WFn64

∞ General Description

∞ Natural Disturbance Regime

∞ Natural Stand Dynamics & Growth-stages

∞ Growth Stage Key

∞ Tree Behavior

- ∞ Black Ash
- ∞ Tamarack
- ∞ Quaking Aspen
- ∞ N. White Cedar
- ∞ Yellow Birch
- ∞ Red Maple

∞ Tables

- ∞ PLS-1 - Historic Abundance of WFn64 Trees in Natural Growth-stages
- ∞ PLS-2 - Abundance of trees throughout succession in WFn64
- ∞ PLS-3 - Historic Abundance of WFn64 Trees Following Disturbance
- ∞ PLS-4 - Ordination of Historic WFn64 Age-classes
- ∞ PLS-5 - Historic Windows of Recruitment for WFn64 Trees
- ∞ R-1 - Suitability ratings of trees on WFn64 sites
- ∞ R-2 - Natural Regeneration and Recruitment of Trees in Mature WFn64 Stands
- ∞ FIA-1 - Structural Situations of Trees in Mature WFn64 Stands
- ∞ PLS/FIA-1 - Abundance of WFn64 trees in Pre-settlement and Modern Times by Historic Growth-stage

∞ Silviculture Systems

∞ Forest Health Considerations

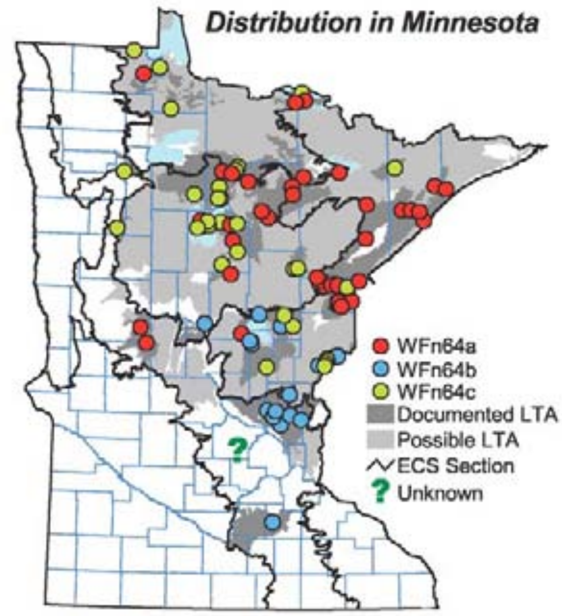
∞ Public Land Survey linked text

∞ Modern Forest linked text

WFn64 – Very Wet Ash Swamp

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights



The range of WFn64 forests in Minnesota (shaded) and distribution of releve samples (red, blue, and green dots).

Very Wet Ash Swamps (WFn64) are a common wetland community found throughout the Laurentian Mixed Forest Province of Minnesota, with a few outliers in the Eastern Broadleaf Forest Province. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

Commercial Trees

As a commercial forest, WFn64 sites are habitat for just a few crop trees. Black ash, tamarack, and quaking aspen are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on WFn64 sites (see Suitability Tables). However, the opportunities for tamarack are limited to the WFn64b type of the community's southern range (see map, blue dots). White cedar, yellow birch, and red maple 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. Paper birch and American elm are ranked as just fair choices of crop trees, but stands can be managed to maintain their presence as minor trees for purposes other than timber production.

Among these species, black ash and tamarack were the dominant native trees that have occupied WFn64 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)**. Paper birch, American elm, and white cedar are likewise native to WFn64 sites but occurred naturally at lower abundance. The consequence of fire suppression, commercial logging, and settlement in the past century has been to diminish the dominance of black ash and to promote substantially more balsam fir than was usual. Past history and land use as also encouraged the ingress of species that were not significant in native MHn35 stands such as red maple, balsam poplar, and quaking aspen. The increased abundance of minor and ingressing species is still modest and doesn't complicate our interpretations or the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

Most native WFn64 stands (55%) were young forest <75 years old **(PLS-1)**. Given that less than 4% of WFn64 forests were described as having been burned or windthrown **(PLS-3)**, it is clear that destructive agents other than these obvious catastrophes were involved to create so much young, WFn64 forest. We suspect that the loss of canopy trees in WFn64 forest was most linked to alterations in the surface water and groundwater regime that maintain WF communities in general. Prolonged ponding/flooding and drought stressed black ash trees and invited disease, pests, and root loss resulting in windthrow. We believe that ponding and drought were equally selective against small-diameter regeneration. This means that "young" WFn64 stands got their start with the most vigorous, drought/flood resistant saplings and poles. Shelterwooding is the silvicultural system that best fits the natural re-initiation of WFn64 forests. Initial entry would be aimed at recruitment of seedlings to the 4-6" diameter classes. Removal of the sheltering trees would occur when it is clear that the mid-canopy trees will dominate the new stand. Because black ash can exhibit excessive growth of equally competitive trees (stagnation), pre-commercial selection of the future crop trees could help to accelerate the differentiation process. Especially important is the idea of a two- or three-step process. WFn64 sites are incredibly prone to post-harvest swamping as removal of too many trees results in a raised water table.

In the historic landscape, 35% of WFn64 forest were mature and between 75 and 135 years old. At this time, senescence of the initial-cohort black ash created regeneration opportunities for coniferous trees and second-cohort black ash ranging from single-tree gaps to gaps up to an acre. No WFn64 trees were restricted to the small-gap strategy, and all trees that gained importance in the mature growth-stage are favored in large gaps. Group selection and variants of shelterwooding approximate the large-gap level of canopy removal. Second cohorts of black ash and recruitment red maple regeneration would be favored with group selection as they come the closest to small-gap behavior. Yellow birch and white cedar should recruit well in the light conditions created by group selection or variants of shelterwooding, depending upon the pattern of advance regeneration or underplanting. In the WFn64b type, patch cutting aimed at rather open conditions would be most appropriate if tamarack is the target species.

Just about 10% of the WFn64 landscape was forest older than 135 years. The hallmark of these forests was the fine-scale mixture of trees and microhabitats of the groundlayer. At this time, black ash was the main native tree to make use of small gaps. Variants of selective harvesting could be used in old WFn64 forests to perpetuate black ash and the structure of old WFn64 forests indefinitely. However, selective small-gap silvicultural systems assure the eventual demise of minor species and overall diversity of canopy trees. The WFn64 conifers such as northern white cedar, tamarack, and white spruce (historically) persisted in old WFn64 forest because of their longevity rather than by subsidy through regeneration. All of these conifers prefer large gaps for establishment and recruitment on these sites. Group selection and variants of shelterwooding could be used in old WFn64 forests to provide regeneration opportunities for the conifers and still maintain the general appearance of old WFn64 forest. Operation on frozen soils is the best approach for maintaining the diversity of groundlayer conditions.

Management Concerns

WFn64 communities indicate poorly drained and structurally weak soils. Frozen soil conditions are required for operation of heavy equipment.

The landscape balance of growth-stages and stand ages for the WFn64 community is nearly identical to its historic condition. We believe that wildlife populations are probably reacting to WFn64 habitat as they always have.

