MHc36

MHc36 – Central Hardwood Forest (Eastern)

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

MHc36, Central Mesic Hardwood Forest (Eastern), is a common hardwood community found mostly within the Western Superior Uplands ecological section of Minnesota (Figure 1). It is common also in the adjacent portions of the Minnesota & NE Iowa Morainal Section; scattered examples occur in the Northern Minnesota Drift & Lake Plain Section in association with historic Indian settlements. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

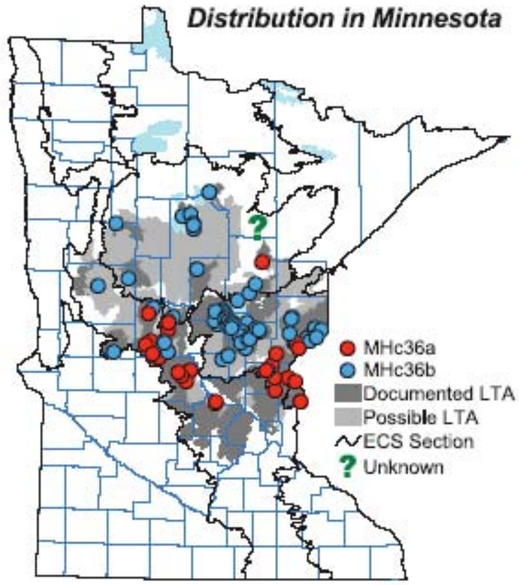


Figure 1. The range of MHc36 forests in Minnesota (shaded) and distribution of releve samples (red and blue dots).

Commercial Trees and Management Opportunities

As a commercial forest, MHc36 sites offer a wide selection of crop trees and possible structural conditions. Sugar maple, northern red oak, basswood, bur oak, and quaking aspen are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on MHc36 sites (see Suitability Tables). Green ash, red maple, paper birch, and big-toothed aspen 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. Bitternut hickory, white oak, and white ash 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, red oak, quaking aspen, big-toothed aspen, basswood, and sugar maple were the dominant native trees that have occupied MHc36 sites for a long time and have had the opportunity through successive generations to adapt to physical conditions typical of these sites **(PLS/FIA-1)**. Historically, American elm was important as well, but its presence as a merchantable tree has been diminished by Dutch elm disease. Paper birch, ironwood, bur oak, white oak, and even some white pine are likewise native to MHc36 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, ironwood, and quaking aspen than was usual. These increases came mostly at the expense of red oak, which no longer dominates MHc36 sites as it once did. Past history and land use has also encouraged the ingress of species that were not significant in native MHc36 stands such as red maple and green ash. The increased abundance of these trees, especially red maple and sugar maple, complicates our interpretations and the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

In the historic landscape most MHc36 forests (75%) were transitioning between the young and mature growth-stages **(PLS-1)**. Roughly these were stands 35-95 years old. The early years of the transition were marked by the decline of quaking or big-toothed aspen. These trees were never the matrix of the forest canopy, but their loss created large-gaps that benefited red oak more than any other species. The decline of aspen resulted in some establishment of red oak, release of advance oak regeneration, and crown release of initial-cohort red oak. A silvicultural approximation of this would be improvement cutting at about age 30, that could involve some additional effort aimed at regeneration of red oak or not, depending upon the current abundance and vigor of advance red oak regeneration.

The late years of the transition involved the gradual loss of red oak accompanied by either limited opportunities of establishment and recruitment of some mid-tolerant species in large gaps, or release of advance regeneration of sugar maple and basswood in any sized gap. Red oak is not senescent at these young ages, so we doubt that its natural pattern of mortality was that of individual, old trees that would be approximated by several entries of thinning from above. More likely, surface fires or pocket diseases accelerated their demise – the fires favoring mid-tolerant replacement and the diseases accelerating conversion to northern hardwoods. Attempts to mimic the surface fire process would involve shelterwood harvests, the variants of which would be dependent upon the existing pattern and composition of advance regeneration or the intention to plant. Presumably, this approach would favor red oak, bur oak, red maple, or green ash when present. Patch cutting, natural shelterwood, or the variants or retention harvesting would approximate the natural conversion of the site from oak cover-type to northern hardwoods. This approach should favor basswood, sugar maple, and historically favored American elm.

In the historic landscape 18% of the MHc36 forests were mature and older than 95 years **(PLS-1)**. In this growth-stage most MHn38 trees maintained their presence by developing banks of seedlings that would recruit to trees in canopy gaps. Wind and surface fires killed or toppled canopy trees to create gaps in the canopy ranging from the size of a single tree crown to about an acre. Variants of selection harvesting, patch cutting, or retention harvesting could be used to approximate single-tree or few-tree gaps. These systems would favor small-gap strategists like sugar maple, American elm, and basswood over all others on MHc36 sites. These systems could be used indefinitely if the goal is to maintain the northern hardwood cover type.

At some point, the manager must decide to prepare mature forests for regeneration. Without fire, advance regeneration in mature MHc36 forests is dominated by shade-tolerant mesic hardwoods. Experience shows that canopy removal without preparation results in a young northern hardwood stand with modest or low amounts of red oak. It seems clear that this happened at least upon occasion naturally as sugar maple and basswood especially could be initial-cohort trees **(PLS-1)** and here they have uncharacteristic young windows of recruitment (0-60 years, **PLS-5**). Experience also shows that if this approach is taken, it should be followed by a commitment to follow the treatment with early cleaning or improvement cutting to select the superior crop trees or thin clusters of stump sprouts. However, if the goal is to create a young oak-dominated stand, management of advance regeneration is required. Historically red oak was “positioned” to re-colonize MHc36 sites because it dominated the advance regeneration. We believe that chronic surface fires “cleansed” MHc36 sites of sugar maple advance regeneration and forced red oak to allocate resources to root growth and caliper more than height. The silvicultural equivalent would most likely involve prescribed burning, underplanting, and monitoring caliper in order to prepare MHc36 sites for canopy removal with the expectation of red oak dominance in the new young stand.

A small proportion (7%) of native MHc36 stands were young forest <35 years old **(PLS-1)**. Surface fires and disease probably worked in concert to weaken MHc36 trees to the point where stands were susceptible to catastrophic windthrow. Severe surface fires too, probably affected MHc36 forests to the point where there were nothing but small-diameter trees available to reference survey corners. We doubt very much that very young MHc36 stands ever resembled a clear-cut. This community usually occurs in topographically rough terrain where it is highly unlikely that the effects of fire or wind were uniform. Patch cutting or variants of shelterwooding would best approximate the natural level of canopy removal that created patches of small-diameter trees picked up at PLS corners. The only real reason to re-initiate a MHc36 stand would be to favor aspen or paper birch, which are the only MHc36 trees with the primary strategy of regenerating in open conditions. We do believe that these trees played a role in helping red oak re-establish its dominance on MHc36 sites in the young growth-stage. On these sites aspen and birch seem incredibly short-lived and they probably served the role of a cover crop for red oak. Both species have the silvicultural potential to train young oaks if sawtimber oak is a management goal. We adhere to the idea that oak establishment is best accomplished in mature forests by mimicking surface fires, but there may be viable strategies of planting or seeding red oak among aspen and birch in young MHc36 stands.

Management Concerns

MHc36 communities occur mostly on medium-textured soils where there are legitimate concerns about heavy equipment compacting or rutting the soil (see Acceptable Operating Season to Minimize Compaction tables). 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. MHc36 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, MHc36 sites are less-well drained because the till plains are flatter and require drying periods far longer than on stagnation moraines.

Today the landscape balance of growth-stages and stand ages for the MHc36 community is nearly identical to its historic condition **(PLS/FIA-1)**. We believe that wildlife populations are probably reacting to MHc36 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 red oak, which is arguably the most valuable species in today’s market. Sugar maple, red maple, and ironwood are the benefactors of modern conditions because logging does not selectively kill these trees as did natural processes. These mesic hardwoods, particularly in the young growth-stage complicate and diminish our silvicultural ability to manage MHc36 stands for red oak. This community along with the southern mesic hardwood (MHs) communities were the stronghold of red oak habitat in Minnesota and all are suffering from conversion to mesic hardwoods under modern management. If red oak is to remain an important commercial tree, conservation and silvicultural experimentation are essential.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 5,368 corners within the primary range of the MHc36 community. At these corners, there were 12,217 bearing trees comprising the species that one commonly finds in MHc36 forests.

The PLS field notes described just 1% of the MHc36 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands, openings, or post-fire thickets. From these data, a rotation of 1,150 years was calculated for stand-replacing fire.

Elsewhere in the MHc36 landscape, the surveyors described lands as windthrown and lacking suitable-sized trees for scribing. Such corners were encountered at about 4% of the time, yielding an estimated rotation of 380 years for windthrow.

Far more common at MHc36 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 sparse forest, scattered timber, or thickets with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked hardwood forests. About 14% of the survey corners were described as such, resulting in a calculated rotation of just 36 years for disturbances that maintained some early and mid-successional trees on MHc36 sites. That more corners were described as burned (20) compared to windthrown (9) suggests that surface fires were the more prevalent cause of partial canopy loss.

Natural Rotations of Disturbance in MHc36 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**1,150 years**
Catastrophic windthrow photograph	**380 years**
Partial Canopy Loss, photograph	**36 years**

Compared to other mesic hardwood (MH) communities in Minnesota, MHc36 rotations of catastrophic disturbance are similar in that they exceed the longevity of any initial cohort species. This means that natural stand dynamics involved a few generations of trees and a shift from large regeneration gaps to smaller ones as stands matured. MHc36 has the shortest rotation of maintenance disturbances (36 years) among MHc communities, and for that reason resembles MHs communities. It shares in common with the southern forests, the persistence of oak throughout succession and oak dominance in the young growth-stage. We believe that frequent surface fires favored oak advance regeneration over sugar maple and that these fires created the large canopy gaps where oak recruits well.

