MHn44

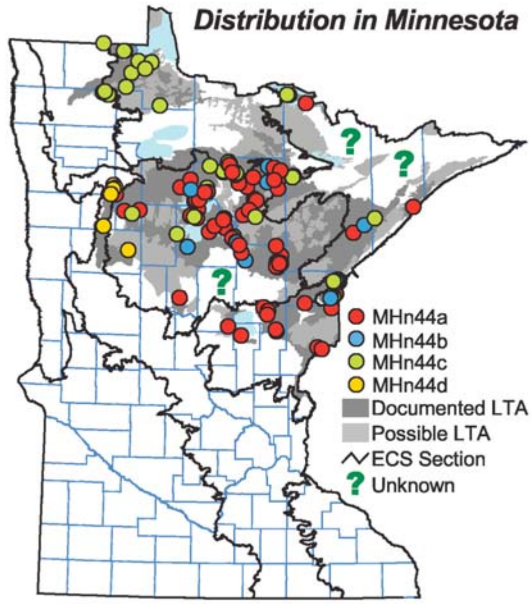
- General Description
- Natural Disturbance Regime
- Natural Stand Dynamics & Growth-stages
- Growth Stage Key
- Tree Behavior
    - Quaking Aspen
    - Balsam Fir
    - Red Maple
    - Paper Birch
    - Basswood
    - White Spruce
    - Northern White Cedar
    - White Pine
    - Black Ash
    - Balsam Poplar
    - Northern Red Oak
    - Bur Oak
- Tables
    - PLS-1 - Historic Abundance of MHn44 Trees in Natural Growth-stages
    - PLS-2 - Abundance of trees throughout succession in MHn44
    - PLS-3 - Historic Abundance of MHn44 Trees Following Disturbance
    - PLS-4 - Ordination of Historic MHn44 Age-classes
    - PLS-5 - Historic Windows of Recruitment for MHn44 Trees
    - R-1 - Suitability ratings of trees on MHn44 sites
    - R-2 - Natural Regeneration and Recruitment of Trees in Mature MHn44 Stands
    - FIA-1 - Structural Situations of Trees in Mature MHn44 Stands
    - PLS/FIA-1 - Abundance of MHn44 trees in Pre-settlement and Modern Times by Historic Growth-stage
- Silviculture Systems
- Forest Health Considerations
- Operability
- Public Land Survey linked text
- Modern Forest linked text

MHn44 – Northern Wet-Mesic Boreal Hardwood-Conifer Forest

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Wet-Mesic Boreal Hardwood-Conifer Forest (MHn44) are a common hardwood community found throughout the Laurentian Mixed Forest ecological Province of Minnesota. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.



The range of MHn44 forests in Minnesota (shaded) and distribution of releve samples (red, blue, green, and yellow dots).

Commercial Trees

As a commercial forest, MHn44 sites offer a wide selection of crop trees and possible structural conditions. This community is widely recognized as the premier pulp-producing habitat in the state. Quaking aspen, balsam fir, red maple, paper birch, basswood, and white spruce are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on MHn44 sites (see Suitability Tables). White cedar, white pine, black ash, balsam poplar, northern red oak, and bur oak 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. Sugar maple is ranked as a fair crop tree, and stands can be managed to maintain its presence as a minor component for purposes other than timber production.

Among these species, quaking aspen, paper birch, balsam fir, and white spruce were the dominant native trees that have occupied MHn44 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)**. White pine, red maple, black ash, balsam poplar, white cedar, bur oak, and red oak are likewise native to MHn44 sites but occurred naturally at lower abundance. The consequence of fire suppression, commercial logging, and settlement in the past century has been to promote more balsam fir than usual at the expense of white spruce. Otherwise, modern MHn44 stands are similar to their historic counterparts, and management interpretations are not complicated by the ingress of atypical species.

Natural Silvicultural Approaches

In the historic landscape, most MHn44 stands (60%) were transitioning between the young and mature growth-stages. Roughly these were stands 35-95 years old. At this time, senescence of the initial-cohort trees created regeneration opportunities for trees ranging from single-tree gaps to large gaps up to an acre. Several silvicultural systems could be used to approximate the natural loss of initial-cohort trees and regeneration typical of transitioning MHn44 forests. Selective harvesting matches best the small-gap mortality pattern, and on MHn44 sites would favor white spruce and balsam fir over all others. Shelterwood variants or group selection would create the large-to-small openings that favor recruitment of white spruce, balsam fir, red maple, and black ash. Paper birch, red oak, bur oak, white cedar, white pine, and basswood should all do well in the larger gaps created by patch cutting or variants of seed-tree harvests.

A significant proportion (24%) of native MHn44 stands were young forest <35 years old. Given that only 4% of MHn44 forests were described as having been burned or windthrown, it is clear that destructive agents other than these obvious catastrophes were involved to create so much young, small diameter MHn44 forest. We suspect chronic disease and possibly surface fire. What seems clear from the historic records is that young, re-initiated MHn44 stands were patchy and offered a mixture of situations where seeding, sprouting, and release of advance regeneration worked together to initiate the next forest. It is highly unlikely that re-initiated MHn44 forests resembled something as uniform as a clear-cut. Clear-cutting with reserves, patch cutting, and variants of seed-tree cutting could all approximate the natural pattern of disturbances that created young MHn44 forests. Clear-cutting with reserves would favor quaking aspen and balsam poplar, which are primarily open regeneration strategists on MHn44 sites. Patch cutting or variants of seed-tree harvests are silvicultural strategies that should work to re-initiate MHn44 stands and favor trees that do well in the open or in large gaps such as paper birch, white cedar, and white pine.

Just about 16% of the MHn44 landscape was forest older than 95 years. The hallmark of these forests is density-dependent mortality of the dominants and the formation of 2-10 acres patches of forest that tend to be either largely deciduous or largely coniferous. The management strategy of creating very large management units (>200 acres) and treatments in several-acre patches with the intent of either regenerating quaking aspen and paper birch or releasing advance regeneration of white spruce and balsam fir would fit our vision of maintaining a MHn44 landscape that is largely older forest. MHn44 sites are chronically infected with diseases and cyclically invaded by pests when populations of the dominant trees reach densities that trigger outbreaks. For this reason it makes no silvicultural sense to manage for monotypes in patches larger than about 10 acres. For this same reason it makes little sense to try to extend rotations beyond the first signs of decline. The salient feature of old MHn44 landscapes is the scattered presence of old, large-diameter white pine and white spruce seed trees that should be conserved or restored. Almost any partial harvesting silvicultural system – patch cutting, seed tree, shelterwooding, or group selection – could be used to encourage either the deciduous components or the coniferous components in 2-10 acre treatments. We advocate an entirely adaptive approach where the vigor of the canopy trees and abundance of advance regeneration would dictate the appropriate silvicultural system for maintaining older MHn44 landscapes.

Management Concerns

MHn44 communities occur on a variety of landforms and parent material ranging from sand to clayey loams. Soil textures have little to do with the distribution of MHn44 forests because the some what-poor to poor drainage is the overriding ecological factor. Soil texture has everything to do with the risk of soil compaction. On dissected glacial lake sediments, the usual texture is silty clay and the risk of compaction and rutting is high. On stagnation moraines and till plains, the usual texture is fine loam and the risk of compaction is high. In these situations the risk of rutting is also high because of hard, impermeable subsoil horizons. On glacial lake sediments, the risks of compaction are low because of the uniform particle sizes, whether fine sand or even silt. On the glacial lake sediments, the soil surface is often saturated and rutting is almost always possible. Because of the usual poor drainage, field inspection is always required to evaluate the chance of operating on unfrozen ground.

The landscape balance of growth-stages and stand ages for the MHn44 community is not much different than it was historically. We believe that wildlife populations are probably reacting to MHn44 habitat as they always have. Other than the loss of white spruce to more balsam fir, there are not great departures in composition from the historical state of MHn44 forests. A potential risk is the attempt to create monotypic patches of MHn44 trees as infection by site-latent diseases and likelihood of pest infestations are higher for monotypic stands. In our experience, naturally regenerated MHn44 stands are adequately mixed regardless of targeted species; the risk is higher for conifer plantations and other sites where herbicides have been used to eliminate deciduous trees and brush.

There is serious risk of swamping on MHn44 sites. The removal of too many trees followed by herbicide applications can seriously reduce the ability of the remaining vegetation to transpire and de-water the soils. Quaking aspen, because of its ability to regenerate vegetatively, played the critical role of helping to de-water MHn44 sites after the loss of forest canopy. Often, MHn44 sites are “lost” to speckled alder, willow, and wetland herbs when sites are denuded, chemically or mechanically, to create white spruce plantations.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 4,074 corners within the primary range of the MHn44 community. At these corners, there were 10,566 bearing trees that one commonly finds in MHn44 forests.

The PLS field notes described about 4% of the MHn44 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands. From these data, a rotation of 430 years was calculated for stand-replacing fire.

Elsewhere in the MHn44 landscape, the surveyors described lands as windthrown without suitable-sized trees for scribing. Such corners were encountered at about 2% of the time, yielding an estimated rotation of 960 years for windthrow.

Far more common at MHn44 sites were references to what we have interpreted as some kind of partial canopy loss, without any explicit mention of fire or windthrow. Most references were to scattered timber, sparse forest, or thickets with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked mesic hardwood forests. About 3% of the survey corners were described as such, resulting in a calculated rotation of 160 years for disturbances that maintained early and mid-successional trees on MHn44 sites. That more corners were described as burned (138) compared to windthrown (37) suggests that surface fires were the more prevalent cause of partial canopy loss.

Natural Rotations of Disturbance in MHn44 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**430 years**
Catastrophic windthrow photograph	**960 years**
Partial Canopy Loss, photograph	**160 years**

Compared to other mesic hardwood (MH) communities in Minnesota, MHn44 rotations of catastrophic disturbance are similar in that they exceed the longevity of any initial cohort species. This means that natural stand dynamics will usually involve a few generations of trees and a shift from large regeneration gaps to smaller ones as stands mature. The rotation of 430 years for catastrophic fire is unusual and the shortest calculated for any northern MH community. We believe that MHn44 sites tended to burn catastrophically more so than other MHn communities because of their tendency to have high populations of conifers in older growth-stages and because of their tendency to occur in landscapes where the matrix vegetation is fire-dependent forest. The rotation of 960 years for stand-regenerating wind is typical of MH communities in the northern (MHn) and central (MHc) floristic regions where wind was not an important disturbance agent. This differs from MH communities in the southern and northwestern floristic regions where wind played a significant role. The rotation of 160 years for maintenance disturbances is typical of MHn communities. Maintenance disturbance was sufficient to keep local populations of early successional trees on MHn44 sites and maintain indefinitely mixed stands of quaking aspen, paper birch, balsam fir, and white spruce. We believe that pocket diseases, e.g. *Armillaria*, were as important as the more obvious fire or windthrow in maintaining MHn44 forests.

Natural Stand Dynamics & Growth-stages

Following stand-regenerating fire or possibly windstorms, the overall pattern of compositional change in MHn44 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 MHn44, quaking aspen and balsam poplar are the species that benefit greatly from fire because they compete poorly with fire-intolerant species like white spruce and fir on these sites in later successional stages.

Views and Summaries for MHn44 sidebar	
PLS-1	**Summary of historic growth-stages:** relative abundance of bearing trees
PLS-2	**View line-graph of historic change:** bearing tree abundance across age-classes
PLS-3	**Summary of historic disturbance:** abundance of bearing trees at burned, windthrown or disturbed sites
PLS-4	**View historic rates of change:** ordination of bearing tree age-classes
PLS-5	**Summary of historic regeneration:** Species ratings regarding their ability to regenerate after disturbance, in gaps, and beneath a canopy
R-1	**Summary of tree suitability for a Native Plant Community:** Species ratings based upon modern forests
R-2	**Summary of understory recruitment in modern forests:** indices of species' success in the understory
FIA-1	**Summary of regeneration in modern forests:** FIA trees in multiple-cohort situations
PLS/FIA-1	**Summary of differences between modern and pre-settlement forests:** relative abundance of bearing trees and FIA trees by growth-stage.

Early in the process of stand maturation, MHn44 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, crown competition among canopy trees causes this. Young MHn44 forests under 35 years had mean distance of just 19 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 and mature forests 95-195 years old both showed mean distances of 21 feet. Bearing trees in old MHn44 forests were 24 feet from their corresponding corners on average. Compared to other communities, these distances are quite typical of naturally stocked forest and slightly tighter than in mesic hardwood communities with sugar maple.

Young Growth-stage: approximately 0-35 years

About 24% of the MHn44 landscape in pre-settlement times was covered by forests estimated to be under 35 years old **(PLS-1)**. About two-thirds of these stands were monotypic. Most common, by far, were survey corners where all of the attending bearing trees were quaking aspen. At survey corners with mixed composition, aspen was still the most cited species, and it was most often mixed with paper birch.