Compositional changes are also not much of a management concern. WFn64 sites were historically dominated by black ash and they still are. Increases in native trees like balsam fir, and ingress of species like red maple and balsam poplar are modest and not likely to complicate the management of these sites for black ash. Conservation of white spruce is recommended as it has been lost as an important species in mature and old WFn64 stands.

The most serious threats to WFn64 forests do not come from the forest management community. Altered hydrology is the death knell of WFn64 sites. Lateral flow of groundwater sustains WFn64 forests, and impeded flow through road beds has converted WFn64 forests to treeless wetlands on the “upstream” sides of roads. The “downstream” sides of roadways are well-drained peaty communities with no natural analogues. Control structures designed to create open-water habitat to benefit waterfowl have also degraded WFn64 habitat. More recently, drought has caused widespread decline of black ash on WFn64 sites, more so than in any other community where black ash occurs. The global warming forecast of greater variability of temperature and precipitation will likely impact communities like WFn64 forests that depend upon a steady flux of groundwater.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 1,113 corners within the primary range of the WFn64 community. At these corners, there were 2,724 bearing trees that one commonly finds in WFn64 forests.

The PLS field notes described about 1% of the WFn64 landscape as recovering from stand-regenerating fire. All such records were of burned-over lands. From these data, a rotation of 1,130 years was calculated for stand-replacing fire.

Elsewhere in the WFn64 landscape, the surveyors described lands as windthrown without suitable-sized trees for scribing. Such corners were encountered at about 3% of the time, yielding an estimated rotation of 480 years for windthrow.

Far more common at WFn64 sites were references to what we have interpreted as some kind of partial canopy loss, without any explicit mention of fire or windthrow. Most references were to sparse forest, thickets, and swampy conditions reflecting perhaps beaver impoundment. Regardless of the general descriptions, the distances to bearing trees were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked wet forests. About 5% of the survey corners were described as such, resulting in a calculated rotation of 110 years for disturbances that maintained early and mid-successional trees on WFn64 sites. Corners described as burned (14) or windthrown (21) are about equal and low for Minnesota. This suggests that surface fires and wind played some role in causing partial canopy loss, but we suspect that altered drainage by beaver and drought were the more prevalent causes.

Natural Rotations of Disturbance in WFn64 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**1,130 years**
Catastrophic windthrow photograph	**480 years**
Partial Canopy Loss, photograph	**110 years**

All northern wet forests (WFn) have similar disturbance regimes and share in common very long rotations of catastrophic fire. It is unlikely that fire played an important role in regenerating these forests. The rotation of 480 years for catastrophic windthrow is also typical of WFn communities. This seems remarkably long, given the tendency of trees to root shallowly on saturated soils and the mechanical weakness of wet soil. Rotations of 300-400 years are a third to a tenth that observed for the surrounding terrestrial forests of the northern floristic region. The rotation of 110 years for maintenance disturbances is the shortest calculated for WFn forests. We believe that of the WFn communities, WFn64 is in the most precarious landscape position regarding water-table fluctuations and that such fluctuations cause stress and tree mortality at the scale of medium-sized gaps. The effect of maintenance disturbance must have been to strongly favor black ash over all other species as it dominates all growth-stages.

Natural Stand Dynamics & Growth-stages

WFn64 forests are among several wetland communities where a particular hydrologic regime translates into dominance of a single species. Here, vernal ponding and the flux of groundwater in shallow aquifers strongly favors black ash. There is no "succession" because black ash dominates all growth-stages. Proximal disturbances like fire and windthrow, while noteworthy in the PLS records, were not the main means of re-setting stands to a youthful structure and composition to be followed by predictable compositional changes that we attribute to stand maturation processes. For wetland dominants like black ash, we favor the approach of considering their vulnerability in light of the hydrologic regimes that allow for their dominance. Storm events that erode drains and lower base water tables, cycles of drought, the ebb and flow of beaver populations, unusual and extended spring ponding, and outbreaks of diseases and pests targeting stressed trees probably had as much to do with the mortality of large black ash on WFn64 sites as did events as obvious as fire or windthrow.

Views and Summaries for WFn64 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.

A second critical difference between terrestrial and wetland communities regarding succession and stand dynamics is that the wetland communities are linked by a single process. For the past 6,000 years the climate of Minnesota has favored the expansion and development of wetland forests. The swamping, or paludification, of terrestrial sites has been a rather unidirectional process of peat accumulation, rising water tables, greater predictability of depth to the water table, and increased acidification by *Sphagnum* mosses. Along the way, different species of trees are favored and tend to dominate wetland forests that are at a particular stage of this process. That is, there is an ontogeny of wetland forest types that is evident both spatially and in the temporal reconstructions of vegetation change preserved in the peat strata. WFn64 forests belong to the "mixed-mire pathway" of wetland development, meaning that WFn64 sites often succeeded alder or willow shrub swamps and will eventually become cedar swamps as long as the peat-accumulation process continues. ***This is significant because the sort-term stand dynamics tend to reflect the long-term ontogeny.*** In this case young, small-diameter WFn64 ash stands tend to have compositional and structural similarities with alder and willow swamps. Old, large-diameter WFn64 stands start to resemble WFn53 cedar swamps. Disturbances that re-initiate WFn64 forests can set back this process, but eventually the gains towards cedar swamp will outweigh the regressions to shrub swamp.

The general compositional dynamics of WFn64 forests is for younger stands to be dominated by black ash and other hardwoods. By comparison with other forest communities, this stage was incredibly long and there was little compositional change for the first 75 years **(PLS-4)**. The eventual senescence of initial-cohort black ash initiates a mature growth-stage where compositional change accelerates. The acceleration is caused by the decline of initial-cohort black ash and the ingress of conifers such as tamarack, white spruce, and white cedar. At about age 135 years, compositional change slows and the stands settle at a balanced mixture of conifers and hardwoods lead by black ash.

The general structural dynamics of WFn64 forests is typical of Minnesota's northern forests. It follows the textbook concept of young forests being densely packed with small diameter saplings followed by older stands that gradually achieve greater tree spacing through self-thinning and crown competition. In young WFn64 stands the average distance of bearing trees to their corners was 22 feet. Such distances are quite in line with fully stocked hardwood forest of similar age. In mature and old WFn64 forests the distance of bearing trees to their corners increased to 25 feet. This is rather tight stocking compared to terrestrial hardwoods and could be the result of stagnation, where stands tend to achieve the condition of having evenly-spaced, similar-diameter, equally competitive trees.

Young Growth-stage: approximately 0-75 years

About 55% of the WFn64 landscape in pre-settlement times was covered by forests estimated to be under 75 years old **(PLS-1)**. Most often these stands were of mixed composition (88%). Essentially all corners were black ash mixed with either balsam fir, American elm, paper birch, quaking aspen, and sometimes balsam poplar. About 18% of all survey corners were monotypic black ash, and no other tree commonly occurred by itself.