Natural Stand Dynamics

Following stand-regenerating fire or windstorms, the overall pattern of compositional change in MHc36 communities is for lots if initial change, which then decelerates as the stand becomes older **(PLS-4)**. This pattern is common for communities where fire overwhelmingly favors a one or two pioneer species and is capable of eliminating late-successional species sensitive to fire. For MHc36 red oak, quaking and big-toothed aspen, and paper birch are the species that benefit greatly from fire because they compete poorly with shade-intolerant species like sugar maple, basswood, American elm, and perhaps ironwood on MHc36 sites in the absence of disturbance.

Early in the process of stand maturation, MHc36 stands achieved tree densities that were fairly stable. Temporal change in tree density followed the textbook concept of young, small-diameter forests being tightly packed – followed by older, large-diameter stands with trees more widely spaced. Presumably, self-thinning and crown competition among canopy trees causes this. Young MHc36 forests under 35 years had mean distance of 22 feet from survey corners to the bearing trees. This is typical of fully stocked hardwood forests of comparable age. Transitioning forests 35-95 years old had bearing trees 26 feet from corners on average; mature forests >95 years had a mean of 25 feet. Compared to other communities, these distances are quite typical of naturally stocked hardwood forest.

Young Growth-stage: 0-35 years
Just 7% of the MHc36 landscape in pre-settlement times was covered by forests estimated to be under 35 years old **(PLS-1)**. There were too few survey corners with a full complement of bearing trees to determine if young MHc36 forests tended to be mixed or monotypic. In describing very young, burned stands, the surveyors indicated that red oak was by far the dominant initial-cohort tree **(PLS-3)**. Among the red oaks, quaking and big-toothed aspen suckers filled-in the matrix, and sprouting basswood were also fairly common. Following fire, the surveyors most often described the structure of the forest as openings, thickets, or just burned-over land.

Young stands recovering from windthrow were more common **(PLS-3)**. There was really very little compositional difference between stands recovering from fire or windthrow, except that the dominance of red oak was even more pronounced, and aspen and basswood did less well than after fire. Most important is the fact that windthrow didn't release advance regeneration of mesic, fire-sensitive trees – meaning that surface fires in older forests must have maintained advance regeneration of oak and mid-tolerants rather than sugar maple, American elm, basswood, and ironwood. Curiously, the surveyors described the structure of windthrown forest in quite different terms than they did for burned forest. Most often, they described windthrown sites as scattered timber or even sparse forest, which suggests to us that stand-regenerating wind events left a lot of scattered, wind-firm oaks and even mesic hardwoods like basswood and elm **(PLS-1)**.

We believe that the only way for red oak to so strongly dominate young forests was for it to have had similar dominance among the advance regeneration of older forests. It seems incredibly unlikely that disturbances as different as fire and wind would create seedbed conditions that would favor red oak over all other species equally. Our interpretation is that surface fires on a rotation of about 36 years (see Natural Disturbance Regime) were the primary disturbance in MHc36 forests that maintained a bank of young red oak seedlings. This idea is supported by the fact that red oaks dominated also the historic forests where we suspected partial canopy loss due to some maintenance disturbance **(PLS-3)**. Any disturbance seemed to result in red oak regeneration.

Averaging the age-class data across the young growth-stage **(PLS-1)** masks what we believe was rather immediate occupation of growing space by quaking or big-toothed aspen. In a restrictive analysis with finer age-classes, it seems that aspen could have represented about 20% of the trees barely large enough to blaze and scribe as a bearing tree. Our interpretation is that following fire, young aspen suckers filled the matrix leaving stump-sprouting species like red oak, basswood, and paper birch at the coarser spacing of mature canopy trees. Rapid self-thinning of the aspen suckers and higher survivorship of the stump sprouts caused the impression of modest, post-disturbance regeneration of aspen and red oak dominance.

Transitional Stage: 35-95 years

The bulk (75%) of the historic MHc36 landscape was forest undergoing considerable compositional change **(PLS-1, PLS-2, PLS-4)**. Stands in this stage far more likely to be mixed (87%) than monotypic (13%). Monotypic conditions were represented mostly by survey corners where all bearing trees were red oak (60%), but some pure sugar maple corners (35%) were starting to appear. At survey corners with mixed composition sugar maple, basswood, and elm were cited more often than initial-cohort red oak and aspen. We believe that this is a clear sign, of succession to mesic hardwoods during the transition.

Succession during the transition stage is initiated by a precipitous decline in aspen between the 30- and 40-year age-classes **(PLS-2)**. The immediate benefactor of aspen's decline was red oak, although we show red oak declining during the transition **(PLS-1)**. Averaging across the lengthy decline obscures a clear peak in red oak abundance in the 40-60 year age-classes where red oaks represented about half the trees in transitioning MHc36 forests. Steady decline of red oak between the 60- and 90-year age classes is the event that creates this lengthy transition. Mesic hardwoods like sugar maple, American elm, and ironwood are the benefactors of red oak's delayed decline during the transition.

The early transition of MHc36 from oak and aspen to mesic hardwoods and sugar maple presents a logical conundrum. This community along with most MHs communities have nearly identical disturbance regimes of long catastrophic rotations and chronic levels of maintenance disturbance that is presumed to be surface fire. The presumption of fire is made because any kind of canopy removal – fire, wind, or disease – resulted in oak regeneration with almost no sugar maple or other fire-sensitive trees. To explain this, we envision a seedling bank of oak and little sugar maple that is maintained by surface fire. To explain rapid succession, we envision a seedling bank of shade-tolerant, fire-sensitive trees unmolested by fire – thus the puzzle. What did the understory of MHc36 and similar hardwood communities look like? In the modern forest there is no puzzle. Sugar maple and basswood are the superior competitors in the understory able to bank seedlings **(R-2)**. Canopy removal results in a young stand of these mesic hardwoods, with very little red oak. Thus, it would seem that advance regeneration had to be solidly fire-maintained oak in the past to explain its post-disturbance success. How then did mesic hardwoods ingress and reach diameters that might usually survive light surface fires? One must imagine episodes where patches of MHc36 forests escaped fire long enough to develop a canopy of mesic hardwoods, but fire would soon rectify the situation and favor advance regeneration of oak beneath a sugar maple and basswood canopy (the exact opposite of today's situation). If this happened, we believe that it was most likely during the self-thinning stage of development as tree density on young MHc36 sites was tight (just 22 feet on average to bearing trees). It is easy to envision ingress of sugar maple during self thinning as it is unequalled in its ability to establish and recruit beneath a canopy on these sites. All of these communities show uncharacteristic peaks of small-diameter sugar maple regeneration very early in succession **(PLS-5)**, thus supporting the idea that self-thinning aspen and oak was prime habitat for young sugar maples. However, the argument also requires self-thinning stands to ward off fire long enough for the hardwoods to reach diameters that might survive surface fires. Were self-thinning stands less likely to burn than older ones? We don't know.

Regardless of this confusion, the actual transition is not hard to understand. It is classic, textbook replacement of rather intolerant trees with shade-tolerant ones. This pattern of replacement fits exactly our observations in modern forests that start the successional cycle enriched in aspen or red oak. Precisely how older red oaks maintained their potency to dominate these sites after historic disturbances is somewhat mysterious if we are forced to envision advance regeneration with but modest presence of red oak as true seedlings.

Mature Growth-stage: >95 years

About 18% of the historic MHc36 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 (92%) than monotypic. Nearly all monotypic survey corners were sugar maple, and some were entirely basswood. Mixed conditions were represented by combinations of sugar maple, basswood, ironwood, and American elm. This degree of mixture is a striking feature of mature MHc36 forests. Although it is clear that sugar maple is the dominant species, and it is also clear that it is unequalled in ability to regenerate and recruit in any stratum (R-2) – mature MHc36 forests were not all sugar maple. Co-dominant species with varying regeneration strategies, varying tolerance of shade, and varying successional position were all present as large trees in mature MHc36 stands in roughly balanced amounts. Our interpretation is that chronic maintenance disturbance, mostly surface fires, created a fine-scale mosaic of hardwoods throughout the MHc36 landscape. Elm was favored in any depression that would hold snowmelt; more exposed areas favored the persistence of oaks; and anything in-between was a mix of sugar maple and basswood.

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 using 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 (large-gap) regeneration strategist***
- ***regeneration window at 0-60 years***

Suitability

MHc36 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 (75%) as trees on these sites in modern forests **(R-1)**. When present, sugar maple is an important co-dominant and sometimes dominant tree, contributing 33% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on MHc36 sites as sampled by releves. All Central mesic hardwood sites (MHc) offer excellent habitat for sugar maple (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, at 4% relative abundance sugar maple was a minor tree in young MHc36 stands **(PLS-1, PLS-2)**. Young sugar maples were present at just 1% of the survey corners described as burned **(PLS-3)**. This result is consistent with its well-known sensitivity to fire. Just a few trees (2%) were recorded at windthrown survey corners. This result is surprising in that there is no particular reason to think that windthrow would select against sugar maples, and they are now quite common in young MHc36 forests where the canopy has been removed by logging **(PLS/FIA-1)**. Small-diameter sugar maple regeneration coming in among larger trees was present at surprisingly high abundance during the post-disturbance window **(PLS-5)**. Today, canopy removal immediately releases the pervasive bank of maple seedlings common in older MHn36 stands. The fact that sugar maple didn't react immediately in the historic record suggests to us that the maple seedling bank was not pervasive or that the regenerating event killed the maple seedlings. We believe that fire accomplished this. Our interpretation is that the reaction of MHc36 stands to fire was to form thicket-like growth that was a mixture of aspen suckers, sprouting trees, sub-trees like ironwood, and tall shrubs. At some point (~self-thinning stage), this re-growth reached a height and degree of canopy closure that favored the establishment and recruitment of shade-tolerant trees like sugar maple. Sugar maple is unequalled among MHc36 trees in its ability to establish and recruit seedlings in the shade **(R-2)**.