In describing young, burned stands the surveyors indicated that aspen and paper birch were the important initial-cohort trees **(PLS-3)**. The ability of quaking aspen to dominate young MHn44 forests is a consequence of its persistence in the mature and old growth-stages. For a pioneer species, quaking aspen shows surprisingly good success in maintaining a presence in older MHn44 forests due to excellent success in establishing seedlings or suckers and recruiting some to mid- and canopy heights **(R-2)**. Apparently quaking aspen was highly successful at maintaining clone rootstocks and scattered seed trees so that they could rapidly repopulate burned areas, even if the burned stand had reached the older growth-stages. Paper birch also maintained a significant presence in older stands and was prepared to re-colonize following fires. Its low abundance though in post-fire stands suggests to us that its main strategy in this circumstance was for mature trees to replace themselves through stump sprouts.

Surprisingly, the surveyors used some fire-sensitive trees such as balsam fir and white spruce as bearing trees at corners they described as burned. Together spruce and fir accounted for 13% of the bearing trees at "burned" corners. This suggests rather strongly that fires were patchy, leaving an unexpected amount of legacy spruce and balsam fir. It is probably significant that these conifers tend to have higher presence in wetter habitats that occur throughout the high water-table landscape typical of the MHn44 community. If wetter habitat was responsible for skips within burns, then one would expect survey corners to pick up at least a few of these trees.

Young stands recovering from windthrow were also dominated by quaking aspen, but much less so than burned stands. About half (51%) of the young bearing trees at windthrown corners were aspen compared to 73% at burned corners **(PLS-3)**. Paper birch, balsam fir, and white spruce were also important initial cohort trees following windthrow, and together accounted for 33% of the post-windthrow trees. Our general impression is that the main effect of windthrow was to regenerate some aspen and release advance regeneration of other species. A variety of tree mixtures were possible depending upon the successional state of the damaged forest and species that were doing well in the understory at that time (see **PLS-5**). It is important to note that windthrow was an uncommon event and not a major means of regenerating MHn44 forests. We favor the idea that MHn44 forests were maintained mostly by "pocket" diseases that tend to create large-canopy gaps rather than widespread tree mortality. Such diseases weaken tree boles and root systems and probably contributed to the effects of powerful storms that the surveyors perceived as extensive windthrow.

Because MHn44 sites have moderately well to somewhat-poorly drained soils due mostly to high water tables, we believe that these sites could be incredibly wet during the post-disturbance years. Removal of the canopy whether by fire, wind, or clear-cutting often results in an elevated water table. This condition apparently favored quaking aspen over any other species, and aspen took on the ecological role of de-watering MHn44 sites in the early successional years. Thus, the effect of canopy removal might have been to expand wetter habitat in MHn44 landscapes and promote establishment of trees in included wetlands that could regenerate beneath a canopy aspen.

Transitional Stage: approximately 35-95 years

About 60% of the historic MHn44 landscape was forest undergoing considerable compositional change as stands approached maturity **(PLS-1, PLS-4)**. Stands in this stage were more often mixed than monotypic. Monotypic conditions were represented mostly by survey corners where all bearing trees were quaking aspen, and much less often by paper birch and balsam fir. At survey corners with mixed composition, quaking aspen is still the most cited species and it was usually mixed with paper birch, balsam fir, and balsam poplar.

The transition stage is driven almost entirely by the behavior of quaking aspen, balsam fir, and white cedar. Initial-cohort quaking aspen decline throughout the period **(PLS-1, PLS-2)**. Aspen's plummet of 76% relative abundance between the 20 and 80-year age classes is responsible for much of the community's compositional "movement" in the transition stage. Initially the decline of quaking aspen is mirrored by a pulse of balsam fir regeneration. The relative abundance of fir increases 27% between age-classes 20 and 40 years. Because quaking aspen are not short-lived or senescent at 20-40 years on wet-mesic habitats, it is exceeding tempting to suspect that balsam fir in some way was the causal agent in aspen decline rather than a benign benefactor of openings beneath dead aspen. Curiously, just as it seems that 40-50 year old MHn44 stands were well on their way to the "spruce-fir climax," the relative abundance of fir collapses to lower levels (~10%) that we see maintained into old-growth. The notion that balsam fir in any way "prepares" sites for paper birch and long-lived conifers, only to altruistically "step aside" has no basis in ecological theory. Nonetheless, the pulse of fir abundance in the first transition stage is observed in most terrestrial forests of the northern floristic region of the state where succession is towards white spruce, white cedar, or white pine rather than sugar maple. On MHn44 sites the effect of the fir pulse is to promote recruitment and regeneration opportunities for paper birch and white spruce. Extension of the transition period to 95 years is mostly the consequence of a pulse of white cedar regeneration that is remarkably similar to that of balsam fir, but successive to it. Between age classes 70 and 90, white cedar abundance increases to about 18% of the trees from nearly nothing. Like fir, cedar abundance drops to low levels following the transition stage. For a short-lived species like balsam fir, its population collapse is not entirely surprising. But for white cedar, a very-long lived tree in any Minnesota habitat, the loss of cedar in 100-150 year old MHn44 stands seems unexplainable by any natural stand-maturation process. The cedar "pulse" is seen among several different northern forest communities and could be the result of regional events and not normal stand dynamics.

Mature Growth-stage: approximately 95-195 years
About 14% of the historic MHn44 landscape was mature forest where the rate of successional change slowed substantially **(PLS-4)**. Stands in this stage were almost always of mixed composition. Just 2% of the survey corners were attended by all quaking aspen trees and no other tree occurred by itself. Most often, mature MHn44 forests were a rather even mixture of quaking aspen, paper birch, balsam fir, and white spruce **(PLS-1)**.

Perhaps the most striking feature of mature MHn44 forests is that they were mixtures of trees that we would normally assign quite different shade-tolerances and regeneration strategies. By age 95 most of the initial-cohort quaking aspen were dead, meaning the current canopy trees of mature MHn44 forests were established and recruited in reaction to conditions not associated with any kind of stand-initiating catastrophe. The successional pattern for MHn44 forests is to be initially deciduous and terminally coniferous. The mature growth-stage was a period where the abundance of deciduous trees and coniferous trees seem to balance, thus forester's common reference to these forests as "mixedwoods." The mixture in MHn44 stands though was patchy and quite unlike the fine-scale integration of hardwood species in MHn communities with sugar maple. Patches of mature MHn44 stands smaller than 10 acres often seem obviously coniferous or obviously deciduous. Groundlayer herbs and shrubs seem to react quite differently to litter derived either from spruce and fir needles versus hardwood litter and this helps to accentuate the sense of patchiness within a stand. We are convinced that mature and very old MHn44 forests could maintain indefinitely this patchy condition.

Maintaining the patchy composition of MHn44 forests requires maintenance disturbances that are density-dependent and mediated by biological agents whose own populations track the abundance of their host trees. In layman's terms, this means that the more successful aspen, paper birch, balsam fir, and white spruce are as monotypes in mature and older MHn44 stands, the more likely it is for them to die and provide at least some regenerative opportunities for the other species. For white spruce and balsam fir, the density dependent cycle of population increase and devastating outbreaks of spruce budworm are well documented. We believe that this is the primary reason that we don't often see pure stands of spruce and fir in northeastern Minnesota. Budworm outbreaks though are regional events that don't explain the 2-10 acre patches that characterize mature MHn44 forests. The size of aspen clones and colonies of root diseases (e.g. *Armillaria*) occur at the scale matching our field observations. Our best guess is that the natural patchiness of MHn44 forests is linked to an underground legacy of rootstocks and their corresponding diseases. We do not know if the mostly coniferous or mostly deciduous patches are stable on the MHn44 landscape, or if they move about in kaleidoscopic fashion where certain points could experience alternating episodes of coniferous or deciduous domination.

The mature growth-stage is also an episode where minor trees are evident and were often the larger trees in mature MHn44 forests. Nearly all of these species got their start during the transition and persisted into the mature growth-stage because of their longevity. We don't believe that the presence of these minor trees directly related to the average MHn44 environmental conditions or successional stage. Because MHn44 is a wet-mesic community, included or bordering wetlands have some influence on these forests. Where the included wetlands are rich and with mineral soils, black ash, American elm, bur oak, and red maple show some presence in MHn44 forests. Where the included wetlands are the more acid *Sphagnum*-dominated peatlands, white cedar and perhaps white pine seem to be more evident as minor trees in mature MHn44 stands.

Very Old Growth-stage: approximately >195 years

Very little of the historic MHn44 landscape, just 2%, was estimated to have been MHn44 stands older than 195 years **(PLS-1)**. Nearly all (99%) of the corners with these large old trees were mixed in composition. Trees that one would find in the initial cohort – quaking aspen, balsam poplar, and paper birch – are still present if not common in very old MHn44 forests. The persistence of paper birch, quaking aspen, and perhaps balsam poplar has the ecological effect of assuring that these trees will dominate MHn44 sites after catastrophic disturbance regardless of how old the damaged forest was. White pine was present in very old MHn44 stands because of its extraordinary longevity, as it had no significant regeneration beyond about age 60 **(PLS-5)**. White spruce has excellent regeneration in the understory of very old MHn44 forests and can support a population of large-diameter trees through replacement. We attribute also the persistence of balsam fir to continuous regeneration in the very old growth-stage because of its excellent ability to establish and recruit seedlings in modern stands **(R-2)**.

We believe that very old MHn44 forests were maintained by the same density-dependent processes as were mature forests. Very old forests differ only in having some very large-diameter and presumably old white pines and white spruce.

Growth Stage Key

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

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

Tree Behavior

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

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

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

To this end, we have performed analyses 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?

Quaking Aspen

- ***excellent habitat suitability rating***
- ***early successional***
- ***open (large-gap) regeneration strategist***
- ***regeneration window at 0-30 years***

Suitability
MHn44 sites provide ***excellent*** habitat for quaking aspen trees. The perfect ***suitability rating*** of 5.0 for quaking aspen is influenced mostly by its very high presence (72%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is an important co-dominant and sometimes dominant tree, contributing 27% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer good habitat for quaking aspen, especially the wet-mesic MHn44 and MHn46 communities. Among northern mesic hardwood communities, MHn44 offers the best opportunity for growing quaking aspen.

Young Growth-stage: 0-35 years
Historically, quaking aspen was the overwhelming dominant in young MHn44 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young aspen represented 73% of the trees at survey corners described as burned, which is by far more than any other tree **(PLS-3)**. Aspen was also the leading species following windthrow, representing 51% of the trees at such survey corners. Young MHn44 corners with aspen trees present were mostly monotypic with all attending bearing trees being aspen. Its dominance in the young growth-stage and its leading abundance following fire and windthrow is why we consider aspen to be an ***early successional*** species on MHn44 sites. Small-diameter aspen regeneration was most abundant in the post-disturbance window **(PLS-5)**. This is typical of early successional species, and we interpret this as aspen showing excellent ability to recruit into under-stocked areas of burned or windthrown stands.

Transition: 35-95 years
Transitioning of young MHn44 forests was driven by the steady loss of initial-cohort aspen, leaving some longer-lived paper birch and allowing some ingress of conifers **(PLS-1)**. We estimate that this decline started immediately and continued to about age 110 years when aspen stabilized at about 24% relative abundance **(PLS-1, PLS-2)**. Small-diameter aspen regeneration was low abundance early in the transition and was not detected beyond the 60-year age-class **(PLS-5)**. In most cases, aspen regeneration was coming in under older aspen. We interpret this as limited replacement of itself in large-gaps as some of the initial-cohort aspen started to senesce. During the transition period, aspen was present at most survey corners and about a quarter of these were still pure aspen. It is possible that aspen establishment and recruitment to bearing-tree size (~4” dbh) during the transition was the consequence of it being the only species present in monotypic pockets.