The surveyors described some young WFn64 forests as having been burned. About 1% of the PLS corners were burned **(PLS-3)**, but often the attending trees were rather large causing us to place the corner in an older growth-stage. At times WFn64 forests develop a continuous grass/sedge groundlayer and such stands might have carried surface fires of sufficient intensity to kill some trees or advance regeneration. More likely though, the survey corners were in uplands that burned, leaving live trees in the wet ash swales that were most fit for bearing trees. Windthrow was far more common, affecting 3% of the PLS corners. Because of the high water table and weak, peaty substrate we believe that windthrow did contribute to the regeneration of WFn64 stands. However, the natural rotations of fire (1,130 years) and windthrow (480 years) were way too long to create the observed balance of growth-stages across the WFn64 landscape **(PLS-1)**. Most of the historic WFn64 forests were in the young growth-stage, composed of ash trees under 8" in diameter. Clearly, small-diameter ash stands were initiated by means other than just fire and wind.

We favor the idea that prolonged drought or prolonged flooding were the primary means of killing canopy black ash. In modern forests, decline of mature ash seems most correlated with the physical effects of altering site's hydrologic regime more so than any disease or pest problems. We believe that this kind of disturbance selects from local ash populations the most vigorous trees, which tends to favor the 4-10" diameter classes. Thus, re-initiation of mature and old WFn64 forests need not involve total site destruction and dependence upon small seedlings or advance regeneration to re-colonize the site. For our interpretation, all that needs to happen is to eliminate ash trees larger than 8" diameter for us to have modeled a survey corner as belonging to the young growth-stage. In modern forests, black ash is unequalled at maintaining a bank of saplings and poles 2-10m tall **(R-2)**, which might explain its immediate dominance and peak presence in the young growth-stage **(PLS-1)**.

Catastrophic regeneration of WFn64 forests probably happened upon occasion. Fire was not impossible and windthrow was sometimes important. Both disturbances favored black ash more than other species. We suspect that events killing most trees resulted in a brief window opportunity for quaking aspen or balsam poplar. Both species show sharp peaks of abundance in the initial age-classes (~20% relative abundance), but collapse by the time a stand is 40 years old. These trees probably performed the ecological function of de-watering WFn64 sites, which can get incredibly wet when the canopy is no longer present to transpire water. The total number of trees contributing to the initial age classes (up to 30 years) is very low and our estimates of aspen and poplar abundance could be unreliable. The lack of small-diameter trees younger than 30 years could be interpreted as further evidence that mortality events in WFn64 forests might have selected for 4-10" trees rather than having stands re-initiate from a legacy of small-diameter regeneration.

Mature Growth-stage: approximately 75-135 years
About 35% of the historic WFn64 landscape was mature forest **(PLS-1)**. Stands in this stage were more often mixed (84%) than monotypic (16%). Monotypic conditions were represented almost entirely by survey corners where all bearing trees were black ash. At survey corners with mixed composition, black ash occurred in combination with a wide variety of trees including: white cedar, American elm, yellow birch, paper birch, white spruce, tamarack, and balsam fir.

The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by the ingress of white cedar and white spruce and by improved success of tamarack **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. The relative abundance of black ash starts to decline from peak abundance of about 80% at age 90 years to about 56% by age 150 years **(PLS-2)**. At about 80 years, there is a burst of white cedar regeneration and establishment of a cedar cohort that persists for the remainder of the mature growth-stage and through the old growth-stage because cedar is long-lived in WFn64 forests. White spruce regeneration was actually present throughout the young growth-stage, but recruitment of tree-sized individuals didn't occur until the beginning of the mature growth-stage. The increase of spruce abundance at about age 80 was the beginning of a trend of steadily rising abundance that continued indefinitely until WFn64 stands were re-initiated by disturbance. During the mature growth-stage the first tree-sized tamaracks appear at about age 90 years. Tamarack's relative abundance rose sharply to about 12% in age-class 120 years, where it stabilized and persisted throughout the old growth-stage.

White spruce and white cedar as species that usually recruit well in large-gaps. Tamarack is favored in the open or in very large gaps. Thus, the success of these conifers in the mature growth-stage would seem to require sizeable openings. However, there is no direct evidence that tree density was any lower during this period. The distance of bearing trees to survey corners was incredibly constant at about 22-25 feet among all growth-stages. Such distances are typical of fully stocked forest. Because black ash is not clonal and because it is long-lived, it is harder to envision a roughly synchronous collapse of initial cohort black ash as one might suggest for a species like quaking aspen. However, it is easy to envision synchronous group mortality of canopy ash due to prolonged flooding, and we believe that this was the primary means of re-initiating WFn64 forests because it favors black ash over the flood-sensitive conifers. Thus, it is unlikely that flooding created the kinds of large-gaps that could benefit conifers during the mature growth-stage. It is also easy to envision synchronous canopy opening in response to ash decline. In modern situations when altered hydrology initiates decline, the response of black ash is to lose crown and depend upon epicormic branching to maintain the bole. For such stands, light-loving species like tamarack could have had success, and yet there would have been enough large-diameter ash for us to have modeled the stand as belonging to the mature growth-stage. What we don't understand though, is why 75-135 year old stands would be more susceptible to decline than younger stands. For now we have no tenable hypothesis as to why 75-100 year-old WFn64 ash stands would provide the light conditions necessary for the magnitude of conifer response that we measured in the historic data. It is though about the time for initial-cohort ash to be dying and white spruce and white cedar could have possibly made use of single-tree gaps. Tamarack could not have made use of single-tree gaps because it performs so poorly in the shade **(R-2)**, but the range of where tamarack was successful was along the periphery of the of the range of WFn64 forests where the climate is marginal and we could imagine greater climatic fluctuations causing synchronous declines of black ash.

Alternatively, canopy architecture and light conditions might not have been the proximal factors that most affected the recruitment success of conifers during the mature growth-stage. It is important to remember that black ash forms monotypic stands because it is unequalled in the handling hydrologic variation that typifies wet forests. In the wetland ontogeny, WFn64 forests are between communities that lack peat-forming mosses (WMn82, WFn55) and communities characterized by continuous moss cover and deep, organic substrates (WFn53, FPn forests). In the course of stand maturation, the tendency of WFn64 forests is to develop increasingly mossy ground cover and deeper, woody peat. The effect of the organics in general is to dampen hydrologic fluctuation and create a poorer substrate, eventually favoring the success of conifers over black ash. We doubt though that enough of a moss layer can develop in the course of a single successional cycle to have a significant hydrologic effect. Our interpretation is that most WFn64 sites already have enough organic capital to support wetland conifers. In years with normal precipitation, the peaty substrate is quite able to dampen annual fluctuations in ponding and water retention into the growing season. Apparently, WFn64 sites find themselves in situations where tree-killing floods occur on a cycle substantially shorter than the natural longevity of the black ash and the conifers typical of this community. The effects of such floods must have been to set back the peat-forming mosses as much as the conifers. Apparently the recovery period for the mosses and conifers is about 75 years.

Old Growth-stage: approximately >135 years

About 10% of the historic WFn64 landscape was estimated to have been WFn64 stands older than 135 years **(PLS-1)**. Nearly all (95%) of the corners with these large old trees were mixed in composition. Nearly all corners were black ash mixed with other species such as: American elm, white cedar, white spruce, tamarack, and balsam fir. At this time it was about equally probable for monotypic survey corners to be all black ash (3%) or all white cedar (2%).