Transition: 35-95 years

As stands transitioned to mature conditions sugar maple increased in abundance **(PLS-1)**. We estimate that this increase started during this transition and continued for the duration of the growth-stage until sugar maples were dominant **(PLS-2)**. Small-diameter sugar maple regeneration was abundant in the G-1 gap window corresponding with the transition stage **(PLS-5)**. At this time, it was about twice as likely for sugar maple bearing trees to be the smallest tree at a survey corner than it was for it to be the largest tree. Also, it occurred almost entirely (89%) at corners of mixed composition. This pattern is typical of an invading species. Young sugar maples were coming in under almost any other tree common in MHc36 forests. It was especially common beneath initial-cohort aspen, red oak, and paper birch. We interpret this as release of seedlings established in the young growth-stage in response to the death of some initial-cohort trees and perhaps in response to a change from thicket-like growth to forest structure. Also common was sugar maple's tendency to be beneath larger sugar maples that must have gotten their start in the young growth-stage. Smaller-diameter maples were also beneath basswood and American elm, suggest that some pockets of mesic hardwoods were forming early in the successional cycle. 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 years

Sugar maple had its peak presence as a canopy dominant or co-dominant in mature stands, which is why we consider sugar maple a ***late-successional*** species – able to replace about any other tree as stands aged **(PLS-1, PLS-2)**. Its steady increase in relative abundance is the result of good establishment and recruitment beginning in the young growth-stage followed by high survivorship. Surprisingly, using our restrictive half-diameter rule, small-diameter sugar maple regeneration was not detected during the mature growth-stage **(PLS-5)**. At this time sugar maples were rather balanced as either the largest or smallest tree at survey corners. This is typical of trees with an extended window of recruitment success, which in sugar maple's case spans 60 years. When sugar maple was the smallest tree, a significant amount (35%) was coming among other sugar maples. Smaller sugar maples were also commonly among larger-diameter basswood and American elm. There were very few instances of smaller-diameter maples below any species like aspen and red oak that might have been in the initial-cohort. Our interpretation is that by the time MHc36 stands were 95 years old, sugar maple was occupying all strata and could indefinitely replace itself in the absence of fire.

Regeneration Strategy
Sugar maple's primary regenerative strategy on MHc36 sites is to develop a pervasive bank of seedlings capable of recruiting in ***small-gaps***. Sugar maples were successful at this beneath almost any other species of tree, including itself. In the historic PLS data the small-gap interpretation is supported by: (1) the fact that sugar maple is dominant in the mature growth-stage of the community when gaps are usually small **(PLS-1, PLS-2)**, and (2) its peak abundance, by far, was at survey corners showing no canopy loss or disturbance **(PLS-3)**. The high percent of sugar maple seedlings below poles or trees (situations 12 and 13) in the FIA data **(FIA-1)** is also a characteristic of species that can bank seedlings and recruit into small gaps. The releve sampling of mature MHc36 forests shows that sugar maple is unequalled at establishing and recruiting individuals in all understory strata, eventually resulting in canopy dominance **(R-2)**. This is especially characteristic of a small-gap species.

There is also evidence that sugar maple was able to capture growing space in ***large-gaps*** as well. In the PLS data, the most compelling argument is that sugar maple's rise in abundance mirrors the breakup of any aspen canopy, and the slower demise of red oak **(PLS-2)**. Normally, we assume fairly large gaps when initial-cohort trees tend to die rather synchronously. Also typical of a large-gap strategist is the high abundance of sugar maple as poles beneath trees (situation 23) in the FIA data **(FIA-1)**. In today's forests, sugar maple regeneration is so pervasive that any level of canopy removal results in maple-dominated gaps.

Historic Change in Abundance
Today, sugar maple is more abundant on MHc36 sites than it once was. In mature forest, there is little difference at it is and was, the dominant (~30-35% abundance) in older stands **(PLS/FIA-1)**. The obvious departure from history is the incredible abundance of sugar maple in today's young stands (30%) in contrast to it's minor presence (4%) historically; obviously sugar maple has replaced red oak in regenerating forests. Sugar maple is especially pervasive in mature forests sampled by releves, with 75% presence as a tree **(R-1)** and 93% presence in the understory **(R-2)**. These presence values seem quite high even when compared with modern forests as sampled by FIA plots. Most likely this is due to our tendency to place releves in the least disturbed forests. Our interpretation is that sugar maple has benefited greatly from the lack of fire disturbance and absence of silvicultural tending on MHc36 sites. It is most evident in young forests, but equally impressive is its dominance in the understory of mature stands. Without prescribed burning or silvicultural tending of understory oaks, sugar maple will eventually replace red oak on MHc36 sites.

Northern Red Oak

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 20-40 years***

Suitability
MHc36 sites provide ***excellent habitat*** for red oak trees. The ***suitability rating*** of 4.9 for red oak is influenced mostly by its very high presence (75%) as trees on these sites in modern forests **(R-1)**. When present, red oak is an important co-dominant and sometimes dominant tree, contributing 31% mean cover in mature stands. The ranking is second, tied with basswood and following sugar maple on MHc36 sites as sampled by releves. All central mesic-hardwood communities provide excellent habitat for red oak (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, at 50% relative abundance northern red oak dominated young MHc36 stands recovering from fire or windthrow **(PLS-1)**. Young red oaks represented 80% of the trees at survey corners described as burned, far ahead of any other tree **(PLS-3)**. Our interpretation is that red oaks got their start on MHc36 sites by sprouting from strong rootstocks. Similarly, red oak dominated the vegetation following windthrow as it represented 87% of the smaller-diameter trees. Most likely, these were well-established seedling-sprouts that were prepared for release. We believe that the fact that any disturbance, even disturbances as different as fire and wind, resulted in good regeneration of red oak is testimony to its dominance as advance regeneration in older forests, maintained by surface fires. Small-diameter red oak regeneration became increasingly common throughout the young growth stage **(PLS-5)**. In the few cases available, red oak regeneration seemed to be coming in under aspen. Because the abundance of small-diameter red oak regeneration increases during the young growth-stage, we believe that it had some ability to recruit into under-stocked areas of burned stands, especially where there was aspen.

Transition: 35-95 years
As stands started to transition to mature conditions red oak increased slightly in abundance, presumably because of its ability to replace or outlive initial cohort aspen. We estimate that this increase started following disturbance until it peaked at about 55% relative abundance in the 50-year age classe **(PLS-2)**. Small-diameter, red oak regeneration coming in among larger trees was most abundant in the G-1 gap window **(PLS-5)**, especially the 30- and 40-year age-classes. In most cases, red oak regeneration was coming in under larger-diameter red oaks, but it was also common to see it among larger aspen. Small-diameter red oak bearing trees were not common among shade-tolerant hardwoods. We interpret this as fair success at establishment and recruitment of seed-origin or seedling-sprout oak under a partial canopy of initial-cohort trees. Also, it seems likely that the collapse of the initial-cohort aspen released some red oak seedlings established during the young growth-stage. After red oak's peak abundance at about age 50-years, its relative abundance steadily declines to about 10% by the close of the transition. The decline of red oak and its replacement by tolerant hardwoods is the major contributor to compositional movement and definition of the transition period **(PLS-4)**. Its rise to prominence and subsequent fall, all within the transition, is the main reason that we consider red oak to be ***mid-successional*** on MHc36 sites.

Mature Growth-stage: >95 years
In forests older than 95 years, the relative abundance of red oak is stable at about 9% **(PLS-1, PLS-2)**. Small-diameter red oak regeneration was not detected in the mature growth-stage using our restrictive half-diameter rule **(PLS-5)**, but it had enjoyed steady recruitment in the preceding growth-stages. At this stage it was about equally likely for red oaks to be the larger tree at a survey corner as it was for them to be the smallest tree. This is typical of a species with a long (70 years) window of recruitment. When red oak was the smaller tree at a corner, it was still most

often beneath larger-diameter red oaks. Unlike the transition, it now was about as common for red oaks to be subordinate to shade-tolerant trees rather than initial-cohort trees. It was most common for red oak to be among larger sugar maples and American elm, but not beneath basswood. We interpret this as red oak's modest ability to establish some true seedlings beneath a canopy. In modern forests, it shows good ability to do so – far more so than other oaks which clearly need more light for establishment **(R-2)**. The ability of red oak to establish or maintain seedlings among tolerant hardwoods in mature forests was probably a key to its success in the young growth-stage and why bur oak and white oak were not part of the initial-cohort.

Regeneration Strategy

We believe that red oak's primary regenerative strategy on MHc36 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the canopy of declining quaking aspen and to some extent other red oaks. In the historic PLS data this interpretation is supported by: (1) the fact that red oak abundance increases in response to the decline of the initial cohort aspen **(PLS-2)**, (2) it is abundant at survey corners showing partial canopy loss **(PLS-3)**, and (3) it shows peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The high percent of red oak poles under trees (situation 23) in the FIA data is also a characteristic of species that tend to regenerate best in large gaps **(FIA-1)**. The releves show that red oak has good regeneration indices (3.2-3.8) beneath a canopy **(R-2)**, and these values are most in line with species that recruit well in large-gaps.