Mature Growth-stage: 95-195 years
In mature MHn44 stands the relative abundance of aspen was stable at about 24% and it persisted into the very old growth-stage at slightly higher abundance **(PLS-1, PLS-2)**. Although much diminished from earlier growth-stages, 24% abundance is still high for an individual species, and was second only to white spruce at this stage. Although aspen can be long-lived on MHn44 sites, persistence must have required some regeneration and recruitment. Thus, we assume that aspen has secondary strategies for behaving like a mid- or late-successional species able to respond to fine-scale or maintenance disturbances. Small-diameter, aspen regeneration was not observed beyond 60-years **(PLS-5)**. Smaller diameter trees though were occasional in mature forests. In most cases, smaller-diameter aspen were among larger white spruce, paper birch, white pine, or older aspen. Surprisingly, the ability of aspen to recruit seedlings or suckers through all height strata in modern MHn44 forests is second only to balsam fir **(R-2)**. This too strongly suggests that it can persist under a regime of fine-scale disturbance on

MHn44 sites. Its excellent regenerative indices are quite in line with species able to recruit into small gaps. Our experience in MHn44 forests is that mortality is rarely a single-tree event, rather several to many trees tend to collapse into gaps that expand over successive years. This behavior is normally ascribed to fungal diseases of roots and lower boles of the trees. Our interpretation for quaking aspen is that the regenerants and seedlings in **R-2** represent a bank of suckers maintained by the adult trees of the stand. They are obviously successful at recruiting into these large gaps allowing aspen to maintain its presence in mature stands. Some studies have suggested that in habitats similar to MHn44, the growth response of aspen suckers in these canopy gaps is subsidized by the parent tree, allowing them to compete with species like white spruce that do very well in partially shaded environments.

Very Old Growth-stage: >195 years

In the very old growth-stage, quaking aspen was an important co-dominant with white spruce **(PLS-1)**. All records of aspen at this stage were at corners with mixed composition. The aspen trees were about evenly represented as the largest or smallest tree at a survey corner, suggesting success in both the canopy and subcanopy. Smaller-diameter aspen were beneath white pine and older aspen more often than beneath white spruce. Our interpretation is that quaking aspen could maintain itself indefinitely as a co-dominant in very old MHn44 stands because this community is susceptible to chronic canopy loss due to disease.

Regeneration Strategies

Quaking aspen's primary regenerative strategy on MHn44 sites is to dominate ***open habitat*** after stand-regenerating disturbance. It was most successful after fire, but any agent or scale of disturbance resulted in aspen regeneration when it was present **(PLS-3)**. In the historic PLS data this interpretation is supported by: (1) the fact that 86% of the bearing trees in young stands were aspen **(PLS-1)**, (2) aspen represented by far, the largest proportion of bearing trees at burned and windthrown corners **(PLS-3)**, and (3) aspen's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. The high percent of aspen as saplings in sapling stands (situation 11) in the FIA data **(FIA-1)** is also characteristic of species that regenerate effectively in the open.

The releve sampling of mature MHn44 forests suggests, however, that aspen is able to function also as a ***large-gap*** strategist with excellent establishment and recruitment in the understory strata **(R-2)**. Modest abundance of aspen in subordinate situations (12, 23, 13) at FIA plots support also the idea that aspen can regenerate in gaps **(FIA-1)**. The persistence of aspen in mature and very old growth-stages is also consistent with the idea of aspen functioning as a large-gap strategist in pre-settlement forests. This had the consequence of aspen being present and prepared to overwhelmingly dominate sites after major disturbance regardless of the timing of such an event.

Historic Change in Abundance

Today, quaking aspen remains the dominant tree in MHn44 forests. It is slightly less abundant in the young growth-stage, but this result could be due to surveyors confusing quaking aspen and balsam poplar as the sum of their abundance is nearly identical to their presence in modern forests **(PLS/FIA-1)**. The abundance of quaking aspen in mature and very old forests has nearly doubled since pre-settlement times. It seems that this increase was at the expense of white spruce as it is generally recognized that spruce seed trees have been lost in the process of commercially coppicing aspen.

Balsam Fir

- ***excellent habitat suitability rating***
- ***late- (mid-) successional***
- ***small-gap (large-gap) regeneration strategist***
- ***regeneration window at 30-50 years***

Suitability
MHn44 sites provide ***excellent habitat*** for balsam fir trees. The ***suitability rating*** of 4.7 for balsam fir is influenced mostly by its high presence (38%) as trees on these sites in modern forests **(R-1)**. When present, balsam fir is a common co-dominant tree, contributing 18% mean cover in mature stands. The ranking is second only to quaking aspen on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer fair-to-good habitat for balsam fir, but MHn44 sites are by far the best (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, balsam fir was a minor tree in young MHn44 stands **(PLS-1, PLS-2)**. Young firs represented 8% of the trees at survey corners described as burned, well behind the fire-tolerant quaking aspen **(PLS-3)**. Nonetheless, the presence of any balsam fir on burned lands is surprising given its well-known sensitivity to fire. As expected, young firs are considerably more abundant at windthrown corners (15%), where we suspect that the effect of canopy removal is to release advance regeneration of fir. Because of balsam fir's affinity for wetter habitats included in the MHn44 landscape, we believe that the few, small-diameter firs showing up in post-burn situations were coming from unburned wetlands near burned survey corners. Fir regeneration first appears at the close of the young growth-stage in the 30-year age-class **(PLS-5)**. Our interpretation is that young firs were absent from the actual burned patches of MHn44, but its widespread presence, especially in habitats less likely to burn, assured local seed sources. Thickets of young quaking aspen were probably fine habitat for seed-origin firs, particularly at the stage where the groundlayer is suppressed and aspen starts to self-thin. Supporting this argument is the performance of balsam fir under a canopy in modern stands, with excellent indices of regeneration **(R-2)**.

Transition: 35-95 years
The transition to mature conditions is due mostly to the decline of initial-cohort quaking aspen, but the beginning of this episode starts with a burst of balsam fir recruitment **(PLS-2)** that adds to the compositional movement **(PLS-4)**. Early in the transition, the abundance of fir rises dramatically to peak abundance of about 30% in the 40 and 50 year age-classes. The zenith is short-lived as the relative abundance of fir plummets to about 10% relative abundance to close the transition period. It is hard to visualize the rise from 5% relative abundance at age 30 to 31% relative abundance at age 40 without a pre-existing, pervasive bank of fir seedlings under 20-30 year old aspen. We believe that young aspen stands offered especially good habitat for establishing balsam fir, because this pulse of fir regeneration is a feature common to many northern forest communities where the initial stages are aspen-dominated and fir is important in later growth-stages. Equally impressive is the collapse of fir populations before the transition stage concludes. Between age classes 50 and 70 years, the relative abundance of fir drops 22%. Although balsam fir is short-lived, it is hard to imaging that the collapse of the transitional cohort didn't involve mortality of a lot of young firs. Whatever the destructive agent, it must have been density-dependent as fir populations never again approach those of the transition stage. Balsam fir's ability to decisively replace the initial-cohort trees and reach peak abundance during the transition stage is why we consider fir somewhat of a ***mid-successional*** species, although its behavior in the older growth-stages is quite typical of a late-successional species.

Mature Growth-stage: 95-195 years
In the mature growth-stage, balsam fir abundance stabilized at about 10% and it persisted at similar abundance into the very old growth-stage **(PLS-1, PLS-2)**. Balsam fir's relative abundance in the mature growth-stage is certainly the result of ingress and recruitment during the transition

stage. Small-diameter fir regeneration was not detected in the mature growth-stage **(PLS-5)**. However, firs were usually the smaller-diameter tree at survey corners rather than the largest tree. The smaller firs were likely regeneration and clearly had an affinity for being beneath paper birch. Less often, smaller firs were coming in under quaking aspen, white cedar, and white spruce. We interpret this as modest, but continued success of recruiting seed-origin trees under the remnants of the initial-cohort canopy and beneath conifers less shade-tolerant than balsam fir.

Very Old Growth-stage: >195 years
In the very old growth-stage, balsam fir was an important tree, occurring almost always at survey corners of mixed composition. At 10% relative abundance, it was behind white spruce, quaking aspen, and paper birch as the most common trees on old MHn44 sites **(PLS-1)**. Small-diameter balsam fir regeneration coming in among larger trees was not detected during the very old growth-stage **(PLS-5)**. Firs were still common, and all survey corners with fir were of mixed composition. Firs were also far more common as the smallest tree at old survey corners. When firs were the smallest tree at a survey corner, they were beneath white spruce, white cedar, and paper birch. In modern forests, balsam fir has excellent ability to establish and recruit seedlings under a canopy **(R-2)**. For this reason, we believe that fir populations in the very old growth-stage were maintained by establishment and recruitment, though none met our half-diameter rule. Other than the curious burst of fir abundance in the transition stage, its persistence and regenerative abilities under a canopy are our reasons for considering balsam fir to be mostly a ***late-successional*** tree in MHn44 forests. The level of fir subordination in the old growth-stage is incredibly high. Our interpretation is that balsam fir was most successful at filling the subcanopy in old forests, but never achieving the height, diameter, or age of the surrounding white spruce.

Regeneration Strategies
Balsam fir's primary regenerative strategy on MHn44 sites is to satiate the groundlayer with seedlings and to then recruit saplings in ***small-gaps***. It was successful at doing this under any other tree, but most often it was paper birch and long-lived conifers. In the historic PLS data this interpretation is supported by: (1) the fact that balsam fir abundance is steady throughout the older growth-stages **(PLS-1, PLS-2)** and, (2) it is most abundant at survey corners in mature, undisturbed conditions **(PLS-3)**. The high percentage of balsam fir seedlings in the FIA data (situations 12 and 13) is also characteristic of species successful in small gaps **(FIA-1)**. Most significant though, is its excellent ability to establish and recruit seedlings under a canopy in modern stands **(R-2)**.

The fir "pulse" described for the transition stage would suggest that balsam fir can function to some extent as a ***large-gap*** strategist. This argument is supported mostly by: (1) the fact that fir, more than any other species, responded strongly to the decline of the initial-cohort aspen **(PLS-2)**, and (2) fir's primary regeneration window was a gap window rather than the ingress window **(PLS-5)**. Also, the high percentage of balsam fir poles beneath trees (situation 23) is also typical of trees that are successful at filling large canopy gaps **(FIA-1)**. Impressed by fir's ability to recruit under a canopy **(R-2)**, we have discounted the idea that large gaps are in any way required for fir germination and establishment. In fact, we believe that fir's competitive advantage is under full shade and probably most obvious under the proximal canopy of initial-cohort quaking aspen. However, fir's response to release in large gaps, such as following windthrow **(PLS-3)**, was excellent and similar to other species that we have described as large-gap strategists.

Historic Change in Abundance
Today populations of balsam fir are considerably higher in MHn44 forests than they were historically **(PLS/FIA-1)**. The increase in fir is evident in all growth-stages at abundances nearly double that of pre-settlement times. Although fire was not a common event in MHn44 communities, it was mentioned more often than windthrow. Also the flora of MHn44 forests includes species of fire-dependent forests, partly because it often occurs on landforms where the matrix vegetation was fire-dependent forest. We believe that mild surface fires were important maintenance events in MHn44 forests and that fire suppression has allowed fir populations to

Red Maple

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window 30-50 years***

Identification Problems

The PLS surveyors did not consistently distinguish between red and sugar maple. Thus, interpretations of PLS data for the more common red maple should always be done knowing that some of these trees were likely sugar maple. MHn44 releve samples show that for plots with maple present: 12% have both species present; 17% are sugar maple without red maple; 71% are red maple without sugar maple.

Suitability

MHn44 sites provide ***excellent habitat*** for red maple trees. The ***suitability rating*** of 4.6 for red maple is influenced mostly by its presence (27%) as trees on these sites in modern forests **(R-1)**. When present, red maple can be an important co-dominant tree, contributing 19% mean cover in mature stands. The ranking is third behind quaking aspen and balsam fir on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer good habitat for red maple, especially the wet-mesic MHn44 and MHn46 communities (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, red maple was nearly absent from young MHn44 stands recovering from stand-regenerating events **(PLS/FIA-1)**. Young red maples represented 1% of the trees at survey corners described as burned **(PLS-3)**. No young red maples were recorded at survey corners affected by stand-regenerating wind. Small-diameter red maple regeneration was first detected in trace amounts in the 30-year age-class at the close of the young growth-stage **(PLS-5)**. Our interpretation is that there was very limited regeneration of red maple under the initial-cohort aspen.

Transition: 35-95 years

As stands transitioned to mature conditions red maple increased in abundance, reaching peak abundance of 4% in the 50-year age-class. This peak was short-lived and limited to just the transition period as red maple constituted no more than about 1% of the bearing trees in the stable growth-stages **(PLS/FIA-1)**. This small peak in abundance during the transition stage is why we tentatively consider red maple to be ***mid-successional*** on MHn44 sites. Small-diameter red maple regeneration was detected as coming in among larger trees during the transition stage, especially in the 30-50 year age-classes **(PLS-5)**. Almost always, it was the smallest tree at a survey corner which is typical of a trees re-colonizing sites by seeding. In most cases, red maple regeneration was coming in under quaking aspen, paper birch, and other hardwoods rather than conifers. We interpret this as modest success at establishment and recruitment of seed-origin maples under a remote or partial canopy of initial-cohort hardwoods.