The most amazing thing about old WFn64 forests is that 56% of all bearing trees were black ash **(PLS-1)**, yet just 3% of the survey corners were monotypic. Chance distributions of trees should have resulted in about 10% monotypic ash corners. Old WFn64 stands are inherently mixed at a fine scale, which allows for a diverse mixture of other trees with varying regenerative strategies to occur about the core population of black ash. In the field, it seems obvious that variety of substrate conditions control the distribution of both canopy tree species and groundlayer plants. Pools of water often in windthrow cradles, nurse logs, moss hummocks, alternating patches of minerotrophic and acidic mosses, raised tree bases, alder stools, etc. create micro-topography with as much as 2 feet of relief with highs and lows that interact differently with the water table. Only a few other forest communities carry the fine-scale biological diversity that is expressed in old WFn64 forests. The significance of both the biological and topographic diversity is that it seemingly helps to carry forward the legacy of most species in old WFn64 forests. All of the trees common in the old growth-stage are present at some level in young, re-initiated stands **(PLS-1)**. Also, this diversity tends to yield a young forest that does not change much **(PLS-4)** after disturbance re-adjusts the relative abundance of WFn64 forest plants.

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?

Black Ash

- ***excellent habitat suitability rating***
- ***early successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 40-50 years***

Identification Problems

The PLS surveyors did not consistently distinguish between black and green ash. WFn64 releve samples show that for plots with ash present: 3% have both species present; 2% are green ash without black ash; 95% are black ash without green ash. Because black ash is so much more abundant today than green ash, we feel that the historical accounts of ash trees in habitats as wet as WFn64 communities were almost always referring to black ash.

Suitability

WFn64 sites provide ***excellent habitat*** for black ash trees. The perfect ***suitability rating*** of 5.0 for black ash is influenced mostly by its very high presence (78%) as trees on these sites in modern forests **(R-1)**. When present, black ash is the dominant or sometimes co-dominant tree, contributing 44% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on WFn64 sites as sampled by releves. All northern wet forest (WFn) communities offer excellent habitat for black ash (see Suitability Tables).

Young Growth-stage: 0-75 years

Historically, black ash was the overwhelming dominant in young WFn64 stands recovering from stand-regenerating disturbances that were exceedingly rare **(PLS-1, PLS-2)**. Young black ash represented 75% of the trees at survey corners described as burned, which is by far more than any other tree **(PLS-3)**. We do not believe though that WFn64 forests burned in the same sense that upland forests did. More likely, the survey corner was burned but not nearby ash swales and the surveyors used small diameter (<8") ash in the unburned wetlands as bearing trees. Black ash was also the leading species following windthrow, representing 73% of the trees at such survey corners. Because of the high water table and weak, peaty soils in WFn64 communities, we believe that windthrow was quite common. Young WFn64 corners with black ash trees present were mostly mixed. Essentially all corners were black ash mixed with either balsam fir, American elm, paper birch, or quaking aspen. About 18% of all survey corners were monotypic black ash, and no other tree commonly occurred by itself. Its dominance in the young growth-stage and its leading abundance following any disturbance is why we consider black ash to be an ***early successional*** species on WFn64 sites. Small-diameter black ash regeneration was exceedingly abundant in the post-disturbance window **(PLS-5)**. In the 20-year age-class, half of all bearing trees were small-diameter black ash. When ash was the smaller tree at survey corners, it was most often coming in among larger black ash. From the beginning, black ash shows the dominant behavior of being able to replace itself. Less often, small-diameter ash were coming in under larger American elm and paper birch. This behavior is typical of early successional species, and we interpret this as black ash showing excellent ability to recruit into under-stocked windthrown, diseased, or rarely burned WFn64 stands.

Mature Growth-stage: 75-135 years

The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by the ingress of white cedar and white spruce and by improved success of tamarack **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. The relative abundance of black ash starts to decline from peak abundance of about 80% at age 90 years to about 56% by age 150 years **(PLS-2)**. Small-diameter ash regeneration coming in among larger trees dropped dramatically from the young growth-stage to nearly nothing in the mature growth-stage, but some ash regeneration was present until the 100-year age-class **(PLS-5)**. At this time though there was great diameter variation among the ash bearing trees and most found themselves as the smaller tree at survey corners. Over half of all these cases were of smaller diameter ash coming in under larger diameter ash. We interpret this as black ash having good success regenerating and replacing itself at the start of the mature growth-stage, but losing some of this ability by the close of the period. If the natural course of stand maturation involved increasingly mossy ground cover, it could explain both the ingress of conifers and the gradual decline of black ash regeneration. It is our field experience that black ash establishment is much better on wet, graminoid-derived mucks than it is on mosses, particularly the minerotrophic *Sphagnum* mosses.

Old Growth-stage: >135 years

In old WFn64 forests the relative abundance of black ash declines slowly and then stabilizes at about 50% in the very old, 200-300 year age-classes **(PLS-1)**. Although diminished from earlier growth-stages, 50% abundance is still high and black ash remained the most abundant and dominant species. In WFn55 forests and wet-mesic hardwood forests, it is not unusual for black ash to be older than 135 years, and very large ash are often older than 200 years. Thus, it is possible for initial-cohort black ash to survive into old growth-stages, but we believe that black ash don't live that long in very wet habitats like WFn64. It seems more likely that the persistence of black ash in old WFn64 forests was the result of continued establishment and recruitment. Small-diameter black ash regeneration was not detected during the old growth-stage using our restrictive half-diameter rule **(PLS-5)**; however, smaller diameter trees were abundant. It was still more common for black ash to be the smaller tree at survey corners, which is typical of trees with regeneration success. When black ash was the smaller diameter tree, it was still most often coming in among larger diameter black ash, but it was also common for black ash to come in among larger tamarack, American elm, white spruce, and white cedar. The most compelling argument for sustained dominance of black ash in old WFn64 forests is its extraordinary regenerative performance in modern forests. Black ash has perfect indices of establishment and recruitment in mature and old forests sampled by releves **(R-2)**. Our interpretation is that black ash can dominate old WFn64 forests by virtue of its exceptional regenerative abilities and because it was favored over other species after disturbance of any scale **(PLS-3)**, including the fine-scale events typical of old forests.