The rotation of 36 years for maintenance disturbances on MHc36 sites would suggest that by the time forests reached the mature growth stage (95 years) they would have experienced events that result in partial canopy loss. Such events clearly favor trees like red oak that depend mostly on large-gaps for regeneration. We believe that most of this was surface fire and they were the main reason that red oak persisted into the old growth-stage on MHc36 sites. We believe also that these fires were particularly effective at diminishing the advance regeneration of trees like sugar maple, thus maintaining a high presence of oak seedlings and saplings in older forests and assuring red oak good opportunity to dominate after a canopy-removing catastrophe.

Historic Change in Abundance

Today, it seems that red oak on MHc36 sites is in some peril because it is being replaced by sugar maple. Mature and old forests still have about as much red oak as they always did, but today it is uncommon to see the oak cover-type in young forests. Historically, red oaks were about half the trees in stands under 35 years, but today they have just 8% relative abundance **(PLS-FIA-1)**. Our interpretation is that the loss of surface fires has resulted in advance regeneration impoverished in oak and enriched in sugar maple – which is released in that ratio by logging the overstory. Learning to silviculturally manipulate the abundance and vigor of advance regeneration of red oak prior to harvest would seem to be the key in reversing red oak's decline. We doubt however that red oak will cease to be a component of future MHc36 forests because it shows high presence even in the least disturbed stands **(R-1, R-2)**. It's ability to recruit some individuals under mature forest conditions is actually rather good, but it will consistently lose to ground to sugar maple and basswood each rotation.

Basswood

- ***excellent habitat suitability rating***
- ***late-successional***
- ***small-gap (large-gap) regeneration strategist***
- ***regeneration window at 0-60 years***

Suitability
MHc36 sites provide ***excellent habitat*** for basswood trees. The ***suitability rating*** of 4.9 for basswood is influenced mostly by its very high presence (87%) as trees on these sites in modern forests **(R-1)**. When present, basswood is an important co-dominant or dominant tree, contributing 24% mean cover in mature stands. The ranking is second, tied with red oak and following sugar maple on MHc36 sites as sampled by releves. All central mesic hardwood communities (MHc) offer excellent habitat for basswood (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, at 14% relative abundance basswood was an important initial-cohort tree in young MHc36 stands **(PLS-1, PLS-2)**. Young basswood represented 6% 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 less successful at windthrown corners where it represented 3% 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 60-year age-class **(PLS-5)**. Our interpretation is that a substantial bank of basswood seedlings and stump sprouts were available to re-colonize MHc36 stands following removal of the canopy by fire or wind.

Transition: 35-95 years
As stands transitioned to mature conditions basswood increased slightly 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)**. At this time it was about twice as common for basswood to be the larger tree at a survey corner as it was to be the smallest one. The larger trees were probably initial-cohort stump sprouts. Small-diameter basswood regeneration was still common early in the transition, but at levels far less than in the young growth stage **(PLS-5)**. In most cases, young basswoods could come in under most species, especially aspen, elm, red oak, and itself. We interpret this as good success at establishment and recruitment of seed-origin basswood during the transition under a canopy of any species. 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 years
The relative abundance of basswood increased throughout the mature growth-stage **(PLS-2)**. The average relative abundance for the entire growth stage is 18% **(PLS-1)**. Its steady gains were most likely the result of good establishment and recruitment for the first 70 years of stand maturation **(PLS-5)** followed by high survivorship as mature, reproducing trees. In mature forests, basswood was about equally likely to be the largest tree at a survey corner as it was for it to be the smallest tree. This is typical of a species with a long, preceding recruitment window. Compared to the transition though, this is an increase in the tendency of basswood to be subordinate to other trees, which we attribute to its excellent ability to continuously establish and recruit seedlings under a canopy **(R-2)**. At this time, it seems that smaller-diameter basswood didn't much care what species overtopped it. It was most common to see recruiting basswood beneath their parent trees, but it was almost as common to see them subordinate to sugar maple, American elm, and a long list of minor species. Its steady increase in abundance in older forests and its obvious ability to replace itself by recruiting seedlings is why we consider basswood to be a ***late-successional*** species on MHc36 sites.

Regeneration Strategies

On MHc36 sites basswood exhibits regenerative flexibility, which allows it to be ever-present throughout the full course of stand maturation. Basswood sprouts effectively following disturbances that kill the main stem, and it is able to carry its parent-tree density into the post-disturbance forest. 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 any other tree species and well as under larger basswoods. We believe that basswood was most successful increasing its presence locally by developing a pervasive bank of seedlings that will recruit ***small canopy gaps.*** In the historic PLS data this interpretation is supported by the fact that basswood abundance rises throughout the successional cycle, including mature forest where we presume small canopy gaps **(PLS-1, PLS-2)**, and (2) it was most abundant at survey corners in mature, undisturbed forest **(PLS-3)**. In the releves, basswood has excellent indices of regeneration (4.2-4.7), which are typical of trees able to bank seedlings and recruit in small gaps.

There is also evidence that basswood was able to capture growing space in ***large-gaps*** as well. In the PLS data, the most compelling argument is that basswood's modest rise in abundance occurs during breakup of any aspen canopy, and the slower demise of red oak **(PLS-2)**. Normally, we assume fairly large gaps when initial-cohort trees tend to die rather synchronously. Also typical of a large-gap strategist is the high abundance of basswood as poles beneath trees (situation 23) in the FIA data **(FIA-1)**. In today's forests, basswood regeneration is so evenly distributed that any size of gap can result in basswood recruitment.

Historic Change in Abundance

Basswood shows little change in abundance since settlement on MHc36 sites. Today, there is slightly less basswood in young forests that there was historically and slightly more in mature forests **(PLS/FIA-1)**. Basswood seems oblivious to the near reversal of abundance in red oak and sugar maple, which is a clear sign that regenerative events are now quite different from what they were naturally. We attribute basswood's steady presence to flexibility in regeneration strategies.

Bur and White Oak

- ***excellent habitat suitability rating for Bur Oak***
- ***fair habitat suitability rating for White Oak***
- ***late-successional***
- ***large-gap regeneration strategists***
- ***regeneration window at 50-60 years***

Identification Problems

The PLS surveyors referenced both white oak and bur oak as witness trees. In some cases, individual surveyors used both terms and we believe they were distinguishing the species. More often white oak was used in a generic sense and included bur oak, making it impossible to segregate the species in our analyses. MHc36 releve samples show that for plots with either oak present: 2% have both species present; 27% are white oak without bur oak; 71% are bur oak without white oak. In spite of the lack of coincidence in the releve data, we believe that they are sufficiently similar for most silvicultural considerations.

Suitability

MHc36 sites provide ***excellent habitat*** for **bur oak** trees. The ***suitability rating*** of 4.4 for bur oak is influenced mostly by its presence (29%) as trees on these sites in modern forests **(R-1)**. When present, bur oak is a co-dominant tree, contributing 12% mean cover in mature stands. The ranking is fourth, following sugar maple, northern red oak, and basswood on MHc36 sites. Except for the rare MHc38 community, central mesic hardwood forests (MHc) all provide excellent habitat for bur oak (see Suitability Tables).

The ***fair suitability rating*** of 2.4 for **white oak** is based upon its 11% presence and 7% mean cover-when-present **(R-1)**. This ranking is eleventh among trees common on MHc26 sites. Except for the odd occurrences of white oak on MHc38 sites, white oak is limited to the poorer central mesic hardwood communities (MHc26, MHc36; see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, bur and white oaks were absent as bearing trees in young MHc36 stands with small-diameter trees **(PLS-1,PLS-2)**. A few bur oaks appeared at burned or windthrown survey corners, but these were large-diameter survivors assigned to older age-classes **(PLS-3)**. Small-diameter, bur and white oak regeneration was not detected coming in among larger trees in the post-disturbance window **(PLS-5)**. Our interpretation is that if bur and white oaks were present in young stands, they were usually the scattered survivors of a catastrophe.

Transition: 35-95 years

As stands transitioned to mature conditions bur and white oaks increased slightly in abundance **(PLS-1)**. We estimate that this started at low abundance at about age 50 and increased modestly in the following age-classes **(PLS-2)**. Bur and white oak regeneration was recorded for the first time during the transition as smaller diameter trees coming in among larger ones in the G-1 gap window **(PLS-5)**. There were so few cases that it is impossible to determine if recruiting bur and white oaks had any correlation with overtopping trees. Neither bur or white oak show much ability to regenerate under a canopy **(R-2)** and they couldn't have been important in transitioning MHc36 stands that were well on their way to being dominated by sugar maple and basswood. Apparently, surface fires burning through MHc36 stands created some large-gaps that favored establishment and recruitment of bur and white oak. Apparently these gaps were better habitat than open ground as we saw no bur or white oak in the young growth-stage. This is not surprising for white oak, but bur oak is a common initial-cohort tree in other communities.

Mature Growth-stage: >95 years

In the mature growth-stage bur and white oaks abundance increases but at a snail's pace, never accounting for more than 5% relative abundance **(PLS-1, PLS-2)**. Their increase in relative abundance is mostly the result of some establishment and recruitment during the transition stage **(PLS-5)** followed by high survivorship. Because of their tendency to increase as stands age, we consider them ***late-successional***, but it is doubtful that they can sustain themselves in mature forest without surface fires creating the large gaps and possibly seedbeds that they need for establishment. Bur and white oak regeneration coming in among larger trees was not detected in mature forests **(PLS-5)**. Once again, there were not enough instances of bur and white oak as smaller diameter trees at corners to draw any conclusions about their behavior or overtopping species. In the releves they have poor regeneration indices, yet modest presence **(R-2)**. This means that when they were found, they were widely scattered individuals that contributed very little cover on the plot. Our interpretation is that mature MHc36 forests were just too shady for recruitment of new bur and white oak individuals, but trees established during the transition were consistently outliving the other species.