Mature and Very Old Growth-stages: 95-195 years and older

In pre-settlement forests red maple was nearly absent from mature and very old MHn44 forests **(PLS/FIA-1)**. Just a few trees, and no small-diameter regeneration were detected in these older growth-stages. For the trees present, most were the smallest diameter tree at survey corners and still were beneath quaking aspen and paper birch rather than conifers. Although few stands older than 95 years contributed to the releve sampling, it is quite clear that red maple is capable of developing a seedling bank and recruiting to all taller strata under a canopy **(R-2)**. This suggests that red maple will be an important component in older MHn44 forests in the future. Our interpretation is that there was historically enough fire in the MHn44 landscape to keep populations of red and sugar maple quite low and that maples were in general infrequent as were mature and very old MHn44 forests **(PLS-1)**. Alternatively, the seral trend for MHn44 is for young stands to be strongly dominated by hardwoods and at some later time (~100 years) flip to conifer domination. It is conceivable that red maple's poor presence during the conifer-dominated stages is related to some sort of direct inhibition by conifers (e.g. allelopathy). This is supported by our observation that smaller-diameter red maples were almost always in the presence of larger-diameter hardwoods but not conifers.

Regeneration Strategies
Red maple's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of initial-cohort quaking aspen and to some extent paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that red maple abundance peaks in response to the decline of the initial-cohort species, and it shows peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The high percent of red maple poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate well in large gaps.

The releve sampling of mature MHn44 forests suggests, however, that red maple is able to function also as a ***small-gap*** strategist with excellent establishment and recruitment in all height strata **(R-2)**. The high percents of red maple as seedlings (situations 12, and 23) in the FIA data support the idea that red maples can develop seedling banks and recruit trees into small gaps **(FIA-1)**.

Historic Change in Abundance
Today red maple is more abundant in MHn44 forests than it was historically. The FIA sampling suggests that it is about twice as common today as it was, but the absolute abundance (~2-3%) is still quite low. Red maple's 27% presence as a tree **(R-1)** and 55% presence in the understory **(R-2)** of stands sampled by releves paints quite a different picture. This balance of understory and tree presence (understory>>canopy) is typical of invading species. It would seem that red maples have made significant progress invading MHn44 stands that have not been recently disturbed.

Paper Birch

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap (open) regeneration strategist***
- ***regeneration window at 40-60 years***

Suitability
MHn44 sites provide ***excellent habitat*** for paper birch trees. The ***suitability rating*** of 4.6 for paper birch is influenced mostly by its high presence (63%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is an occasional co-dominant tree, contributing just 8% mean cover in mature stands. The ranking is fourth behind quaking aspen, balsam fir, and red maple on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer good habitat for paper birch (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, paper birch was an occasional tree in young MHn44 stands recovering from fire or windthrow **(PLS-1, PLS-2)**. Young paper birch represented 6% of the trees at survey corners described as burned, well behind the dominant quaking aspen **(PLS-3)**. Our interpretation is that this percentage is about what one would expect from stump sprouts if an older stand were burned. Birch's sprouting ability is the main reason we consider it to be an initial-cohort tree with some abilities to regenerate in ***open*** conditions. Young birch trees responded slightly better to windthrow, representing 10% of the trees at survey corners in windthrown timber. Windthrow, however, was rare and not an important means of regenerating trees on MHn44 sites. Because paper birch increases during the young growth-stage **(PLS-2)** we believe that it had some ability to recruit into under-stocked areas of burned stands or to seed-in below the emerging canopy of quaking aspen. Small-diameter, paper birch regeneration coming in among larger trees was scant in the post-disturbance window **(PLS-5)**, but increases steadily throughout the young growth-stage. Nearly all of these small-diameter trees were coming in under quaking aspen.

Transition: 35-95 years
As stands transitioned to mature conditions paper birch increased in abundance, presumably because of its ability to outlive or replace initial cohort aspen **(PLS-1, PLS-2)**. Possibly paper birch benefited from the pulse of balsam fir regeneration at the beginning of the transition stage (see Stand Dynamics). Throughout northern Minnesota, paper birch was historically more associated with conifers than with other hardwoods, and it is common to see birch thrive after ingress of balsam fir. The transition stage offered a good window of opportunity for birch regeneration, especially in the 40-60 year age-classes **(PLS-5)**. Recruitment of paper birch during this stage probably involved some release of seedlings established in the young growth-stage in openings created as the initial-cohort aspen died. The rather high percentages of birch, suggest also that such openings were also good habitat for both establishment and recruitment. Most of the smaller birch in transitioning stands were coming in under aspen. The fir pulse might have helped create opportunities for paper birch regeneration, but it was not the role of a nurse crop as birch mostly overtopped fir at corners where they were both present.

Mature Growth-stage: 95-195 years
Paper birch had peak presence as a co-dominant in mixed mature stands, which is why we consider birch a ***mid-successional*** species – able to replace initial cohort trees but dropping in relative abundance as stands aged **(PLS-1, PLS-2)**. Small-diameter birch regeneration was not detected in the age-classes of the mature growth-stage **(PLS-5)**. Birch bearing trees in mature stands showed substantial diameter variation and were about evenly mixed as the largest tree or smallest tree at survey corners. Most likely, this is the consequence of a long period of at least some birch recruitment beginning at stand initiation and lasting until about age 70. When present as the smaller-diameter tree, paper birch was coming in under aspen, white spruce, and older paper birch.

Very Old Growth-stage: >195 years

Paper birch persisted in the very old growth-stage at about 12% relative abundance **(PLS-1, PLS-2)**. If persistence requires regeneration and recruitment, then we must assume that paper birch has secondary strategies that make it able to respond to fine-scale or maintenance disturbances. The ability of paper birch to establish and recruit seedlings through all height strata in modern MHn44 forests is just fair **(R-2)**, suggesting that it probably responded more to larger gaps created by maintenance disturbances rather than small, single-tree gaps. We suspect that pocket-diseases create the several-tree gaps where paper birch is successful in mature and old MHn44 forests today.

Regeneration Strategies

Paper birch's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of quaking aspen. In the historic PLS data this interpretation is supported by: (1) the fact that paper birch abundance peaks in response to the decline of the initial cohort species **(PLS-1, PLS-2)**, and (2) it has good establishment in a gap window **(PLS-5)**. The high percent of paper birch 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. In the releve data paper birch has just fair ability to establish and recruit seedlings under a canopy **(R-2)**. The index values of 2.2-3.2 in the regenerating layer are most in line with species that do well in the open or rather large gaps.

Paper birch was also able regenerate and sometimes dominate ***open habitat*** after stand-regenerating fires. We believe that the initial cohort of young birch was composed of stump sprouts and far fewer seed-origin trees. Birch's modest regenerative ability after fire is evident in the PLS data by: (1) its presence in young stands **(PLS-1)**, (2) its presence at burned survey corners **(PLS-3)**, and (3) its fair regeneration in the post-disturbance window **(PLS-5)**.

Historic Change in Abundance

Today, paper birch remains an important co-dominant tree on MHn44 sites **(PLS/FIA-1)**. In modern stands birch abundance is about the same as it was historically and shows similar distribution among the growth-stages.

Basswood

- ***excellent habitat suitability rating***
- ***mid- (late-) successional***
- ***large-gap regeneration strategist***
- ***regeneration window 40-50 years***

Suitability

MHn44 sites provide ***excellent habitat*** for basswood trees. The ***suitability rating*** of 4.4 for basswood is the consequence of balanced presence (18%) and mean cover when present (21%, **R-1**). The ranking is fifth, following quaking aspen, balsam fir, red maple, and paper birch on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer excellent habitat for basswood, especially communities that are better-drained than MHn44 (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, basswood was nearly absent from young MHn44 stands recovering from stand-regenerating events **(PLS/FIA-1)**. Young basswoods represented just 1% of the trees at survey corners described as burned **(PLS-3)**. No young basswoods were recorded at survey corners affected by stand-regenerating wind. Small-diameter basswood regeneration was at low abundance throughout the post-disturbance window **(PLS-5)**. Our interpretation is that the initial regeneration was from stump sprouts and that young MHn44 forests offered limited chances for seed-origin basswood.

Transition: 35-95 years

As stands transitioned to mature conditions basswood increased in abundance, reaching peak abundance of 3% in the 70-100 year age-classes. This peak was short-lived and limited to just the transition period as basswood constituted no more than about 1% of the trees in the stable growth-stages **(PLS/FIA-1)**. This small peak in abundance during the transition stage is why we tentatively consider basswood to be ***mid-successional*** on MHn44 sites. Small-diameter basswood regeneration was present early in the transition, especially in the 40-50 year age-classes **(PLS-5)**. In most cases, basswood regeneration was coming in under quaking aspen. We interpret this as modest success at establishment and recruitment of seed-origin basswoods under a remote or partial canopy of initial-cohort trees.

Mature and Very Old Growth-stages: 95-195 years and older

In pre-settlement forests basswood was nearly absent from mature and very old MHn44 forests. Small-diameter basswood regeneration was not detected in these older growth-stages **(PLS-5)**. Although few stands older than 95 years contributed to the releve sampling, it is quite clear that basswood is capable of developing a seedling bank and recruiting to all taller strata under a canopy **(R-2)**. Thus, it seems odd that basswood abundance dropped to trace amounts in older MHn44 stands, especially given its late-successional, small-gap performance in communities where sugar maple is the climax dominant. The seral trend for MHn44 communities is for young stands to be strongly dominated by hardwoods and at some later time (~100 years) flip to conifer domination. It is conceivable that basswood's poor presence during the conifer-dominated stages is related to some sort of direct inhibition by conifers (e.g. allelopathy). The loss of white spruce from older, modern forests may explain why basswood shows some traits of a ***late-successional*** species in the releve and FIA data.

Regeneration Strategy

Basswood's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of initial-cohort quaking aspen and to some extent paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that basswood's abundance peaks in response to the decline of the initial-cohort species, and (2) it shows peak establishment in a gap window (40-50 years) rather than post-disturbance or ingress windows **(PLS-5)**. The high percent of basswood poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate well in large gaps. Basswood has good regeneration indices (3.2-3.5) in modern forests sampled by releves **(R-2)**. These indices are most in line with the large-gap strategy. Basswood's regenerant index is the lowest (3.2), suggesting that establishment is a bit of a bottleneck. Once established seedlings have a good chance of recruiting to higher strata.

Historic Change in Abundance

Today basswood is more abundant in MHn44 forests than it was historically. However, its relative abundance in either the PLS and FIA data does not exceed 1% by growth-stage. Basswood's 18% presence as a tree **(R-1)** and 34% presence in the understory **(R-2)** of stands sampled by releves paints quite a different picture. This translates roughly to 4.8% relative abundance. This balance of understory and tree presence (understory>>canopy) is typical of invading species. It would seem that basswoods have made significant progress invading MHn44 stands that have not been recently disturbed.

White Spruce

- ***excellent habitat suitability rating***
- ***late-successional***
- ***small-gap (large-gap) regeneration strategist***
- ***regeneration window at >120 years***

Identification Problems

The PLS surveyors did not distinguish between white and black spruce. Thus, interpretations of PLS data for the more common white spruce should always be done knowing that some of these trees were likely black spruce. MHn44 releve samples show that for plots with spruce present: 4% have both species present; 9% are black spruce without white spruce; 87% are white spruce without black spruce. White spruce and black spruce are not at all alike in their ecology on MHn44 sites. We believe that the occurrence of black spruce in MHn44 releves is incidental because MHn44 often occurs next to peatland forests, and the following account is just for white spruce in upland habitat.

Suitability

MHn44 sites provide ***excellent habitat*** for white spruce trees. The ***suitability rating*** of 4.1 for white spruce is influenced mostly by its high presence (29%) as trees on these sites in modern forests **(R-1)**. When present, white spruce is an important co-dominant tree, contributing 10% mean cover in mature stands. This ranking is sixth, following quaking aspen, balsam fir, red maple, paper birch, and basswood on MHn44 sites. Northern mesic hardwood communities in general are not good habitat for white spruce (see Suitability Tables). MHn44 provides excellent habitat for white spruce because it has lower nutrient status than other mesic hardwood forests, which seems to be spruce's preference.

Young Growth-stage: 0-35 years

Historically, white spruce was a minor tree in young MHn44 stands **(PLS-1, PLS-2)**. Young spruce were present at 5% of the survey corners described as burned, well behind the fire-tolerant quaking aspen **(PLS-3)**. Nonetheless, the presence of any white spruce on burned lands is surprising given its sensitivity to fire. White spruce was substantially more abundant at windthrown corners, representing 8% of the trees. Because of spruce's affinity for wetter habitats included in the MHn44 landscape, we believe that the few, small-diameter spruce showing up in post-burn situations were coming from unburned wetlands near burned survey corners. Alternatively, it is possible that some of the post-fire spruce records were black spruce as it is substantially more tolerant of fire. Small-diameter white spruce regeneration was not detected in the young growth-stage **(PLS-5)**. Our interpretation is that white spruce were absent from the actual burned patches of MHn44, but could be important in stands originating after windthrow or perhaps in extensive disease pockets.