Regeneration Strategies

Because black ash dominated all growth-stages and canopy situations in WFn64 forests, it is obvious that all of its regenerative strategies were successful. We believe that it primary strategy was to establish a pervasive bank of seedlings, and that it was as dominant in the understory as it was in the overstory. We doubt very much that stand-regenerating events eliminated entirely the advance regeneration of black ash. This seedling bank reacted positively to openings of any size, but the balance of historic and modern data would suggest that recruitment was best in gaps that span our concepts of both ***large-gaps*** and ***small-gaps***. Although no other tree could rival black ash in the open, WFn64 sites are notorious for swamping after canopy removal, and considerable growing space and resources are directed to wetland graminoids and speckled alder rather than tree growth. In the historic PLS data our interpretation of black ash's gap strategy is supported by (1) its dominance throughout the mature and old growth-stages where we presume most initial cohort trees were mostly dead **(PLS-1, PLS-2)**, (2) its peak presence at survey corners showing partial canopy loss due to maintenance disturbance **(PLS-3)**, and (3) its extended regeneration success to the 100-year age class **(PLS-5)**. In the FIA data, black ash has its highest combined presence as seedlings or saplings under taller trees (situations 12, 13, and 23), which is typical of trees able to use large or small gaps for recruitment **(FIA-1)**. Most impressive though is black ash's regenerative performance in modern WFn64 forests sampled by releves. Its perfect indices of regeneration in the understory means that no other tree had greater presence, cover, and continuous vertical stratification **(R-2)**. These perfect scores are the hallmark of a small-gap strategist.

Historic Change in Abundance

Today, black ash remains the dominant tree in WFn64 forests, but it has lost total dominance to a mixture of species lead by balsam fir **(PLS/FIA-1)**. In young forests black ash were 72% of the trees compared to just 55% today. It seems likely that in young WFn64 forests regenerated by logging or altered drainage, black ash are not quite as favored as they were after natural disturbances.

The decline of black ash is evident also in the mature growth stage where they were historically 71% of the trees and are now 56% of the trees. Highly unusual is the fact that there is about as much old WFn64 forest (>135 years) as there ever was. These stands have not been affected by logging, yet the decline of black ash is both evident and proportionally similar to the declines in the young and mature growth stages. Black ash was historically 56% of the trees in the old growth-stage and it is now just 36% of the trees. This fact makes us suspect that black ash's problems are a reaction to something apart from logging and exploitation. In the past 10 years, the decline of mature black ash has been evident and seems restricted to the WFn64 community. Because our comparison is between PLS bearing trees and the 1990 FIA cycle, we suspect that there was undocumented decline of mature black ash prior to that time as well. Our best guess is that altered drainage is the primary reason for the decline of black ash in modern times. Most management activities and development projects fail to appreciate the dependence of black ash and wet forests in general on the horizontal flux of groundwater. Drainage impeded by roadbeds, control structures, uncontrolled beaver populations, etc. have probably all contributed to the decline in black ash. For these reasons and the impending arrival of emerald ash borers, we consider black ash to be in some peril on WFn64 sites, deserving of silvicultural attention and conservation efforts.

Tamarack

- ***excellent habitat suitability rating (restricted to WSU and MIM)***
- ***late-successional***
- ***open (large-gap) regeneration strategist***
- ***regeneration window at 0-20 years***

Suitability

WFn64 sites provide ***excellent habitat*** for tamarack trees. The ***suitability rating*** of 4.0 for tamarack is influenced mostly by its high mean cover when present (21%) as trees on these sites in modern forests **(R-1)**. Tamarack can be an important co-dominant when present. Tamarack's presence is just 9% 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 second, tied with quaking aspen and following only the dominant black ash on WFn64 sites as sampled by releves. Tamarack's success in WFn64 forests seems to be restricted to the Western Superior Uplands ***(WSU)*** Subsection and the Minnesota and Iowa Moraines ***(MIM)*** Section. Northern wet forests in general are not habitat for tamarack, with WFn64 being the exception (see Suitability Tables).

Young Growth-stage: 0-75 years

Historically, tamarack was a minor tree in young WFn64 stands **(PLS-1, PLS-2)**. Most young tamarack bearing trees were recorded in the initial age-class and were present at corners described as burned or windthrown. They represented 8% of the trees at survey corners described as burned, second to the dominant black ash **(PLS-3)**. We doubt that WFn64 sites ever burned like upland forests, but it seems possible that fires in adjacent uplands might have crept through WFn64 forests and done enough damage to kill the trees. In conifer-dominated peatlands, tamarack is the usual early-successional tree to re-colonize burned, organic substrates. Thus, its immediate presence in burned WFn64 stands is expected, far more so than black ash. Young tamarack represented 13% of the trees survey corners described as windthrown. Tamarack does well in open peatlands, and it seems that windthrown WFn64 habitat was a favorable canopy condition for tamarack establishment. Small-diameter, tamarack regeneration coming in among larger trees was present throughout post-disturbance window that correlates with the young growth-stage **(PLS-5)**. Amazingly, all tamarack records in the first 75 years was small-diameter regeneration, meaning that there is little evidence that post-disturbance seedlings and saplings ever became trees. In modern WFn64 forests, tamarack has a poor record of recruitment under a canopy, and especially has trouble recruiting seedlings to heights over 2m **(R-2)**. Our interpretation is that canopy removal in WFn64 forests provided an establishment window for tamarack, but historically the canopy of black ash and perhaps even speckled alder closed fast enough to prevent much recruitment to tree size.

Mature Growth-stage: 75-135 years

The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by improved success of tamarack and the ingress of white cedar and white spruce **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. During this time the first tree-sized tamaracks appear at about age 90 years, and its relative abundance rises sharply to about 12% in the 120-year age-class, where it stabilizes and persists throughout the old growth-stage. Because this increase starts late in the growth-stage, the average relative abundance of tamarack is just 2% in mature forests. Small-diameter tamarack regeneration coming in among larger trees was detected until the 100-year age-class **(PLS-5)**, but there were too few records to determine if tamarack had a preference for coming in under a certain species. Because of tamarack's poor record of recruitment under a canopy **(R-2)**, and because of its peak presence at windthrown corners **(PLS-3)**, one would suspect that tamarack's rise to importance would have required more open conditions. It is possible that tamarack benefited from canopy gaps created by the senescence and death of initial-cohort black ash. It seems likely to us that 90-120 years might represent a reasonable estimate of the natural longevity of canopy black ash on WFn64 sites. Tree density, though, is remarkably constant among the WFn64 growth-stages at about 23 feet on average from survey corners to bearing trees. Such distances are typical of undisturbed, closed-canopy forest. Because of the geographic restriction of WFn64 releves with tamarack, we tested the idea that the sharp rise in tamarack abundance could be the result of a regional event, unrelated to inherent stand dynamics. In other tamarack communities that share the range of WFn64 forests (e.g. FPs63), we found tamarack behaving in its normal, early successional, open-habitat role. In these communities tamarack increased at times that were not coincident with the tamarack rise in WFn64 forests. Our best guess is that the late increase in tamarack abundance near the close of the mature-growth stage was the result of successful recruitment in large gaps that formed when initial-cohort black ash started to die. However, we believe that this success was limited to the WSU and MIM regions where climatic or hydrological settings somehow favored the punctuated demise of initial-cohort ash.