Regeneration Strategy

The primary regenerative strategy bur and white oak on MHc36 sites is to fill ***large-gaps***. In the historic PLS data this interpretation is supported by: (1) the fact that bur and white oak first appear as bearing trees during the transition where we presume the formation of large gaps **(PLS-1, PLS-2)**, (2) they were most abundant (barely) at survey corners showing partial canopy loss **(PLS-3)**, and (3) they showed peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The high percent of bur and white 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 MHc36 forests is consistent with the idea that bur and red oak need considerable sunlight for regeneration. The indices for these oaks in the regenerating strata are more in line with open regeneration strategists **(R-2)**, but we couldn't consider open habitat as an alternative strategy because they are absent from young PLS corners and barely present in open, regenerating forests sampled by FIA plots.

Historic Change in Abundance

Bur and white oak occur in modern MHc26 forests at almost exactly the same abundance as they did historically **(PLS/FIA-1)**. Their presence in releves **(R-1)** seems a bit high in comparison to their abundance at FIA plots, suggesting that these trees are possibly favored in less disturbed stands.

Quaking & 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 0-30 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. MHc36 releve samples show that for plots with aspen present: 5% have both species present; 43% are big-toothed aspen without quaking aspen; 52% are quaking aspen without big-toothed aspen. We consider quaking and big-toothed aspen to be ecologically equivalent for most silvicultural considerations.

Suitability

MHc36 sites provide ***excellent habitat*** for **quaking aspen** trees. The ***suitability rating*** of 4.3 for quaking aspen is influenced mostly by its presence (20%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is a co-dominant tree, contributing 16% mean cover in mature stands. This ranking is fifth, following sugar maple, northern red oak, basswood, and bur oak on MHc36 sites. Quaking aspen has excellent success on the drier central mesic hardwood (MHc) sites: MHc26, MHc36, and MHc37 (see Suitability Tables).

MHc36 sites provide ***good habitat*** for **big-toothed aspen** trees. The ***suitability rating*** of 3.3 for big-toothed aspen is based upon its 17% presence and 10% mean cover-when-present **(R-1)**. This ranking is ninth among trees common on MHc36 sites. Except for the rare MHc38 community, MHc36 and MHc26 are the best central mesic hardwood (MHC) communities for big-toothed aspen (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, aspen was an important tree in young MHc36 stands recovering from stand-regenerating disturbance **(PLS-1)**. Obscured by averaging across the entire growth-stage is an immediate peak of aspen abundance in the first class to achieve diameters where surveyors could scribe the tree. As much as 40% of the post-disturbance trees may have been aspen **(PLS-2).** Young aspen represented just 6% of the trees at survey corners described as burned, which is well behind the dominant red oak **(PLS-3)**. This is surprising in that aspen can dominate post-fire regeneration in other communities, especially the similar MHc26 community. Aspen was also underrepresented at windthrown corners where it represented just 4% of the bearing trees. Thus it would seem that the relative abundance of aspen in the initial age-class is about 4-times greater than its representation at survey corners where the forest had just recently been re-initiated by fire or wind. The only explanation that we can conjure up is that the surveyors might have been reluctant to use aspen as bearing trees, given the likely option of using the longer-lived red oaks. Sample sizes for both the initial age-class for **PLS-2** and disturbed survey corners in **PLS-3** are sparse enough to suspect some error due to chance, but it seems clear that aspen's best chances on MHc36 sites were early, if not immediate following catastrophe.

Transition: 35-95 years

The loss of aspen during the first few age-classes of the transition cause successional movement during this period **(PLS-4)**. The steepest decline was between the 30- and 40-year age classes where the abundance of aspen falls to about 15% **(PLS-2)**. This trend slowed, but continued throughout the transition stage until there were very few initial-cohort aspen left. During the transition, aspen was almost always the largest tree at a survey corner, which is typical of a fast-growing initial-cohort tree. Small-diameter, aspen regeneration coming in among larger trees falls to nearly nothing by age 40 **(PLS-5)**. When aspen was the smaller tree at a corner, it was overtopped by larger aspen or paper birch. Bearing-tree sized aspen were nonexistent beneath tolerant hardwoods. Our interpretation is that aspen's only real opportunity on MHc36 sites was in the initial-cohort and the early transition is characterized by that cohort's decline with little replacement. For this reason, we consider aspen to be ***early-successional*** on MHc36 sites.

Mature Growth-stage: >95 years

By the beginning of the mature growth-stage, the initial-cohort aspen were gone and its relative abundance was barely detectable at about 1-2% **(PLS-1)**. Small-diameter aspen regeneration was not detected during the mature growth-stage **(PLS-5)**. At this time, aspen were still more common as the larger tree at a survey corner, suggesting that perhaps a few old veterans of the young growth-stage were still around. 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 MHc36 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 has fair indices of regeneration for regenerants and seedlings (2.8), 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 MHc36 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 the persistence of aspen in mature MHc36 forests. Big-toothed aspen is even less successful 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 in the initial-cohort following major disturbances.

Regeneration Strategy

Quaking aspen's primary regenerative strategy on MHc36 sites is to occupy ***open habitat*** after stand-regenerating disturbance. Its modest success could follow either fire or windthrow **(PLS-3)**. In the historic PLS data this interpretation is supported by: (1) the fact that aspen was most abundant in very young forests **(PLS-1, PLS-2)**, and (2) aspen's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. The fairly 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 can regenerate effectively in the open **(FIA-1)**. However both species seem to occur in the full spectrum of possible structural situations, which matches to some extent its historic occurrence at survey corners across the spectrum of disturbance **(PLS-3)**. The most compelling argument for the open strategy is the fact that both quaking and big-toothed aspen show just fair-to-poor ability to establish seedlings or recruit seedlings/suckers when beneath a hardwood canopy **(R-2)**. It seems likely to us that the MHc36 landscape, especially the stagnation moraines, had enough inclusions of the drier, aspen-enriched MHc26 community where surface fires could regenerate patches of aspen within the matrix of tolerant hardwoods.

Historic Change in Abundance

Today, aspen is more abundant on MHc36 sites than it was historically. It was never common in mature forests, and it is not today. The main departure from history is in the young growth-stage where it now represents 18% of the trees as compared to just 10% in the past **(PLS/FIA-1)**. We attribute this change to the tendency to manage stands by coppicing aspen, even when aspen is a minor component of the cover-type.

Green Ash

- ***good habitat suitability rating***
- ***late-successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 60-70 years***

Identification Problems
The PLS surveyors did not distinguish among green, white, and black ash. Nearly all references were just to "ash." Black and white ash are far less common than green ash on MHc36 sites. About 76% of the time, the releves involve only green ash. Interpretations of PLS data for the more common green ash should be done knowing that some of these trees were likely white or black ash. For this treatment, we decide to treat "ash" records as green ash, and we suspect that the ecology of all ash species on this upland habitat is similar enough for most silvicultural applications.

Suitability
MHc36 sites provide ***good habitat*** for green ash trees. The ***suitability rating*** of 3.9 for green ash is influenced mostly by its presence (33%) as trees on these sites in modern forests **(R-1)**. When present, green ash is a minor co-dominant tree, contributing 7% mean cover in mature stands. This ranking is sixth, tied with red maple, among trees common on MHc36 sites. Green ash has been invading central mesic hardwood forests since settlement of the area and has been most successful on MHc36 sites and the wetter MHc47 community (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, at 3% relative abundance green ash were a minor tree in young MHc36 stands **(PLS/FIA-1)**. Young green ash represented 2% of the bearing trees at burned survey corners and 1% of the trees at windthrown corners **(PLS-3)**. Small-diameter green ash regeneration coming in among larger trees was not detected in the post-disturbance window **(PLS-5)**. Because there wasn't a lot of young forest in general (7%, **PLS-1**), the number of young ash bearing trees is quite low, which makes interpretation difficult. Our guess is that surface fires kept advance regeneration of ash low as it did for most mesic species. The few bearing trees showing up at burned corners could well have been small-diameter ash trees that survived in wet swales. Its post-disturbance abundance is similar to the other shade-tolerant, fire-sensitive trees like sugar maple, ironwood, and American elm. Perhaps all of these species were present in wetter inclusions recently burned or disturbed forests.

Transition: 35-95 years
As stands transitioned to mature conditions green ash increased ever so slightly in abundance **(PLS/FIA-1)**. Nearly all of the ash records were small-diameter regeneration coming in among larger trees, especially in the 60-70 year age-classes **(PLS-5)**. When green ash was the smaller tree at a survey corner, it was coming in only among larger mesic hardwoods including sugar maple, American elm, and basswood. It seems clear that ash's success was tied to that of the mesic hardwoods, meaning that its regenerative success didn't begin until succession was well underway in some patches of MHc36 forests. In modern forests, green ash has good ability to establish seedlings beneath a mesic canopy, but recruitment to heights over 2m would seem to require more light and release than is usually available **(R-2)**. Our interpretation is that the transition offered the forest floor conditions and occasional large gaps for the establishment and recruitment of some green ash.

Mature Growth-stage: >95 years
Historically, green ash had its peak presence as a minor co-dominant in mature stands, which is why we consider it a ***late-successional*** species **(PLS/FIA-1)**. Its steady increase in relative abundance is the result of modest establishment and recruitment in the transition period. Small-diameter green ash regeneration was present at low abundance until the 90-year age-class **(PLS-5)**. We interpret this as green ash establishing a modest seedling bank early in the mature growth-

stage as it does in modern stands where it is commonly present (50%) as seedlings. Recruitment to heights over 2m seems unlikely without some kind of opening above green ash seedlings **(R-2)**.