Transition: 35-95 years

As stands transitioned to mature conditions white spruce increased in abundance **(PLS-1)**. The increase starts modestly at the beginning of the transition, but at about 70 years the abundance of white spruce rises steadily for the remainder of the transition (**PLS-2**). Small-diameter white spruce regeneration was abundant in the G-1 gap window that corresponds with the transition **(PLS-5)**. Throughout the transition all white spruce bearing trees were the smallest tree at the survey corner, which is typical of an ingressing species. Small spruces were coming in exclusively under quaking aspen and paper birch. This is not at all in line with the common anecdote among Minnesota foresters that balsam fir serves as a nurse crop for white spruce. This perspective comes mostly from observations in modern forests where it is far more common (~2 times in our releves) to have fir in stands without spruce than to have white spruce without any fir. The coincidence of spruce ingress and the pulse in fir abundance makes it tempting to interpret a causal link. But in this case, it doesn't seem that young spruce liked to come in directly beneath the firs on MHn44 sites. Our best guess is that the fir helps to create seedbeds that favor white spruce, but recruitment was limited to gaps in the hardwood canopy.

Mature Growth-stage: 95-195 years
In the mature growth-stage, white spruce achieved dominance by about age 100 **(PLS-1, PLS-2)**. At this stage white spruce bearing trees were about equally abundant as the smallest tree at survey corners as is was the largest tree. This diameter variation and high presence is the signature of a community dominant that is having success regenerating and overtopping other trees. Small-diameter white spruce regeneration was abundant throughout the I-1 ingress window that corresponds with the mature growth-stage **(PLS-5)**. At this time, most spruce regeneration was still coming in under older paper birch and quaking aspen, suggesting a preference for replacing hardwoods. Unlike the transition period, there was some white spruce regeneration under conifers. Most often smaller white spruce were beneath parent trees, but there were also cases of it coming in under balsam fir. Our interpretation is that the mature growth-stage represents the point in stand development where it is evident that white spruce is the climax species for MHn44 sites – able to replace any other tree and maintain populations in all height strata.

Very Old Growth-stage: >195 years
In the very old growth-stage white spruce was the dominant tree. At 33% relative abundance, it was slightly ahead of quaking aspen as the most common tree on very old MHn44 sites **(PLS-1)**. White spruce's importance in the old growth-stage is the main reason that we consider it to be a ***late-successional*** species on MHn44 sites. Small-diameter white spruce regeneration coming in among larger trees was at its peak in the I-1 ingress window that applies to the very old growth-stage **(PLS-5)**. When white spruce was the smallest tree at a survey corner, they were still mostly coming in under less tolerant trees such as paper birch and quaking aspen. There was, however, significant regeneration under itself. Our interpretation is that white spruce was the climax dominant of MHn44 sites and that there were some rather pure pockets of white spruce, but fine-scale and maintenance disturbances assured a mixed composition at coarser scales.

Regeneration Strategy
White spruce's primary regenerative strategy on MHn44 sites is to satiate the groundlayer with seedlings and to then recruit saplings in ***small gaps***. It was successful at doing this under any other tree including itself, but most often it was coming in other trees less tolerant of shade. In the historic PLS data this interpretation is supported by: (1) the fact that white spruce abundance peaks in the old growth-stage when we assume a full canopy and lower strata **(PLS-1, PLS-2)**, (2) it is most abundant at survey corners in a mature, undisturbed condition **(PLS-3)**, and (3) its best recruitment window is an ingress window **(PLS-5)**. White spruce has fairly high abundance as understory saplings (situations 12 and 13) at FIA subplots, which is also consistent with a small-gap strategy **(FIA-1)**.

The releve data paint a different picture. The ability of white spruce to establish seedlings is just good-to-fair under a canopy in mature MHn44 forests **(R-2)**. Its regeneration indices (2.8-3.5) are more in line with species that recruit in ***large-gaps***. The bottleneck seems to be in establishing seedlings as recruitment is good in large gaps. On organic seedbeds, increased solar radiation is known to improve germination and seedling establishment. Our interpretation is that white spruce is certainly and able small-gap species, but establishment and recruitment are better in large-gaps.

Historic Change in Abundance
Today white spruce has been nearly eliminated from MHn44 sites **(PLS/FIA-1)**. This is true of all growth-stages in spite of considerable plantation efforts. For a mesic hardwood community, the proportion of MHn44 sites in the mature and old, spruce-dominated forests on the pre-settlement landscape was rather low **(PLS-1)**. Our interpretation is that there is significantly less white spruce on the MHn44 landscape because there are even fewer very old stands. Mostly, this is the consequence of the fact that MHn44 sites offer such good management opportunities for short-rotation quaking aspen, and that white spruce has done poorly in response to coppicing silvicultural strategies.

Northern White Cedar

- ***good habitat suitability rating***
- ***mid- successional***
- ***large-gap (open) regeneration strategist***
- ***regeneration window at 80-90 years***

Suitability

MHn44 sites provide ***good habitat*** for white cedar trees. The ***suitability rating*** of 3.8 for white cedar is influenced mostly by its high mean cover when present (32%) as trees on these sites in modern forests **(R-1)**. White cedar can be an important co-dominant when present. White cedar's presence is 7% among releve samples of this community. For long-lived conifers with greater cover-when-present than presence, we often suspect the loss of seed source, and believe that they would increase significantly if they were planted more often or if seed trees were more numerous. The ranking is seventh among trees common on MHn44 sites as sampled by releves. MHn44 communities in general offer a variety of habitat for white cedar, depending mostly on the presence of cedar-dominated wetlands in the landscape (see Suitability Tables). MHn44 is good mostly because of its wet-mesic soils and the tendency of it to be close to wetlands where cedar is more abundant.

Young Growth-stage: 0-35 years

Historically, white cedar was nearly absent in young MHn44 stands **(PLS/FIA-1)**. Young cedars represented 1% of the trees at survey corners described as burned, well behind most other species **(PLS-3)**. Young cedars represented 3% of the trees at survey corners described as windthrown. White cedar does well as a cultivar in open environments, and it seems that windthrown MHn44 habitat was the most favorable canopy condition for cedar although the sample numbers are quite low. Small-diameter white cedar regeneration coming in among larger trees was not detected in age-classes of young growth-stage **(PLS-5)**. Our interpretation is that young cedars were so infrequent historically on MHn44 sites that there are just too few records to ascribe a behavior or reaction to open conditions.

Transition: 35-95 years

As stands transitioned to mature conditions white cedars were essentially absent at the start, but peak at age 90 where its abundance exceeded 10% of the bearing trees. This peak spans age classes 80-120 where cedar abundance averaged about 5%, however the total number of trees in these age classes is low and when averaged by growth-stage, white cedar abundance was just 1% **(PLS/FIA-1)**. Variation in cedar abundance is one of the main reasons that the transition period was extended to 95 years based upon the ordination **(PLS-4)**, well beyond abundance changes relating to the demise of initial-cohort aspen. Small-diameter white cedar regeneration was first detected at age 70 and is followed by the peak of larger trees. This is typical of ingressing species. Apparently white cedar enjoyed an episode of good regeneration and recruitment at the end of the transition stage **(PLS-5)**. The arrival and success of white cedar at about age 90 seems too punctuated to be a response to gradual, stand-maturation processes like thickening duff or the accumulation of woody substrates for seedlings. Also, this cedar peak is duplicated in other ecological systems (e.g. FDn43, WFn53) where forest floor conditions are quite different. We are unaware of any stand-scale process that might explain a pulse of cedar regeneration and recruitment. Because it is an attribute of communities across ecological systems, it seems possible that this was a regional phenomenon with cedar benefiting from a widespread and favorable condition *ca.* 1780-1800 AD. Survey corners with cedar regeneration and trees were evenly distributed throughout northeastern Minnesota regardless of community class.

Mature Growth-stage: 95-195 years

In the mature growth-stage, white cedar had an episode of sustained abundance at about 6% from 90-140 years. This is why we consider white cedar a ***mid-successional*** species – able to replace or outlive initial cohort trees but dropping in relative abundance as stands aged **(PLS-2)**. However, when averaged across the entire growth stage, the relative abundance of white cedar didn't exceed 1% **(PLS/FIA-1)**. Regeneration during the mature growth-stage was limited to the beginning of the growth-stage and was not detected after 100 years **(PLS-5)**. Thus, the mature growth-stage represents a period where stand conditions became unfavorable for cedar, and much of cedar's regenerative attempt in the transition was lost. In modern, closed-canopy MHn44 forests does poorly in the understory **(R-2)**, suggesting that significant levels of light are required for germination and seedling establishment. Our impression of mature MHn44 forests is that there was probably a double canopy of tall white spruce and mid-canopy fir. It seems likely that this level of shading could have discouraged white cedar. Given the longevity of white cedar though, the historic loss of established trees in the mature growth-stage is puzzling. Such loss is not evident in the later growth-stages of modern MHn44 forests **(PLS/FIA-1)**, which suggests that the short-lived pulse of success may have been a regional event.

Very Old Growth-stage: >195 years

In the very old growth-stage, white cedar was a minor co-dominant **(PLS/FIA-1)**. We believe that white cedar's presence in old stands was mostly a consequence of its longevity, or perhaps resistance of selected individuals to a regional event that killed lots of white cedar. Small-diameter, white cedar regeneration coming in among larger trees was not detected during this very old stage **(PLS-5)**. As was the case for mature MHn44 forests, we suspect that cedar regeneration in the very old growth-stage was quite limited due to shady, forest floor conditions.

Regeneration Strategies

White cedar's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of quaking aspen and paper birch, although in later growth-stages it showed success beneath conifers. In the historic PLS data this interpretation is supported by: (1) the fact that white cedar abundance responds to the decline of initial-cohort quaking aspen and short-lived paper birch in the transition growth-stage **(PLS-2)**, (2) it is more abundant at survey corners showing partial canopy loss due to windthrow **(PLS-3)**, and (3) it has peak regeneration in a gap window rather than an ingress or post-disturbance window **(PLS-5)**. The high percent of white cedar poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate well in large gaps.

The releve sampling of mature MHn44 forests suggests, however, that white cedar has very limited ability to regenerate under much shade **(R-2)**. The regenerant and seedling indices for white cedar (1.3-0.8) are more in line with trees that do well in ***open*** environments. These low indices are influenced mostly by low presence. One hypothesis is that the establishment of white cedar follows events that remove much of the canopy or at least the leaves of canopy trees, and that cedar regeneration grows slowly until released in persistent canopy gaps. In Minnesota, there is some evidence that cedar regeneration comes in distinct cohorts. Age-classes often date to major fire years or local fire scars. Successive years of spruce budworm defoliation might be enough to initiate cedar cohorts in MHn44 forests – but after such outbreaks, the cedar regenerants may sit in suppression until more permanent gaps open above them. Alternatively, poor establishment of cedar could be due entirely to seedling depredation by white-tailed deer as populations now far exceed their natural levels throughout the range of white cedar in Minnesota.

Historic Change in Abundance

Today, white cedar has increased in abundance substantially on MHn44 sites. While young stands are similar to their historic counterparts, mature and very old forests have much higher amounts of white cedar than they once did **(PLS/FIA-1)**. It is important to note, that mature and very old MHn44 stands now represent only about 4% of the landscape, compared to about 16% at pre-settlement times. The increase of cedar in older MHn44 forests is almost certainly related to fire-suppression and cedar's longevity. Cedar is very sensitive to fire and just stopping direct mortality due to fire in the early 1900's could account for more cedar in stands that are now mature or very old. A secondary effect of fire suppression may have been the formation of increasingly organic seedbeds on MHn44 sites that could have favored more establishment and regeneration of white cedar than usual – at least before these sites became prime aspen and deer habitat later in the century. Although the abundance of white cedar in younger MHn44 forests was naturally low, its absence in the FIA samples of forests under 95 years is still alarming.

White Pine

- ***good habitat suitability rating***
- ***mid- (late) successional***
- ***large-gap (open) regeneration strategist***
- ***regeneration window at ~40 years***

Suitability
MHn44 sites provide ***good habitat*** for white pine trees. The ***suitability rating*** of 3.8 for white pine is the result of modest, but balanced presence (14%) and mean cover when present (16%, **R-1**). The ranking is eighth among species common on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer just fair-to-good habitat for white pine, and it is limited to just the poorer communities (see Suitability Tables). Among these, MHn44 and MHn35 offer the best opportunity for growing white pine.