Mature Growth-stage: 75-135 years
In the old growth-stage tamarack had sustained abundance at about 12% **(PLS-1, PLS-2)**. Its persistence in the old growth-stage is the main reason that we consider tamarack to be a ***late-successional*** species on WFn64 sites. Small-diameter tamarack regeneration coming in among larger trees was not detected during the old growth-stage **(PLS-5)**. In modern mature and old WFn64 forests tamarack is present as either scattered seedlings or as an important co-dominant tree, and almost never in the mid-canopy. This pattern is reflected in the indices of regeneration for WFn64 tamarack **(R-2)**. We believe that whatever causes some WFn64 sites to essentially convert from black ash to tamarack was a short-term phenomenon that was more likely in older ash swamps and was more likely in the MIM and WSU regions. We do not suspect that this same event was recurring and therefore, a means of sustaining tamarack in old WFn64 forests. In old forests, essentially all of the tamarack was the largest tree at survey corners suggesting to us that after its burst of success in the mature growth-stage, tamarack persisted in the old growth-stage due mostly to its longevity.

Regeneration Strategies
The regenerative behavior of tamarack on WFn64 sites is puzzling in that its window of establishment is immediate after disturbance, yet its window of recruitment comes late in the life of a stand – as much as 100 years following disturbance. Thus, tamarack's establishment strategy is to establish seed-origin trees in the post-disturbance years as would an ***open*** regeneration strategist. Tamarack's recruitment strategy seems to be to fill ***large-gaps***, especially during the decline of the initial-cohort black ash, which can start as early as age 75 years. Tamarack's leanings towards regenerating in the open or in large-gaps is evident in the historic PLS data by (1) its higher presence at disturbed survey corners **(PLS-3)** and (2) by having its peak regeneration in the post-disturbance window **(PLS-5)**. Tamarack's requirement of more open conditions is especially evident from its behavior in modern, closed canopy forests as sampled by releves **(R-2)**. Tamarack has just fair ability to germinate seedlings under a canopy, but survival and recruitment from ankle-high seedlings to 10m is poor, and typical of trees that regenerate in the open. No conclusions can be drawn from the FIA sampling of modern WFn64 forests where just 3 trees were recorded **(FIA-1)**. Our interpretation is that tamarack's primary strategy on WFn64 sites is to establish and maintain a scant, but ever present seedling bank and to then recruit into the taller strata when large-gaps form in the overstory of black ash. This delayed recruitment of tamarack is not at all typical of its behavior in other communities where at least some recruitment is coincident with establishment early in the life of a stand.

Historic Change in Abundance
Today, tamarack has been eliminated from WFn64 sites as there is very little old WFn64 forest **(PLS/FIA-1)**. Just 3 tamarack trees were among the 9,824 total FIA trees representing WFn64 forests. It's modest presence of 9% in our releves seems large by comparison, and suggests strongly that tamarack is persisting only in protected, old wet-forests. The historic loss of tamarack is a statewide phenomenon, especially in upland and wet forest settings. Both logging and outbreaks of larch sawflies have been blamed for the historic demise of tamarack.

Quaking Aspen

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

Identification Problems

The PLS surveyors normally distinguished between quaking aspen and balsam poplar, but it is possible that some references to aspen might have included balsam poplar. Thus, interpretations of PLS data for the more common quaking aspen should always be done knowing that some of these trees could have been balsam poplar. WFn64 releve samples show that for plots with these trees present: 29% are balsam poplar without quaking aspen; 71% are quaking aspen without balsam poplar. We consider quaking aspen and balsam poplar to be ecologically equivalent for most silvicultural considerations. However, the lack of coincident occurrence in the releves would suggest that there are certain conditions that favor one tree over the other.

Suitability

WFn64 sites provide ***excellent habitat*** for quaking aspen trees. The ***suitability rating*** of 4.0 for quaking aspen is influenced by a balance of its presence (12%) and mean cover when present (16%, **R-1**). The ranking is tied for second with tamarack, and follows only the dominant black ash on WFn64 sites as sampled by releves. The ash-dominated northern wet forests (not WFn53) in general offer excellent habitat for quaking aspen (see Suitability Tables).

Young Growth-stage: 0-75 years

Historically, quaking aspen was a minor, but important tree in young WFn64 stands recovering from stand-regenerating disturbance **(PLS/FIA-1)**. Young aspen were not recorded as present at survey corners described as burned or windthrown **(PLS-3)**. This was quite surprising given that aspen had its peak abundance, nearly 20% in the initial 20- and 30-years age classes **(PLS-2)**. This initial burst of aspen regeneration collapsed to nearly nothing by the 40-year age class and averaged just 2% presence across the whole growth-stage. Aspen abundance continued to decline and was only sporadically present in the older growth-stages. For this reason, we consider aspen to be an ***early successional*** species on WFn64 sites. In spite of aspen's modest abundance, we believe that it played an important role in de-watering WFn64 sites after they have lost the transpiring function of the tree canopy. This was important because WFn64 sites can revert to an alder/sedge condition after major disturbances that can slow the recovery of trees.

Mature Growth-stage: 75-135 years

By the time WFn64 forests reached maturity, quaking aspen represented slightly less than 1% of the bearing trees **(PLS-FIA-1)**. It played no important role in the gradual decline of black ash and ingress of conifers which typifies the mature growth-stage. No small-diameter aspen regeneration was detected at this time **(PLS-5)**. The few trees present tended to be the larger trees at the survey corners. We believe that there was no regeneration of aspen at this time, and thus no means of sustaining the local populations.

Mature Growth-stage: 75-135 years

Quaking aspen was absent from old WFn64 forests. The ecological significance of this and its scant occurrence in mature forests is that its success after catastrophic disturbance must have been accomplished mostly by seeding in on disturbed sites. Given the grassy and brushy nature of WFn64 sites, it is hard to imagine a lot of aspen seeding unless the regenerating disturbance also eliminated a lot of the sedges, grasses, and alder. Alternatively, patches of WFn64 forests tend to be linear with lots of edge between it and upland forest types that often have lots of quaking aspen because they are wet-mesic. It is possible that some of aspen's post-disturbance success was due to their ability to sucker into the wet forest from adjacent uplands rather than being persistent in old forests.

Regeneration Strategy
Aspen's primary regenerative strategy on WFn64 sites is to occupy ***open*** habitat after stand-regenerating disturbance. It seems though that fire and windthrow were not the major means of creating open habitat for quaking aspen as aspen bearing trees were not present at survey corners described as such **(PLS-3)**. Temporary ponding or flooding might have left good seedbed conditions for quaking aspen. In the historic PLS data the open-strategy interpretation is supported by: (1) the fact that aspen was most abundant in the initial 20- and 30-years age classes, (2) its near absence in mature and old forests suggests that it could not effectively use gaps for regeneration, 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 in young sapling and pole stands (situations 11 and 22) in the FIA data **(FIA-1)** is also characteristic of species that regenerate effectively in the open. The releve sampling of mature WFn64 forests corroborates this argument. Aspen has just fair ability to establish and recruit seedlings under a canopy **(R-2)**. Its indices of success for establishing seedlings (2.5-2.7) are most in line with trees that regenerate best in the open.

Historic Change in Abundance
Today, quaking aspen is more important on WFn64 sites than it was historically **(PLS/FIA-1)**. Quaking aspen has gained about 3-4% relative abundance in all growth-stages. While this seems modest, it is significant in that historically aspen was mostly absent from WFn64 forests after 40 years. Because the soils are poorly drained, we doubt that the increase in aspen abundance is the consequence of aspen building extensive clonal rootstocks. More likely, logging has left some sites more receptive to aspen seeding.