Regeneration Strategies

Ash's primary regenerative strategy on MHc26 sites is develop a bank of seedlings that can fill canopy gaps. We are uncertain about the size of the gaps needed. The PLS data argue for green ash's ability to fill ***small-gaps*** because green ash has peak abundance in the mature growth-stage where we presume small-gaps **(PLS/FIA-1)**, and (2) it was present most often at survey corners classified as mature and not recently disturbed **(PLS-3)**. The FIA data are also vague about gap size. Green ash is equally abundant in all subordinate situations (12, 23, 13) at 17% **(FIA-1)**. High abundance in 12 and 13 situations is usually a property of small-gap strategists, whereas high abundance in situation 23 is usually a property of large-gap species. The releve data present a clearer picture. Green ash's regenerant and seedling indices are just good (3.8), which is typical of large-gap species **(R-2)**. Especially important is the low index (2.5) for saplings, which is usually a clear indication that recruitment demands more light that is offered in a single-tree gap. Because we favor releve data in ambiguous situations, we believe that green ash's primary regeneration strategy involved ***large-gaps***.

Historic Change in Abundance

Today, green ash occurs at almost exactly at the same abundance as it did historically **(PLS/FIA-1)**. Our interpretation is that as long as MHc36 sites are dominated by mesic hardwoods, green ash along with some white and black ash will occur as minor species.

Red Maple

- ***good habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 40-80 years***

Identification Problems
The PLS surveyors did not consistently distinguish between red and sugar maple. Although most references were just to "maple," explicit references to "soft maple" were interpreted as red maple and references to "sugar" or "hard maple" were interpreted as sugar maple. Because sugar maple is dominant on MHc36 sites, especially with regard to cover, we were forced to assign most generic "maple" references to sugar maple in our PLS analyses. From the perspective of presence today, red maple is actually rather common. MHc36 releve samples show that for plots with maple present: 17% have both species present; 15% are red maple without sugar maple; 68% are sugar maple without red maple. We consider sugar maple and red maple to be ecologically similar for most silvicultural considerations, but there seemed to be enough difference in the modern data to treat the species separately. The low number of explicit references to "soft maple" complicate our interpretation of the historic data.

Suitability
MHc36 sites provide ***good habitat*** for red maple trees. The ***suitability rating*** of 3.9 for red maple is influenced mostly by its presence (28%) as trees on these sites in modern forests **(R-1)**. When present, red maple is a minor co-dominant, contributing just 7% mean cover in mature stands. This ranking is sixth, tied with green ash, among tree common on MHc36 sites. Among central mesic hardwood communities (MHc), red maple is favored only on the driest and poorest end of the gradient (MHc26) and on the wettest and richest end (MHc47, see Suitability Tables). Presumably, red maple cannot compete with sugar maple in the more mesic MHc communities like MHc36.

Young Growth-stage: 0-35 years
Historically, red maple was present in just trace amounts (<1%) in young MHc36 stands recovering from catastrophic disturbance **(PLS-1, PLS-2)**. There were no records of red maple at survey corners showing any disturbance **(PLS-3)**. A few red maple bearing trees occurred as small-diameter regeneration in the young growth-stage **(PLS-5)**, but this is not enough to draw any conclusions about natural establishment. The FIA data show low abundance (3%) of red maple in the post-harvest stands (situation 11, **FIA-1**). We believe that fire eliminated most red maple from MHc36 sites at least through most of the young growth-stage.

Transition: 35-95 years
As stands transitioned to mature conditions red maple bearing trees start to consistently appear **(PLS-2)**, but still at levels below a percent **(PLS/FIA-1)**. The stretch of age-classes of 40-80 years is where the surveyors included some soft maple in their notes **(PLS-5)**. Still, there were not enough records to draw conclusions about the behavior of red maple from historic data. In modern stands, the FIA data show a clear peak of red maple abundance in MHc36 stands 40-80 years old. This reason, coupled with the continuity of soft maple bearing tree references during the transition is why we believe that red maple is a ***mid-successional*** tree.

Mature Growth-stage: >95 years
Red maple had but trace presence as a bearing tree in the mature growth-stage **(PLS-FIA-1)**. The FIA data show red maple in decline by the time a MHc36 stand reaches maturity. The releve sampling of modern mature forests shows considerable amounts of red maple as either a tree with 28% presence **(R-1)** or in the understory at 51% presence **(R-2)**. It is hard to look at these data and not suspect that red maple was present also in mature stands historically. It is clear to us that our choice to assign generic references of "maple" bearing trees has hampered our interpretation. It is significant that the regeneration indices of red maple (3.3-4.0) in releves is more in-line with

large-gap species, which are usually mid-successional species that take advantage of large gaps that form when the initial-cohort trees die rather synchronously – which is precisely when the few explicit references to soft maple appear in the survey notes. Our interpretation is that mature MHc36 had some red maple, but it was in slow decline as sugar maple exerted its dominance.

Regeneration Strategy

Red maple's primary regenerative strategy on MHc36 sites is to fill ***large-gaps***. The limited evidence for this in the PLS data is consistent reference to soft maple during the decline of initial-cohort aspen and red oak **(PLS-2)**, when we usually assume the formation of large canopy gaps. In the FIA data, the high presence of red maple in subordinate situations (12, 23, and 13) suggest that red maple can recruit in gaps of any size **(FIA-1)**. In releves, the regeneration indices match best with large-gap strategists **(R-2)**. The recruitment bottleneck at 2m, suggests strongly that red maple seedlings require more than single-tree gaps to recruit to the canopy.

Historic Change in Abundance

Populations of red maple have been expanding in Minnesota. Statewide, red maple abundance has at least doubled since pre-settlement times. This is most evident in communities historically dominated by intolerant or mid-tolerant hardwoods, unlike the MHc36 community where sugar maple prevails. We have estimated that red maple abundance has increased from trace amounts in historic stands to about 3% today in all growth-stages **(PLS/FIA-1)**. This muted increase is related to the necessity of assigning surveyor references to generic maple to sugar maple. Our best guess is that the behavior of red maple on MHc36 sites is not so different than that of sugar maple, which would lead us to believe that it is substantially more abundant in modern young forests, but occurs at about the same abundance as it always did in mature ones.

Paper Birch

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

Identification Problems

Often, the PLS surveyors distinguished yellow from paper birch, but not always. MHc36releve samples show that for plots with birch present: 7% are yellow birch without paper birch; 93% are paper birch without yellow birch. For this analysis, tree records were biased towards paper birch because we assigned generic references to "birch" to the more common paper birch. Thus, our interpretation of paper birch's historic behavior could possibly include some yellow birch.

Suitability

MHc36 sites provide ***good habitat*** for paper birch trees. The ***suitability rating*** of 3.5 for paper birch is influenced mostly by its presence (33%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is a minor co-dominant tree, contributing just 7% mean cover in mature stands. The ranking is eighth among trees common on MHc36 sites as sampled by releves. In general, the better-drained central mesic hardwood communities (not MHc47) offer excellent-to-good habitat for paper birch. Among these, MHc36 is the poorest choice for growing paper birch commercially (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, at about 5% relative abundance paper birch was a minor initial-cohort tree in young MHc36 stands **(PLS-1, PLS-2)**. Young paper birch were present at low abundance in young, post-disturbance MHc36 stands (1-2%, **PLS-3**). Small-diameter regeneration was detected throughout the young growth-stage **(PLS-5)**. At this stage it was about twice as likely for a paper birch to be the largest tree at a survey corner as it was for it to be the smallest one. This pattern is typical of initial-cohort trees reproducing mostly from established rootstocks, which would be stump-sprouts in the case of paper birch. However, there were cases of birch as the smaller tree which leads us to believe that stump-sprouting was augmented by some seed-origin paper birch. In the releves, paper birch shows almost no ability to establish or recruit seedlings beneath a canopy **(R-2)**, suggesting that the open conditions provided its best chance of regeneration. Between the stump-sprouts and seed-origin trees paper birch has peak abundance in the young growth-stage, which is why we consider it to be ***early-successional*** on MHc36 sites.

Transition: 35-95 years

As stands transitioned to mature conditions paper birch decreased in abundance, but ever so slightly **(PLS-1)**. We estimate that this decrease started immediately after disturbance and continued for the life of the stand. At this time, paper birch was still more often the largest tree at survey corners, suggesting that these were initial-cohort trees. Small-diameter paper birch regeneration was present throughout most the transition **(PLS-5)**. Smaller birch could be beneath almost any other species of tree, but it was most often among larger paper birch. We interpret this as limited success at establishment and recruitment of seed-origin paper birch in gaps as the canopy of initial-cohort birch, aspen, and red oak started to decline. This is somewhat contrary to our observations in modern forests where paper birch shows almost no ability to establish seedlings under a canopy **(R-2)**. The gaps that formed in the declining initial-cohort canopy must have been fairly large for paper birch to have regenerative success during the transition stage. Its success though, was limited and not enough to maintain the current population of trees.

Mature Growth-stage: >95 years

During the mature growth-stage the abundance of paper birch continued to decline, but very slowly **(PLS-1)**. Its presence was most likely the result of modest, but persistent establishment and recruitment for the first 70 years of stand maturation **(PLS-5)**. Small-diameter paper birch regeneration was not detected during the mature growth-stage **(PLS-5)**. At this time, paper birches were still more common as the larger tree at a survey corner, suggesting that some of the trees established in the young growth-stage, if not the initial-cohort, were still around. This is typical of a tree in decline, lacking the means of sustaining its local populations by establishment and recruitment. We interpret its presence as the smaller tree as it having some success in the subcanopy, but relying more on survivorship than a large pool of small trees as does sugar maple. When paper birch was the smallest tree, it was most favored when coming in under itself. Thus, some paper birch regeneration could be due to birch's tendency to form rather pure pockets within the maple-dominated matrix of MHc36 forests. We believe that paper birch was able to perpetuate itself as a minor species in older MHc36 forests by doing well in patches where sugar maple had yet to totally dominate, perhaps in response to surface fires.