Young Growth-stage: 0-35 years
Historically, white pine was nearly absent from young (0-35 years) MHn44 stands **(PLS-1, PLS-2)**. Young white pines represented just 1% of the trees at survey corners described as burned, which is quite surprising given its abilities in fire-dependent forests **(PLS-3)**. White pines represented just 4% of the trees at survey corners affected by stand-regenerating wind. Both fire and windthrow, however, were infrequent and were not an important means of regenerating white pine. Small-diameter white pine regeneration coming in among larger trees was not detected in the young growth-stage **(PLS-5)**. Our interpretation is that white pine had limited ability to compete with young quaking aspen under open conditions on MHn44 sites.

Transition: 35-95 years
As stands transitioned to mature conditions white pine increased slightly in abundance **(PLS-1)**. This is the beginning of a modest, but steady trend of increasing white pine presence throughout the course of stand maturation **(PLS-2)**. Small-diameter white pine regeneration coming in among larger trees was only observed in the G-1 gap window that corresponds with the early years of the transition **(PLS-5)**. In all cases, white pine regeneration was coming in under quaking aspen. We interpret this as limited success at establishment and recruitment of seed-origin white pines under a partial canopy of initial-cohort aspen. White pine's ability to decisively replace the initial-cohort trees is why we consider white pine to be primarily a ***mid-successional*** species, although it remains important in the older growth-stages. Though low, the presence of white pine trees in the transition stage is steady in comparison to the spotty occurrence of small-diameter white pine regeneration. Though we did not detect white pine regeneration at young, post-disturbance corners, we suspect that the amount of trees present in the transition stage must have been supplemented by some regeneration in the young growth-stage and that established white pine seedlings were released at this time.

Mature Growth-stage: 95-195 years
In the mature growth-stage, white pine continues to increase (slightly) in relative abundance **(PLS-1, PLS-2)**. White pine's rise is mostly the result of modest establishment and recruitment during the transition stage **(PLS-5)** followed by high survivorship. Small-diameter white pine regeneration coming in among larger trees was not detected in the mature growth-stage. At this time white pine was almost always the largest tree at survey corners. For the few corners where white pines had the smaller diameters, they were still coming in below quaking aspen. Our interpretation is that there was almost no establishment of white pine under the supercanopy of white spruce and mid-canopy of balsam fir that characterizes mature MHn44 stands. This is strongly supported by white pine's poor record of establishment in mature stands sampled by releves **(R-2)**. Where there were patches of mature MHn44 forest with an aspen canopy yet to be invaded by spruce and fir, we suspect that white pine was still recruiting some trees.

Very Old Growth-stage: >195 years
In the very old growth-stage white pine was a minor co-dominant, occurring always at survey corners of mixed composition. At 4% relative abundance, it was well behind white spruce and what must have been second or third-cohort quaking aspen, paper birch, and balsam fir **(PLS-1)**. Because white pine has peak abundance in the old growth-stage consider it to be secondarily a ***late-successional*** tree. However, white pine's presence in old stands is hardly a peak and can be explained entirely by its incredible longevity. This idea is supported by the fact that we detected no small-diameter white pine regeneration at very old MHn44 corners **(PLS-5)**, and in all cases white pines were the largest tree at the survey corner.

Regeneration Strategies
White pine's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this beneath the declining canopy of initial-cohort quaking aspen. In the historic PLS data this interpretation is supported by: (1) the fact that white pine abundance rises in response to the decline of the initial cohort species **(PLS-1, PLS-2)**, and (2) it shows peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The presence of white pine 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 MHn44 forests suggests, however, that white pine has poor ability to establish and recruit seedlings under a canopy **(R-2)**. White pine's regeneration indices of 1.2 for regenerants and 1.0 for seedlings are far more in line with trees that do well in the ***open***. Our interpretation is that the collapse of the initial-cohort aspen on MHn44 sites must have created quite large gaps that white pine could exploit for a limited time.

Historic Change in Abundance
Today, white pine is roughly as abundant as it was historically on MHn44 sites, but its distribution among the growth-stages is a bit different. Its near absence in young stands is much like the historic condition **(PLS/FIA-1)**. Today, in mature stands (95-195 years) it has substantially higher presence (4%) than it did historically and this may be the consequence of conservation efforts. Very old MHn44 forests are now so rare that white pine's slight decline from 4% historically to 2% presence today is probably meaningless.

Black Ash

- ***good habitat suitability rating***
- ***mid- (late) successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at ~90 years***

Suitability

MHn44 sites provide ***good habitat*** for black ash trees. The ***suitability rating*** of 3.4 for black ash is influenced mostly by its higher presence (19%) as trees on these sites in modern forests **(R-1)**. When present, black ash is a minor co-dominant tree, contributing just 9% mean cover in mature stands where it is present. The ranking is ninth among trees common on MHn44 sites as sampled by releves. Northern mesic hardwood communities in general offer limited habitat for black ash, favoring communities like MHn44 and MHn46 with their somewhat poorly to moderately well-drained soils (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, black ash was a rare tree in young MHn44 stands recovering catastrophic disturbance **(PLS/FIA-1)**. Young black ash represented only 1% of the trees at survey corners described as burned **(PLS-3)**. Windthrow was infrequent and black ash represented just 3% of the survey corners affected by stand-regenerating wind **(PLS-3)**. Small-diameter black ash regeneration coming in among larger trees was not detected in the young growth-stage **(PLS-5)**. Our interpretation is that the young growth-stage offered few opportunities for black ash, and that its slight presence is the result of windthrow removal of the canopy and release of seedlings established in older growth-stages.

Transition: 35-95 years

As stands transitioned to mature conditions black ash increased in abundance **(PLS-1)**. We estimate that this increase started at low abundance at the beginning of the growth-stage and lasted throughout **(PLS-2)**. Small-diameter black ash regeneration was present in trace amounts during the transition stage **(PLS-5)**. In most cases, ash regeneration was coming in under aspen and paper birch, but the sample size is very small. We interpret this as limited success at establishment and recruitment of seed-origin ash under a partial canopy of initial-cohort trees. It is possibly significant that black ash recruitment is coincident with that of white cedar, as either might suggest moister seedbed conditions relating to stand development. In the releves though, these species seem to be slightly negatively correlated because they infrequently occur together on MHn44 sites. The fact that black ash trees are more consistently present at the close of the transitional stage and less so in older forests is why we believe it was predominantly ***mid-successional***.

Mature Growth-stage: 95-195 years

In the mature growth-stage, black ash averaged about 1% presence **(PLS/FIA-1)**, but it was sporadically distributed among the age-classes. Small-diameter black ash regeneration was not detected during this growth-stage **(PLS-5)**. For the small number of ash bearing trees at survey corners estimated to be of mature age, black ash was almost always the smallest tree at the corner. These trees were beneath aspen and paper birch rather than conifers. Our interpretation is that there were always enough wet inclusions on MHn44 sites for there to be a few mature seed trees around. During the transition and the mature growth-stages black ash has success establishing seedlings, but rarely were trees recruited to the canopy. This idea is strongly supported by our observations of black ash recruitment in the understory of older, modern stands **(R-2)**. Black ash in these forests has excellent recruitment at heights under 10m, but significantly poorer recruitment to taller strata.

Very Old Growth-stage: >195 years

In the very old growth-stage black ash was nearly absent **(PLS/FIA-1)**. We believe that black ash's presence in old stands was mostly a consequence of very modest recruitment around inclusions of wet ash forests. However, we did not detect small-diameter ash regeneration using our stringent half-diameter rule **(PLS-5)**. Alternatively, black ash is long-lived on MHn44 sites and trees established during the transition stage were capable of surviving into the old growth-stage.

Regeneration Strategies
Black ash's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of quaking aspen and paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that black ash abundance responds to the decline of initial-cohort quaking aspen and short-lived paper birch in the transition, and (2) it has peak regeneration in a gap window rather than an ingress or post-disturbance window **(PLS-5)**.

However, it is clear in the modern data that black ash is behaving as would a ***small-gap*** strategist. Most supportive of this idea is black ash's excellent indices of regeneration at heights under 10m **(R-2)**. Today it seems quite capable of building a seedling bank, but recruitment to tree-sized individuals seems to be a bottleneck. The very high presence of black ash seedlings at FIA subplots (situations 12 and 13) is also characteristic of seedling bankers that usually are able to exploit single-tree gaps **(FIA-1)**. Our interpretation is that black ash is a successful tree in wet habitats included within MHn44 uplands and that seedling banks spread from these inclusions. Recruitment to the tree stratum requires gaps of at least several trees.

Historic Change in Abundance
Today, black ash has increased in abundance substantially on MHn44 sites, but it still is an infrequent tree at about 2-5% relative abundance **(PLS/FIA-1)**. Most MHn44 ash is in the understory, present in 62% of the releves as seedlings and saplings **(R-2)** and 59% of the comparable situations (13 and 23) at FIA subplots **(FIA-1)**. Normally, the imbalance of seedling presence versus trees is the signature of an invading species expanding its range. We believe though that this invasion will continue to be more in the understory than the overstory. The considerable difference of 19% presence in the releves **(R-1)** versus about 5% as trees (situation 33) in the FIA sampling may be important. Apparently black ash is more successful in ecologically intact stands sampled by releves when compared to the average MHn44 stand.

Balsam Poplar

- ***good habitat suitability rating***
- ***early successional***
- ***open regeneration strategist***
- ***regeneration window at 0-30 years***

Suitability
MHn44 sites provide ***good habitat*** for balsam poplar trees. The ***suitability rating*** of 3.3 for balsam poplar is the consequence of balanced presence and mean cover when present (13% for both) on these sites in modern forests **(R-1)**. Only the wet-mesic northern mesic hardwood communities, MHn44 and MHn46, offer good habitat for balsam poplar (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, balsam poplar was a minor tree in young MHn44 stands recovering from stand-regenerating disturbance **(PLS/FIA-1)**. Young balsam poplars represented just 1% of the trees at survey corners described as burned or windthrown **(PLS-3)**. Small-diameter poplar regeneration was in general low during the post-disturbance years **(PLS-5)** and was only observed coming in among its more abundant cousin, quaking aspen. Though the sample size is small, balsam poplar was most abundant immediately following disturbance, which is why we consider it to be an ***early successional*** species.

Transition: 35-95 years
The transitioning of young MHn44 forests was mostly driven by the steady loss of initial-cohort quaking aspen **(PLS-1)**. The behavior of balsam poplar parallels that of quaking aspen and for that reason mostly, we suspect that initial-cohort poplars probably declined as well during the transition stage **(PLS-FIA-1)**. Small-diameter balsam poplar regeneration was steadily coming in among larger trees until about age 30, however some regeneration was detected up to age 60 years in the transition stage **(PLS-5)**. Again, balsam poplar seemed limited to coming in among either quaking aspen or itself. We interpret this as very limited regeneration success in large-gaps as some of the initial-cohort aspen started to senesce.

Mature and Very Old Growth-stages: 95-195 years and older
Throughout the mature and the very old growth-stages, balsam poplar bearing trees are nearly absent and sporadically distributed among age-classes. There are insufficient data to make any interpretations concerning its historic behavior or regenerative success in forests this old.

Regeneration Strategy
Balsam poplar's primary regenerative strategy on MHn44 sites is to dominate ***open habitat*** after stand-regenerating disturbance. There are too few records to determine if fire or windthrow affected poplar differently, but in other communities fire is usually considered beneficial. In the historic PLS data this interpretation is supported only by the fact that balsam poplar bearing trees are more consistently present in young stands and we detected the most poplar regeneration in the post-disturbance window **(PLS-5)**. The high percent of balsam poplat as saplings in sapling stands (situation 11) and poles in pole stands (situation 22) in the FIA data **(FIA-1)** is characteristic of species that regenerate effectively in the open. The releve sampling of mature MHn44 forests is also consistent with the idea that balsam poplar needs rather open habitat for establishment and recruitment. Its indices in the regeneration strata (2.3-2.7, **R-2**) are quite in line with open strategists, but it is possible that very large gaps might allow for some recruitment as well.

Historic Change in Abundance
Today, balsam poplar is considerably more abundant on MHn44 sites than it was historically **(PLS/FIA-1)**. This is particularly true of the young growth-stage where it is now 6% of the FIA trees compared to just 1% at survey corners of similar age. Our interpretation is that the practice of clear-cutting MHn44 sites has favored balsam poplar more than fire or windthrow did historically.

Northern Red Oak

- ***good habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 40-50 years***

Suitability
MHn44 sites provide ***good habitat*** for red oak trees. The ***suitability rating*** of 3.2 for red oak is influenced mostly by its 17% mean cover when present on these sites in modern forests **(R-1)**. Though an important co-dominant when present, red oak occurred in just 7% of the stands sampled by releves. The ranking is eleventh among trees common on MHn44 sites. Northern mesic hardwood communities in general offer good habitat for red oak within its range (not MHn45), especially the better drained communities (see Suitability Tables). Among these, MHn44 offers the poorest opportunity for growing red oak.