Northern White Cedar

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

Suitability
WFn64 sites provide ***good habitat*** for white cedar trees. The ***suitability rating*** of 3.9 for white cedar is the consequence of balanced presence (15%) and mean cover when present (12%, **R-1**). For long-lived conifers with balanced presence and cover, we suspect some loss of seed source, and believe that they might increase significantly if they were planted more often or if seed trees were more numerous. The ranking is fourth among trees common on WFn64 sites as sampled by releves. Northern wet forests (WFn) in general offer good-to-excellent habitat for northern white cedar (see Suitability Tables). This is especially true of the WFn53 community where cedar is a strong dominant. Among the WFn communities, WFn64 is the poorest habitat.

Young Growth-stage: 0-75 years
Historically, white cedar was a minor tree in young WFn64 forests **(PLS-1, PLS-2)**. Young cedars represented 3% of the trees at survey corners described as burned **(PLS-3)**. We do not believe though that WFn64 forests burned in the same sense that upland forests did. More likely, the survey corner was burned but not nearby ash/cedar swales and the surveyors used some small-diameter (<8") cedar in the unburned wetlands as bearing trees. White cedar was substantially more important after windthrow, representing 13% of the trees at such survey corners. White cedar does well as a cultivar in open environments, and it seems that windthrown WFn64 habitat was the most favorable canopy condition for cedar. Small-diameter white cedar regeneration coming in among larger trees was not detected during the young growth-stage **(PLS-5)**. All cedar records in the young growth-stage were as the largest tree at a corner. Apparently, the effect of wind was to leave the better-established, larger-diameter cedars that we modeled to be under 75 years old.

Mature Growth-stage: 75-135 years
The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by the ingress of white cedar and white spruce and by improved success of tamarack **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. White cedar first appears as small-diameter regeneration in age-classes 70 and 80 years, and then is never again detected. This burst of regeneration, initiated a corresponding burst of cedar recruitment and trees, which peaked at nearly 15% relative abundance in the 80-year age class. Following this peak, cedar abundance drops steadily throughout the remainder of the mature growth-stage and into the old growth-stage where it stabilized at about 4% relative abundance. Thus, it would seem that the beginning of the mature growth-stage offered a brief, but effective window of opportunity for white cedar. Recruitment and survivorship must have been excellent as we measured just a fair amount of small-diameter regeneration **(PLS-5)** that translated into considerable tree abundance. Our interpretation is that advance regeneration of white cedar responded favorably to the decline of initial-cohort black ash during the mature growth-stage. This idea is supported by the fact that white cedar has good ability to establish and recruit seedlings under a canopy in mature WFn64 forests **(R-2)**, and its advance regeneration should have been able to react to openings in the ash canopy. Because cedar peaks in the mature growth-stage we consider white cedar to be ***mid-successional*** in WFn64 forests. It is important to note that the pulse of cedar regeneration and recruitment success at about age 80 years is duplicated in other ecological systems (e.g. FDn43, MHn44) where the initial-cohort trees are not nearly as long-lived as black ash. In those cases, and perhaps this one, it is possible that the pulse of cedar success was a regional phenomenon from unknown, but favorable conditions *ca.* 1780-1800 AD.

Mature Growth-stage: 75-135 years

In the old growth-stage white cedar was a minor co-dominant tree **(PLS-1)**. We believe that white cedar's presence in old stands was mostly a consequence of its longevity. We believe that trees established during its regenerative pulse in the mature growth-stage persisted, almost indefinitely, until the next catastrophic event. Small-diameter white cedar regeneration coming in among larger trees was not detected during this very old stage **(PLS-5)**. At this time, white cedar bearing trees were almost always the largest tree at survey corners, which is typical of a tree that has essentially stopped reproducing. Nearly all of these large, old trees were standing above small diameter black ash.

Regeneration Strategy
White cedar's primary regenerative strategy on WFn64 sites is to fill ***large-gaps***. It is most successful at this when gaps are forming within a declining canopy of black ash. In the historic PLS data this interpretation is supported by: (1) the fact that white cedar abundance responds to the decline of initial-cohort black ash in the mature growth-stage **(PLS-2)**, and (2) 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 WFn64 forests shows that white cedar has good ability to establish seedlings and recruit to higher strata under a full canopy **(R-2)**. Its indices of regenerative success (3.0-3.7) are most in line with species that do well in large-gaps. For this reason, and cedar's high abundance in windthrown situations suggests that the gaps needed to be fairly large for successful establishment and recruitment.

Historic Change in Abundance
Today, white cedar is about as abundant as it ever was in young and mature WFn64 forests. In old forests though, white cedar's abundance is much higher (31%) than it was historically (4%, **PLS/FIA-1**). In fact, the main reason that we modeled WFn64 FIA subplots to be >135 years old was due to the presence of large-diameter cedars. Land management agencies have for many years in Minnesota avoided cutting cedar because there has been little success in regenerating it. We believe that the overall abundance of old WFn64 forests enriched in white cedar is the result of this policy.

Yellow Birch

- ***good habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at ~70 years***

Identification Problems

The PLS surveyors usually distinguished yellow from paper birch, but not always. Thus, interpretations of PLS data for yellow birch on WFn64 sites should always be done knowing that some of these trees were likely paper birch. WFn64releve samples show that for plots with birch present: 16% have both species present; 39% are yellow birch without paper birch; 45% are paper birch without yellow birch. For this analysis, tree records were biased towards paper birch because we assigned generic references to "birch" as paper birch, only because of a very slight higher presence of paper birch **(R-1)**. Thus, the account below is based upon explicit reference to yellow birch. On WFn64 sites, these trees are different and not silviculturally equivalent.

Suitability

WFn64 sites provide ***good habitat*** for yellow birch trees. The ***suitability rating*** of 3.2 for yellow birch is influenced mostly by its presence (14%) as trees on these sites in modern forests **(R-1)**. When present, yellow birch is a minor co-dominant tree, contributing 8% mean cover in mature stands. The ranking is fifth among common trees on WFn64 sites as sampled by releves. Northern wet forest communities in general offer fair-to-excellent habitat for yellow birch (see Suitability Tables). Its performance increases as soil drainage gets better. WFn64 forests are intermediate in this respect.

Young Growth-stage: 0-75 years

Historically, yellow birch was present in just trace amounts in young WFn64 stands recovering from stand-regenerating events **(PLS-1, PLS-2)**. No young yellow birches were recorded at survey corners described as burned or windthrown **(PLS-3)**. Small-diameter, yellow birch regeneration was not detected throughout the post-disturbance window that correlates with the young growth-stage **(PLS-5)**. Our interpretation is that stand-regenerating disturbances effectively eliminated yellow birch from WFn64 sites and that recovery was slow, favoring the older growth-stages.