Regeneration Strategies
On MHc36 sites paper birch exhibits regenerative flexibility, which allows it to be a minor, but ever-present tree throughout the full course of stand maturation **(PLS-2)**. Paper birch 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 higher abundance in the young growth stage **(PLS-1)** could be due to the fact that that it was a much better at sprouting than sugar maple should an older stand burn. We believe that paper birch was most successful increasing its presence locally after catastrophic disturbance and out-competing other trees in the ***open***. In the historic PLS data this interpretation is supported by the fact that paper birch abundance peaks in the young growth-stage **(PLS-1)**, and (2) its primary window of regeneration was during the post-disturbance years **(PLS-5)**. Paper birch has very poor indices of establishment and recruitment under the canopy of modern forests **(R-2)**. These indices (0.8-2.0) are quite in line with trees limited to regenerating in the open.

In stands sampled by FIA plots, paper birch has high presence as poles in tree stands (situation 23), which is typical of species that prefer ***large-gaps*** for recruitment **(FIA-1)**. Also, paper birch's long window of regeneration (to 70 years, **PLS-5**) suggests that it must have had some success in large gaps as initial-cohort aspen, birch, and red oak died. Though this success was limited and not sufficient to maintain its population of trees, it was enough to leave some paper birch in older stands ready to re-colonize when MHc36 stands were finally disturbed.

Historic Change in Abundance
Today, paper birch is about as abundant as it always was **(PLS/FIA-1)**. It is slightly less abundant in modern stands under 35 years old, and slightly more abundant in mature ones. Apparently, birch's reaction to logging is about what it was to fire and windthrow. Our interpretation is that birch is maintaining its presence on MHc36 sites mostly by vegetative means with little opportunity for establishing new seedlings without exposure of the mineral soil.

(PLS-1) Historic Abundance of MHc36 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the MHc36 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 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.

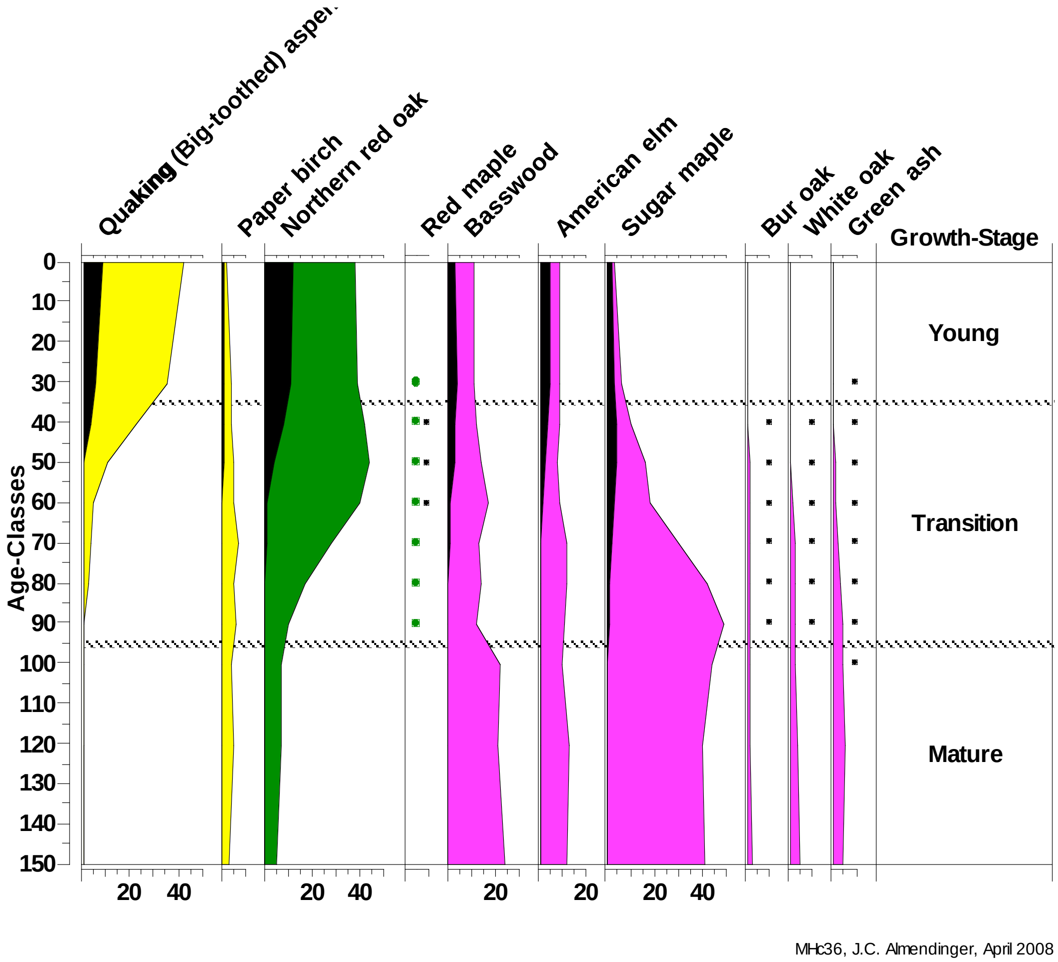
Dominant Trees	Forest Growth Stages in Years		
	0 - 35	35 - 95	> 95
	Young	T1	Mature
Red Oak	**50%**	‖	**9%**
Quaking (Bigtooth) Aspen[1]	**10%**	|	**1%**
Paper Birch	**5%**	|	**2%**
Ironwood	**4%**	⌉	**8%**
Bur Oak[2]	**–**	⌉	**5%**
White Pine	**1%**	⌉	**3%**
American Elm[3]	**6%**	⌉	**10%**
Basswood	**14%**	⌉	**18%**
Sugar Maple	**4%**	⌉⌉	**36%**
Miscellaneous	**6%**		**8%**
Percent of Community in Growth Stage in Presettlement Landscape	**7%**	**75%**	**18%**

1. The PLS surveyors did not consistently distinguish the more prevalent quaking aspen from big-toothed aspen on MHc36 sites.
2. The PLS surveyors did not consistently distinguish the more prevalent bur oak from white oak on MHc36 sites.
3. American elm is now largely absent as a tree in MHc36 forests.

See linked text on brief methods and silvicultural application for Table PLS-1, file *Figures_Tables_Documentation*

(PLS-2) Abundance of trees throughout succession in MHc36

Graphed for the individual species of MHc36 trees is their relative abundance (%) as PLS bearing trees by age class. Species with good-to-excellent suitability have graphs colored as follows: early successional (yellow); mid-successional (green); late-successional (magenta). The data were smoothed from adjacent classes (3-sample moving average). Black insets show the proportion of bearing trees that were small-diameter trees that were presumably recruiting to bearing tree size (~4" dbh, see PLS-5). For infrequent trees, the presence of large-diameter (colored) and small-diameter (black) trees is indicated by dots.



See linked text on brief methods and silvicultural application for Table PLS-2, file *Figures_Tables_Documentation*

(PLS-3) Historic Abundance of MHc36 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent MHc36 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.

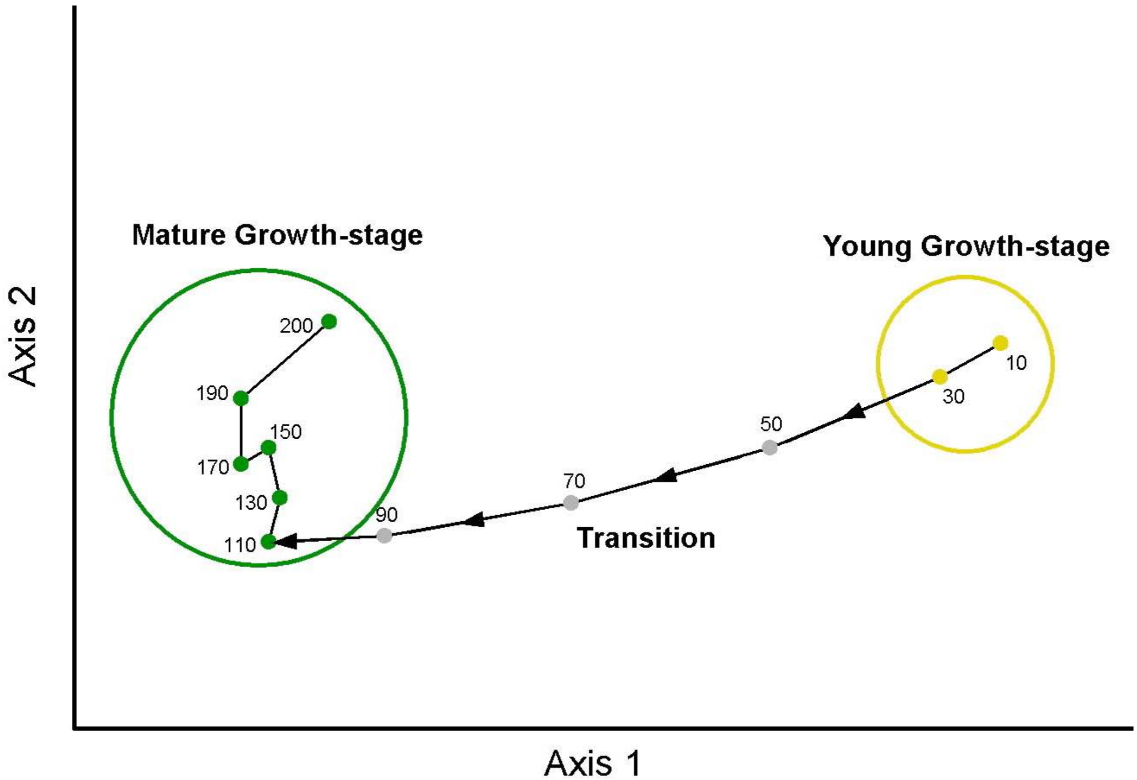
Tree	Burned		Windthrown		Maintenance		Mature	
Quaking (Big-toothed) aspen[1]	8	6%	14	4%	48	3%	417	5%
Northern red oak	100	80%	296	87%	1177	82%	1901	22%
Bur oak[2]	4	3%	11	3%	59	4%	352	4%
Sugar maple	1	1%	6	2%	69	5%	3167	37%
Basswood	8	6%	9	3%	46	3%	1686	20%
Paper birch	2	2%	3	1%	27	2%	551	7%
Green ash	2	2%	2	1%	12	1%	237	3%
Bitternut hickory	0	0%	0	0%	0	0%	134	2%
Red maple	0	0%	0	0%	0	0%	7	0%
Total (% of grand total, 10356)	125	1%	341	3%	1438	14%	8452	82%