Young Growth-stage: 0-35 years
Historically, northern red oak was nearly absent in young MHn44 stands recovering from a stand-regenerating event **(PLS/FIA-1)**. Young red oaks were not recorded as present at either burned or windthrown survey corners **(PLS-3)**. In the 20 and 30 year age-classes there are a few red oak records, but they are not enough for interpretation.

Transition: 35-95 years
As stands transitioned to mature conditions red oak increased in abundance. Red oak abundance peaks in the 40-60 year age-classes, however this peak was only to about 2% relative abundance. These age classes are the largest samples for the community, so we believe that the peak is real and for this reason we consider red oak to be a ***mid-successional*** species on MHn44 sites. Some small-diameter red oak regeneration was coming in among larger trees during the transition stage until about age 50 **(PLS-5)**. In most cases, red oak regeneration was coming in under aspen and sometimes under older red or bur oaks. We interpret this as poor, but measurable success at establishment and recruitment of seed-origin oak under a partial canopy of initial-cohort trees.

Mature and Very Old Growth-stages: 95-195 years and older
Throughout the mature and the very old growth-stages, red oak bearing trees are nearly absent and sporadically distributed among age-classes. There are insufficient data to make any interpretations concerning its historic behavior or regenerative success in forests this old.

Regeneration Strategy
Red oak's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***. It was most successful at this when gaps formed in the declining canopy of initial-cohort 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 peaks (slightly) in response to the decline of the initial cohort species, (2) it is most abundant (slightly) at survey corners showing partial canopy loss **(PLS-3)**, and (3) its peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. More convincing, is the high percent of red oak poles under trees (situation 23) in the FIA data **(FIA-1)**, which is characteristic of species that tend to regenerate best in large gaps. In the releve sampling of mature MHn44 forests, the indices of regeneration in the understory (2.0-2.8) are quite in line with large-gap species and leaning towards the larger, more open versions of such gaps **(R-2)**. As commonly observed in other communities, red oak's sapling index (SA-index) is the lowest, suggesting that recruiting red oak seedlings to heights taller than 2m is a regenerative bottleneck under a closed canopy.

Historic Change in Abundance
Today, red oak is about as abundant now as it was historically **(PLS/FIA-1)**. In either case, red oak is infrequent and never reaches 2% relative abundance in any age-class or growth-stage. Its

inclusion in this discussion is entirely the consequence of its performance in MHn44 forests sampled by releves. Though infrequent as a tree, its occurrence in 7% of the releves **(R-1)** is far higher than in the historic PLS data or on FIA plots. More impressive is it's 30% presence in the understory **(R-2)**. The high ratio of understory presence to tree presence is a property of invading species, and to some extent we suspect that red oak is having limited success doing this in the ecologically intact MHn44 stands preferentially sampled by releves. On the other hand, large-seeded species like red oak with effective dispersal agents like blue jays or squirrels often have wider distributions as seedlings as compared to trees. That is, acorns relying on their stored energy can germinate and live for a while in habitats where they have little chance of becoming a tree.

Bur Oak

- ***good habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 40-60 years***

Suitability

MHn44 sites provide ***good habitat*** for bur oak trees. The ***suitability rating*** of 3.1 for bur oak is influenced mostly by its presence (14%) as trees on these sites in modern forests **(R-1)**. When present, bur oak is a minor co-dominant tree, contributing 9% mean cover in mature stands when present. The ranking is twelfth among trees common on MHn44 sites. Northern mesic hardwood communities offer the full spectrum of habitat for bur oak ranging from none to excellent (see Suitability Tables). It is favored in the wet-mesic communities, preferring the richer MHn46 sites to MHn44.

Young Growth-stage: 0-35 years

Historically, bur oak was nearly absent in young MHn44 stands recovering from a stand-regenerating disturbance **(PLS/FIA-1)**. Young bur oaks were present at just 1% of the survey corners described as burned **(PLS-3)**. Bur oak seemed to prefer windthrown stands a bit more than burned ones as young bur oaks were present at 4% of such survey corners. Small-diameter bur oak regeneration coming in among larger trees was present throughout the young growth-stage at levels suggesting poor but measurable success regenerating following disturbance **(PLS-5)**. Our interpretation is that bur oak enjoyed limited success filling richer microhabitats on recently disturbed MHn44 sites.

Transition: 35-95 years

As stands transitioned to mature conditions bur oak increased (slightly) in abundance **(PLS/FIA-1)**. Bur oak abundance peaks in the 50-90 year age-classes at 4-5%, but when averaged across the entire growth-stage its abundance just slightly exceeded 1%. This peak at 50-90 years is the main reason that we consider bur oak to be a ***mid-successional*** species on MHn44 sites. Some small-diameter bur oak regeneration was coming in among larger trees during the transition, especially at survey corners estimated to be 40-60 years old **(PLS-5)**. When bur oak was the smallest tree at a corner it showed a strong preference for coming in under aspen and less often under paper birch and older bur oaks. We interpret this as poor, but measurable success at establishment and recruitment of seed-origin oaks under a partial canopy of initial-cohort trees.

Mature and Very Old Growth-stages: 95-195 years and older

By about age 100, bur oak abundance had dropped to about 1%. Throughout remainder of the mature and the very old growth-stages, bur oak abundance never recovers and is sporadically recorded among age-classes **(PLS/FIA-1)**. There are insufficient data to make any interpretations concerning its historic behavior or regenerative success in forests this old.

Regeneration Strategy

Bur oak's primary regenerative strategy on MHn44 sites is to fill ***large-gaps***, much more so than in the open or in small-gaps. It was most successful at this when gaps formed in the declining canopy of initial-cohort quaking aspen and to some extent under paper birch and other bur oaks. In the historic PLS data this interpretation is supported by: (1) the fact that bur oak abundance peaks in response to the decline of the initial cohort species, (2) it is most abundant by far at survey corners showing partial canopy loss **(PLS-3)**, and (3) its peak establishment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The high percent of bur oak poles under trees (situation 23) in the FIA data **(FIA-1)** is characteristic of species that tend to regenerate best in large gaps. However, it is also common as seedlings (situations 12 and 13), suggesting that the gaps may not need to be particularly large. In the releve sampling of mature MHn44 forests, the indices of regeneration in the understory (3.0-3.2) are quite in line with large-gap species **(R-2)**.

Historic Change in Abundance

Today, bur oak is about as abundant now as it was historically in MHn44 forests **(PLS/FIA-1)**. Bur oak was but a minor tree in either case never exceeding 2% relative abundance in any age-class. Its inclusion in this discussion is entirely the consequence of its performance in MHn44 forests sampled by releves. Though infrequent as a tree, its occurrence in 14% of the releves **(R-1)** is far higher than in the historic PLS data or on FIA plots. More impressive is it's 30% presence in the understory **(R-2)**. The high ratio of understory presence to tree presence is a property of invading species, and to some extent we suspect that bur oak is having some success doing this in the ecologically intact MHn44 stands preferentially sampled by releves. On the other hand, large-seeded species like bur oak with effective dispersal agents like blue jays or squirrels also often have wider distributions as seedlings as compared to trees. That is, lots of acorns germinate and live for a while in habitats where they have little chance of becoming a tree.

(PLS-1) Historic Abundance of MHn44 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the MHn44 community by growth-stage. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow, green, and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

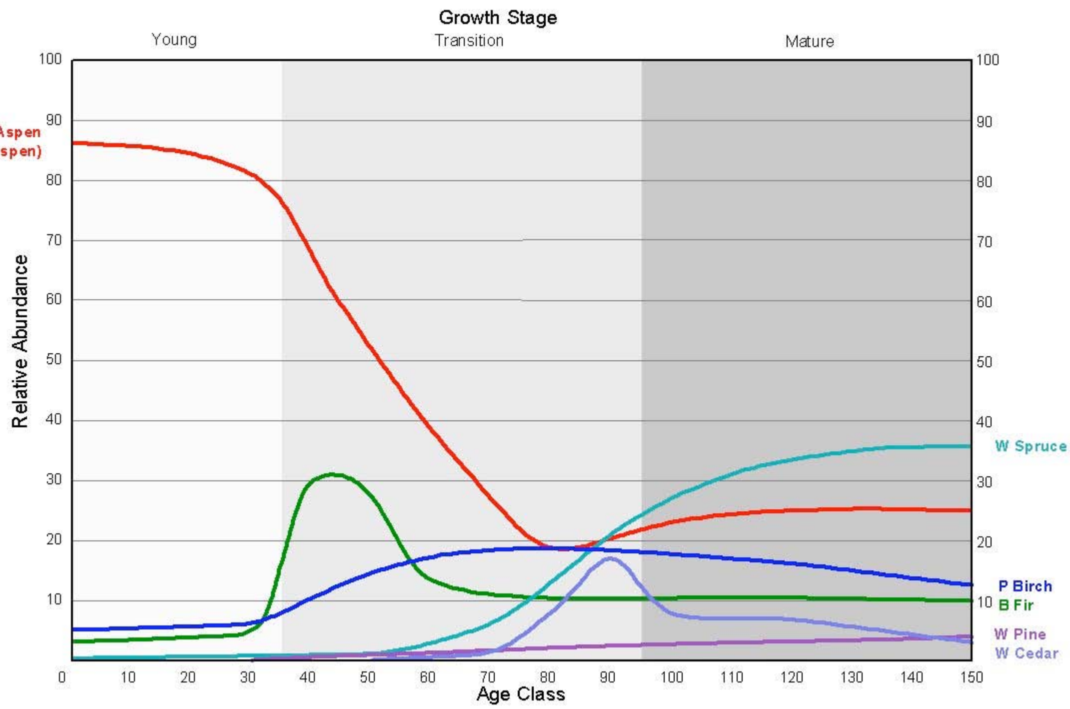
Dominant Trees	Forest Growth Stages in Years				
	0 - 35	35 - 95	95 - 195	~ 195	> 195
	Young	T1	Mature		Very Old
Quaking Aspen	**86%**	||	**24%**	)	**28%**
Paper Birch	**5%**	)	**18%**	|	**12%**
Balsam Fir	**3%**	)	**10%**	/	**10%**
White Spruce	**1%**	))	**34%**	|	**33%**
White Pine	**–**	)	**1%**	)	**4%**
Miscellaneous	**5%**		**13%**		**13%**
Percent of Community in Growth Stage in Presettlement Landscape	**24%**	**60%**	**14%**		**2%**

PLS-1
Trees included in Table PLS-1 are species with greater than 3% relative abundance in at least one growth-stage. Species that are now abundant in MHn44 forests, but were rare historically appear in Table **PLS/FIA-1**.

Public Land Survey linked text

(PLS-2) Abundance of trees throughout succession in MHn44

Caption: Graphed for the different species of MHn44 trees is their relative abundance (%) as PLS bearing trees by age class. The data were initially smoothed from adjacent classes and then by visually fitting lines to illustrate general trends.



Documentation for Figure PLS-2

**Public Land Survey linked text

(PLS-3) Historic Abundance of MHn44 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent MHn44 forests. The columns represent our interpretation of disturbance at the survey corners. Shading associates trees that peak in the same disturbance category.

Tree	Burned		Windthrown		Maintenance		Mature	
Quaking aspen	251	73%	71	51%	221	73%	4620	49%
White pine	3	1%	6	4%	4	1%	91	1%
White cedar	3	1%	4	3%	3	1%	123	1%
Black ash	3	1%	4	3%	2	1%	88	1%
Bur oak	2	1%	5	4%	23	8%	206	2%
Balsam poplar	4	1%	2	1%	5	2%	49	1%
Northern red oak	0	0%	0	0%	2	1%	58	1%
Balsam fir	29	8%	21	15%	8	3%	1482	16%
Paper birch	22	6%	14	10%	15	5%	1546	16%
White spruce	16	5%	11	8%	16	5%	819	9%
Red maple	4	1%	0	0%	1	0%	184	2%
Basswood	4	1%	0	0%	2	1%	131	1%
Sugar maple	3	1%	2	1%	1	0%	90	1%
Total (% of grand total, 10274)	344	3%	140	1%	303	3%	9487	92%

PLS-2

Table PLS-3 includes only trees ranked as having excellent, good, or fair suitability for MHn44 sites. Tree sums will not match the totals in the Natural Disturbance Regime text, because trees of poorer suitability were included in that analysis.

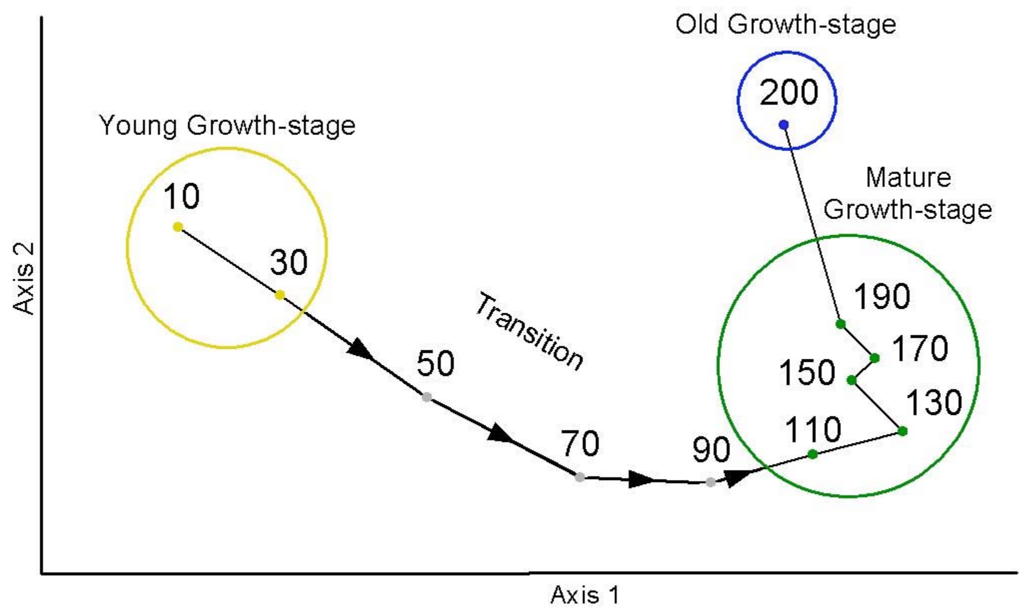
PLS survey corners were assigned to four disturbance categories:

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

Public Land Survey linked text

(PLS-4) Ordination of Historic MHn44 Age-classes

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



PLS-4

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

(PLS-5) Historic Windows of Recruitment for MHn44 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 30-110 years	I-1 >110 years
Yes	Quaking Aspen	0-30	Excellent	Poor to 60	--
Minor	Balsam Poplar	0-30	Poor	Poor to 50	--
Minor	Paper Birch	40-60	Fair	Good to 70	--
No	Red Oak	40-50	Poor	Poor to 50	--
No	Bur Oak	40-60	Poor	Poor to 60	--
No	Balsam Fir	30-50	Poor	Good to 60	--
No	Basswood	40-50	Poor after 20	Poor to 60	--
No	Red Maple	30-50	Poor after 20	Poor to 70	--
No	White Pine	40	--	Poor to 60	--
No	Sugar Maple	60	--	Poor to 70	--
No	Black Ash	90	--	Poor to 90	--
No	White Cedar	80-90	--	Good 70-100	--
No	White Spruce	120-150+	--	Good	Excellent

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 quaking aspen, 30-110 years
- **I-1:** ingress of seedlings under canopy of white spruce, quaking aspen, paper birch, and balsam fir, >110 years

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

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

PLS-5

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

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

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

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

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

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

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

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

(R-1) Suitability ratings of trees on MHn44 sites

This table presents an index of suitability for trees in MHn44 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 MHn44			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Quaking aspen (Populus tremuloides)	72	27	5.0
Balsam fir (Abies balsamea)	38	18	4.7
Red maple (Acer rubrum)	27	19	4.6
Paper birch (Betula papyrifera)	63	8	4.6
Basswood (Tilia americana)	18	21	4.4
White spruce (Picea glauca)	29	10	4.1
White cedar (Thuja occidentalis)	7	32	3.8
White pine (Pinus strobus)	14	16	3.8
Black ash (Fraxinus nigra)	19	9	3.4
Balsam poplar (Populus balsamifera)	13	13	3.3
Northern red oak (Quercus rubra)	7	17	3.2
Bur oak (Quercus macrocarpa)	14	9	3.1
Sugar maple (Acer saccharum)	10	12	2.9

*Suitability ratings: excellent, good, fair

R-1

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

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

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

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

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

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

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

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

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

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

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

(R-2) Natural Regeneration and Recruitment of Trees in Mature MHn44 Stands

This table presents an index of regeneration for MHn44 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 MHn44 communities. Changes in the index values from one stratum to another can be used to estimate regenerative bottlenecks, whether establishment (R-index) or recruitment (SE-, SA-, or T-indices).

Natural regeneration indices for germinants, seedlings, saplings, and trees common in the canopy of Northern Wet-Mesic Boreal Hardwood-Conifer Forest – MHn44					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Quaking aspen (Populus tremuloides)	79	4.3	4.2	4.5	5.0
Balsam fir (Abies balsamea)	69	4.7	4.2	4.5	4.3
Black ash (Fraxinus nigra)	62	4.3	4.3	4.0	3.0
Red maple (Acer rubrum)	55	4.3	4.3	4.2	4.0
Paper birch (Betula papyrifera)	50	2.7	2.2	3.2	4.3
Basswood (Tilia americana)	34	3.2	3.5	3.5	3.8
Sugar maple (Acer saccharum)	31	4.0	4.0	3.7	2.8
White spruce (Picea glauca)	30	3.0	2.8	3.5	3.8
Bur oak (Quercus macrocarpa)	30	3.0	3.0	3.2	3.0
Northern red oak (Quercus rubra)	30	2.8	2.8	2.0	2.8
Balsam poplar (Populus balsamifera)	23	2.7	2.3	2.5	3.3
White cedar (Thuja occidentalis)	8	1.3	0.8	2.3	3.8
White pine (Pinus strobus)	7	1.2	1.0	2.0	3.8

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

% presence: the percent of 175 MHn44 sample plots with that species present under 10m (33 feet) tall (R, SE, SA layers)
R-index: index of representation as true seedling or under 10cm (4 inches) tall
SE-index: index of representation as seedlings over 10cm and under 2m (0.3-6.6 feet) tall
SA-index: index of representation as saplings 2-10m (6.6-33 feet) tall
T-index: index of representation as a tree >10m (33 feet) tall
All indexes: equally weight (1) presence, (2) mean cover when present, and (3) mean number of reported strata, the frequency distributions of which are segmented equally by area into 5 classes.

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

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

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

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

(FIA-1) Structural Situations of Trees in Mature MHn44 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples MHn44 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
White Pine	61	2%	3%	-	3%	-	92%
Paper Birch	1609	5%	30%	11%	27%	7%	20%
Red Oak	97	6%	12%	10%	22%	9%	40%
Balsam Poplar	546	26%	24%	16%	11%	9%	13%
Quaking Aspen	9641	32%	15%	16%	8%	10%	19%
White Spruce	180	2%	9%	9%	18%	17%	44%
White Cedar	56	-	14%	13%	23%	13%	38%
Bur Oak	252	13%	19%	8%	17%	19%	24%
Basswood	232	9%	11%	16%	25%	20%	19%
Red Maple	522	8%	16%	15%	27%	25%	9%
Balsam Fir	1266	6%	17%	23%	23%	23%	8%
Sugar Maple	241	10%	20%	21%	14%	32%	3%
Black Ash	239	18%	9%	30%	9%	29%	5%

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

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

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

FIA linked text

(PLS/FIA-1) Abundance of MHn44 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 MHn44 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 - 195		~ 195	> 195	
	Young		T1		Mature			Old	
Quaking Aspen	86%	78%	| |		24%	40%	⌉	28%	43%
Paper Birch	5%	3%	⌉		18%	14%	|	12%	14%
Balsam Fir	3%	5%	⌉		10%	17%	)	10%	16%
White Spruce	1%	0%	⌉⌉		34%	1%	|	33%	0%
White Pine	–	0%	⌉		1%	4%	⌉	4%	2%
Red Maple	1%	3%			1%	2%		1%	0%
Basswood	--	1%			1%	1%		1%	0%
Black Ash	1%	2%			1%	2%		--	5%
Balsam Poplar	1%	6%			--	3%		1%	2%
White Cedar	--	0%			1%	4%		1%	18%
Bur Oak	1%	1%			1%	2%		2%	0%
Red Oak	--	0%			--	1%		1%	0%
Miscellaneous	2%	2%			9%	12%		9%	0%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	24%	21%	60%	75%	14%	4%		2%	0%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 4,074 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 10,595 FIA subplots that were modeled to be MHn44 sites.

Public Land Survey linked text
FIA linked text

Silviculture Systems for MHn44: No arrow - least favorable, ⇧ Favorable, ⇧⇧ Very Favorable

	Silviculture Systems	Clearcut	Patch Cutting	Group Seedtree	Dispersed Seedtree	Uniform Shelterwood	Group Shelterwood	Irregular Shelterwood	Group Selection	Strip Selection	Single Tree Selection
	Regeneration Strategy										
Quaking Aspen	Open (large-gap)										
Balsam Fir	Small-gap (large-gap)										
Red Maple	Large-gap (small-gap)										
Paper Birch	Large-gap (open)										
Basswood	Large-gap										
White Spruce	Large-gap (open)										
N. White Cedar	Large-gap (open)										
White Pine	Large-gap (open)										
Black Ash	Large-gap (small-gap)										
Balsam Poplar	Open										
N. Red Oak	Large-gap										
Bur Oak	Large-gap										

Forest Health

Quaking Aspen

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

WATCHOUTS!

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

• Harvest during the winter to ensure adequate regeneration.

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

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

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

Balsam Fir

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Spruce budworm	“	“
Stem decay	“	Volume loss

WATCHOUTS!

• In northeast and north central counties, use a rotation age of 45-50 years and presalvage/ salvage stands as budworm defoliation starts to cause topkill in the dominant trees. Promote mixed species in regeneration.

• Discriminate against balsam fir regeneration in white spruce stands and in areas where budworm outbreaks are common.

• 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 roots and stem, dead branches, and dead or broken tops.

Red 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.

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.

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.

White Spruce

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Spruce budworm	"	"
Yellow-headed spruce sawfly	Seedlings and saplings	Topkill, mortality
White pine weevil	Seedlings to pole-sized	Forking, multi-stemmed
Spruce decline	Pole-sized and larger	Growth loss, mortality
Spruce beetle	"	Mortality
Stem decay	"	Volume loss

WATCHOUTS!

• Both white pine weevil and yellow-headed spruce sawfly damage can be prevented by planting/ regenerating seedlings under a light overstory until the seedlings are at least 12-20 feet tall.

• Inspect young, open-grown plantations in early June for YHSS larvae. Use contact insecticides on seedlings with active feeding. Repeat inspection in mid to late June.

• In northeast and north central counties, presalvage/ salvage stands as budworm defoliation starts to cause topkill in the dominant trees.

• Along the North Shore, salvage spruce beetle-caused mortality. Contact the RFHS for more information about prevention, timing and sanitation.

• If a white spruce plantation does not respond to its first commercial thinning or mortality losses increase, it may be declining. Contact the RSS or the RFHS for more information.

• 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 roots and stem, dead branches, and dead or broken tops.

White Cedar

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Stem decay	“	Volume loss

WATCHOUTS!

• Encourage and preserve all white cedar regeneration. Consider retaining white cedar during harvests to ensure a local seed source.

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

White Pine

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

WATCHOUTS!

• Protect seedlings and saplings from browse damage.

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

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

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

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

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

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.

MHn44 - 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 MHn44 that are more susceptible to compaction and rutting.

- Lady fern (*Athyrium filix-femina*)
- Black ash (U) (*Fraxinus nigra*)
- Mountain maple (*Acer spicatum*)
- Palmate sweet coltsfoot (*Petasites frigidus*)
- American elm (U) (*Ulmus americana*)
- Nodding trillium (*Trillium cernuum*)
- Balsam fir (C) (*Abies balsamea*)
- Woodland horsetail (*Equisetum sylvaticum*)
- Side-flowering aster (*Aster lateriflorus*)
- Highbush cranberry (*Viburnum trilobum*)

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

Foot Notes

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

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

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

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

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

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

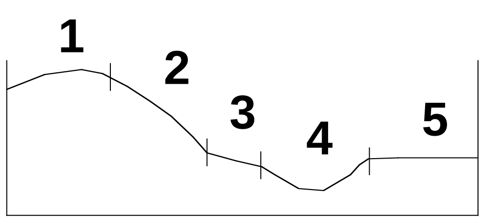
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

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

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

4. Landscape Position

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



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

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

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

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

   W Winter – the ground is snow covered or partially frozen

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

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

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

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

Public Land Survey linked text

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

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

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

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

Modern Forest linked text

Releve Samples

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

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

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

For more information on the releve method and NPC Classification:

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

FIA Samples

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

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

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

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

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

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

Link to the USFS website, north central