1. The PLS surveyors did not consistently distinguish the more prevalent quaking aspen from big-toothed aspen on MHc36 sites.
2. The PLS surveyors did not consistently distinguish the more prevalent bur oak from white oak on MHc36 sites.

See linked text on brief methods and silvicultural application for Table PLS-3, file *Figures_Tables_Documentation*

(PLS-4) Ordination of Historic MHc36 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.



See linked text on brief methods and silvicultural application for Table PLS-1, file *Figures_Tables_Documentation*

(PLS-5) Historic Windows of Recruitment for MHc36 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 0-30 years	G-1 30-90 years	I-1 >90 years
Minor	Red maple[1]	0-20	Fair	Poor	--
Yes	Quaking aspen	0-30	Excellent	Poor to 50	--
Yes	Big-toothed aspen[1]	0-30	Good	Fair to 70	--
Yes	Paper birch	0-40	Good	Fair to 70	--
Yes	Basswood	0-60	Excellent	Good to 70	--
Minor	Sugar maple	0-60	Excellent	Good	--
Yes	Northern red oak	20-40	Good	Excellent	--
No	White ash[1]	40-70	--	Poor to 70	--
Minor	Red maple[1]	40-80	Poor	Fair	--
No	Bur oak	50-60	--	Poor to 80	--
No	White oak[1]	50-60	--	Poor to 80	--
No	Bitternut hickory	50-60	--	Fair to 70	--
No	Green ash	60-70	--	Poor to 90	--

Recruitment windows from ordination PLS-4:

- **P-D:** post-disturbance filling of understocked areas, 10-30 years
- **G-1:** gap filling during decline of initial-cohort red oak, quaking aspen, and basswood, 30-90 years
- **I-1:** ingress of seedlings under canopy of sugar maple and basswood, with some elm, ironwood, and red oak, >90 years

1. Red maple, big-toothed aspen, white ash, and white oak were only occasionally distinguished from their more abundant counterparts: sugar maple, quaking aspen, green ash, and bur oak respectively. Interpretations for this table were based upon reconciling the FIA data of the less common with the PLS data of the more common trees.

-- : 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; **light green** = trees with peak regeneration in gaps formed during the decline of the initial cohort

See linked text on brief methods and silvicultural application for Table PLS-5, file *Figures_Tables_Documentation*

(R-1) Suitability Ratings of Trees on MHc36 Sites

This table presents an index of suitability for trees in MHc36 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 MHc36			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Sugar maple (Acer saccharum)	**75**	**33**	**5.0**
Northern red oak (Quercus rubra)	**75**	**31**	**4.9**
Basswood (Tilia americana)	**87**	**24**	**4.9**
Bur oak (Quercus macrocarpa)	**29**	**12**	**4.4**
Quaking aspen (Populus tremuloides)	**20**	**16**	**4.3**
Green ash (Fraxinus pennsylvanica)	**33**	**7**	**3.9**
Red maple (Acer rubrum)	**28**	**8**	**3.9**
Paper birch (Betula papyrifera)	**33**	**6**	**3.5**
Big-toothed aspen (Populus grandidentata)	**17**	**10**	**3.3**
Bitternut hickory (Carya cordiformis)	**12**	**9**	**2.7**
White oak (Quercus alba)	**11**	**7**	**2.4**
White ash (Fraxinus americana)	**6**	**13**	**2.2**
*Suitability ratings: **excellent**, **good**, **fair**			

See linked text on brief methods and silvicultural application for Table R-1, file *Figures_Tables_Documentation*

(R-2) Natural Regeneration and Recruitment of Trees in Mature MHc36 Stands

This table presents an index of regeneration for MHc36 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 MHc36 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 regenerants, seedlings, saplings, and trees common in the canopy of Central Mesic Hardwood Forest (Eastern) – MHc36					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Sugar maple (Acer saccharum)	93	5.0	5.0	5.0	5.0
Basswood (Tilia americana)	90	4.2	4.3	4.7	5.0
Northern red oak (Quercus rubra)	70	3.8	3.8	3.2	5.0
Red maple (Acer rubrum)	51	4.0	4.0	3.3	3.5
Green ash (Fraxinus pennsylvanica)	50	3.8	3.8	2.5	3.5
Bitternut hickory (Carya cordiformis)	35	3.8	3.5	2.8	2.8
Quaking aspen (Populus tremuloides)	31	2.8	2.8	1.8	3.8
Bur oak (Quercus macrocarpa)	23	1.7	1.7	2.2	4.0
Big-toothed aspen (Populus grandidentata)	16	2.0	1.8	1.7	3.5
Paper birch (Betula papyrifera)	15	1.0	0.8	2.0	3.5
White oak (Quercus alba)	6	1.2	1.0	1.2	3.3
White ash (Fraxinus americana)	5	2.3	2.0	2.8	3.3

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

% presence: the percent of 122 MHc36 sample plots with that species present under 10m tall (R, SE, SA layers)
R-index: index of representation as true seedling or under 10cm tall
SE-index: index of representation as seedlings under 2m tall
SA-index: index of representation as saplings 2- 10m tall
T-index: index of representation as a tree >10m 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.

See linked text on brief methods and silvicultural application for Table R-2, file *Figures_Tables_Documentation*

(FIA-1) Structural Situations of Trees in Mature MHc36 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples MHc36 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
Sugar maple	734	3%	8%	11%	19%	11%	29%
Basswood	567	2%	5%	8%	24%	8%	50%
Red maple	117	3%	14%	8%	27%	8%	32%
Northern red oak	373	4%	8%	2%	18%	2%	66%
Bitternut hickory	8	0%	50%	25%	12%	25%	0%
White ash	1	0%	0%	0%	0%	0%	100%
Green ash	18	0%	6%	17%	17%	17%	44%
Bur oak	72	1%	11%	4%	18%	4%	49%
Paper birch	194	3%	14%	5%	37%	5%	35%
Quaking aspen	174	18%	9%	8%	10%	8%	45%
Big-toothed aspen	38	16%	0%	16%	5%	16%	47%
White oak	13	0%	0%	0%	15%	0%	85%

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

See linked text on brief methods and silvicultural application for Table FIA-1, file *Figures_Tables_Documentation*

(PLS/FIA-1) Abundance of MHc36 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 MHc36 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 - 35		35 - 95		> 95	
	Young		T1		Mature	
Red Oak	50%	8%	ǀǀ		9%	14%
Quaking Aspen (incl. Bigtooth)	10%	18%	ǀ		1%	3%
Paper Birch	5%	4%	ǀ		2%	4%
Basswood	14%	10%	⎫		18%	20%
American Elm	6%	5%	⎫		10%	3%
Ironwood	4%	12%	⎫		8%	7%
Bur Oak (incl. White)	–	1%	⎫		5%	6%
White Pine	1%	0%	⎫		3%	0%
Sugar Maple	4%	30%	⎫⎫		36%	33%
Red Maple	--	3%			--	3%
Green Ash (incl. Black & White)	3%	4%			4%	3%
Miscellaneous	3%	5%			4%	4%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	7%	7%	75%	71%	18%	21%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 5,368 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 2,107 FIA subplots that were modeled to be MHc36 sites.

See linked text on brief methods and silvicultural application for Table PLS/FIA-1, file *Figures_Tables_Documentation*

Forest Health

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.

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.

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.

Trembling 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.

Bigtooth 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.

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.

MHc36 - 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	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 MHc36 that are more susceptible to compaction and rutting.

Lady fern (*Athyrium filix-femina*)
Jack-in-the-pulpit (*Arisaema triphyllum*)
Virginia creeper (*Parthenocissus spp.*)
Green ash (C) (*Fraxinus pennsylvanica*)
Black ash (U) (*Fraxinus nigra*)

Side-flowering aster (*Aster lateriflorus*)
Graceful sedge (*Carex gracillima*)
Virginia waterleaf (*Hydrophyllum virginianum*)
Starry sedge (*Carex rosea*)
American elm (U) (*Ulmus americana*)

(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

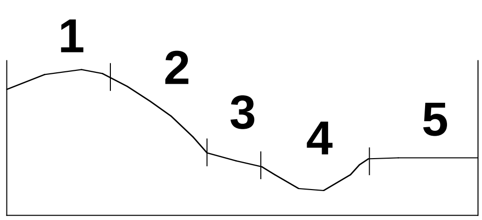
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

   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

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

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