Mature Growth-stage: 75-135 years

The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by the ingress of white cedar and white spruce and by improved success of tamarack **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. The abundance of yellow birch increased at the end of the young growth-stage and the beginning of the mature growth-stage, peaking in abundance in the 60-80 year age-classes at about 3% relative abundance. This peak was responsible for the average abundance of 1% in both growth-stages **(PLS/FIA-1)**. Because yellow birch has a distinct peak of abundance in the mature growth-stage, we consider it to be ***mid-successional*** on WFn64 sites. Small-diameter yellow birch regeneration coming in among larger trees was first detected and peaked in the 70-year age-class **(PLS-5)** and persisted throughout the mature growth-stage. The PLS data are too sparse to suggest that yellow birch had a preference for coming in among certain overstory trees. In modern forests yellow birch shows good ability to establish seedlings and excellent ability recruiting them to heights above 2m **(R-2)**. Our interpretation is that yellow birch had limited success building a bank of seedlings late in the young growth-stage and that some trees were recruited into the canopy when gaps formed in the initial-cohort black ash canopy during the mature growth-stage.

Mature Growth-stage: 75-135 years

By the time stands reached the old growth-stage yellow birch had dropped out of the picture and was present in just trace amounts **(PLS/FIA-1)**. Small-diameter yellow birch regeneration was not detected during this growth-stage **(PLS-5)**. The paucity of yellow birch trees and possible absence of small-diameter regeneration in the old growth-stage, might explain why it was largely absent from young WFn64 stands. Apparently there was no old-forest legacy to pass on to stands recovering from major disturbance.

Regeneration Strategy

Yellow birch's primary regenerative strategy on WFn64 sites is to fill ***large-gaps***. In the historic PLS data the idea that yellow birch is a large gap strategist is supported by the fact that it responded to gaps during the decline of initial-cohort black ash **(PLS-2)**, and (2) its window of regeneration is in the gap window **(PLS-5)**. In the FIA data **(FIA-1)**, yellow birch regeneration is present *only* as seedlings (situations 12 and 13). This is a property of trees that we normally consider small-gap strategists. The sampling of yellow birch in the FIA data though, just 11 trees, is too sparse for drawing conclusions. The releve sampling of mature WFn64 stands, shows that yellow birch is capable of building a seedling bank with excellent chances of the seedlings reaching heights over 2m **(R-2)**. Its regenerant and seedling indices are good (3.5), which is typical of large-gap species.

Historic Change in Abundance

Today yellow birch is about as abundant as it ever was, present at about 1% relative abundance in all growth-stages **(PLS/FIA-1)**. Its presence as a tree and especially as regeneration in the releve sampling of WFn64 forests is considerably higher than it is in either the PLS or FIA data. This suggests to us that yellow birch has had modest success in older, unmanaged stands.

Red Maple

- ***good habitat suitability rating***
- ***early successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 30-40 years***

Suitability

WFn64 sites provide ***good habitat*** for red maple trees. The ***suitability rating*** of 3.1 for red maple is the consequence of balanced presence (10%) and mean cover when present (11%, **R-1**). The ranking is sixth among trees common on WFn64 sites as sampled by releves. Northern wet forest communities with black ash as the dominant (not WFn53) offer good-to-excellent habitat for red maple (see Suitability Tables). Red maple's success improves with soil drainage, meaning that WFn55 sites are better than WFn64 sites.

Young Growth-stage: 0-75 years

Historically, red maple was present at just 1% relative abundance in young WFn64 stands recovering from stand-regenerating events **(PLS/FIA-1)**. Young red maples were not recorded at all at survey corners described as burned, and just a single tree was recorded at a windthrown corner **(PLS-3)**. This suggests to us that the presence of red maple in young WFn64 stands was not related to establishment and recruitment in the open. Small-diameter, red maple regeneration was first detected and most abundant in the 30- and 40-year age-classes providing fair chances of recruitment **(PLS-5)**. Its peak presence as a tree follows its establishment in these age classes but declines steadily. For this reason, we consider red maple to be an ***early successional*** species on WFn64 sites. We believe, though unlike most early successional trees, that red maple did well establishing itself beneath the emerging canopy of black ash, mostly because is has good establishment in modern stands under a canopy **(R-2)** and because it has good representation in pole stands (situations 12 and 22) that were sampled by FIA plots **(FIA-1)**.

Mature Growth-stage: 75-135 years

The mature growth-stage is the period of greatest compositional change in WFn64 forests **(PLS-4)**. This change was driven by the ingress of white cedar and white spruce and by improved success of tamarack **(PLS-1)**. Compositional adjustments in the mature growth-stage were far more subtle than the transitioning of terrestrial forests because it all happens about a slowly declining, dominant population of black ash. The abundance of red maple decreases steadily throughout the mature growth-stage. The trend of red maple decline starts from peak abundance of about 5% in the 30-year age-class until it stabilized at about 1% presence in the 100-year age-class. Small-diameter red maple regeneration was not detected in the mature growth-stage **(PLS-5)**. The decline of red maple throughout the mature growth-stage probably represents the gradual loss of trees established earlier (at 30-40 years) and poor success at regeneration much beyond the 40-year age class.

Mature Growth-stage: 75-135 years

By the time stands reached the old growth-stage red maple had dropped out of the picture and was present in just trace amounts **(PLS/FIA-1)**. Small-diameter red maple regeneration was not detected during this growth-stage **(PLS-5)**. The paucity of red maple trees and possible absence of small-diameter regeneration in the old growth-stage, might explain why it was largely absent in the post-disturbance years of young WFn64 stands. Apparently there was no old-forest legacy to pass on to stands recovering from major disturbance.

Regeneration Strategies

Red maple's regenerative strategies on WFn64 sites is based entirely upon its performance in modern forests. It seems that it is most likely to fill ***large-gaps***. The releve sampling of older WFn64 stands shows that red maple is very capable of developing a seedling bank. It has good success establishing and recruiting seedlings beneath a canopy **(R-2)**. Its indices of regeneration success (3.5-3.8) are most in line with species that do well in large-gaps, and borders on values where ***small-gap*** species are successful. Red maple's performance in the FIA plots is similar. Its highest abundance is as poles in tree stands (situation 23), which we consider a trait of large-gap species. However, it also has good presence as seedlings (situations 12 and 13), which we tend to consider a trait of small gap species. The historic PLS data did not record enough red maples for reasonable interpretation.

Historic Change in Abundance

Today red maple is about as abundant as it ever was, present at about 1% relative abundance in all growth-stages **(PLS/FIA-1)**. Its presence as a tree and especially as regeneration in the releve sampling of WFn64 forests is considerably higher than it is in either the PLS or FIA data. This suggests to us that red maple has had modest success in older, unmanaged stands.

(PLS-1) Historic Abundance of WFn64 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the WFn64 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 - 75	~75	75 - 135	~135	> 135
	Young		Mature		Old
Balsam Fir	6%		1%		2%
Paper Birch	4%		3%		3%
American Elm	6%		5%		6%
Black Ash	72%		71%		56%
White Cedar	1%		8%		4%
Tamarack	1%		2%		12%
White Spruce	1%		5%		13%
Miscellaneous	9%		5%		4%
Percent of Community in Growth Stage in Presettlement Landscape	55%		35%		10%

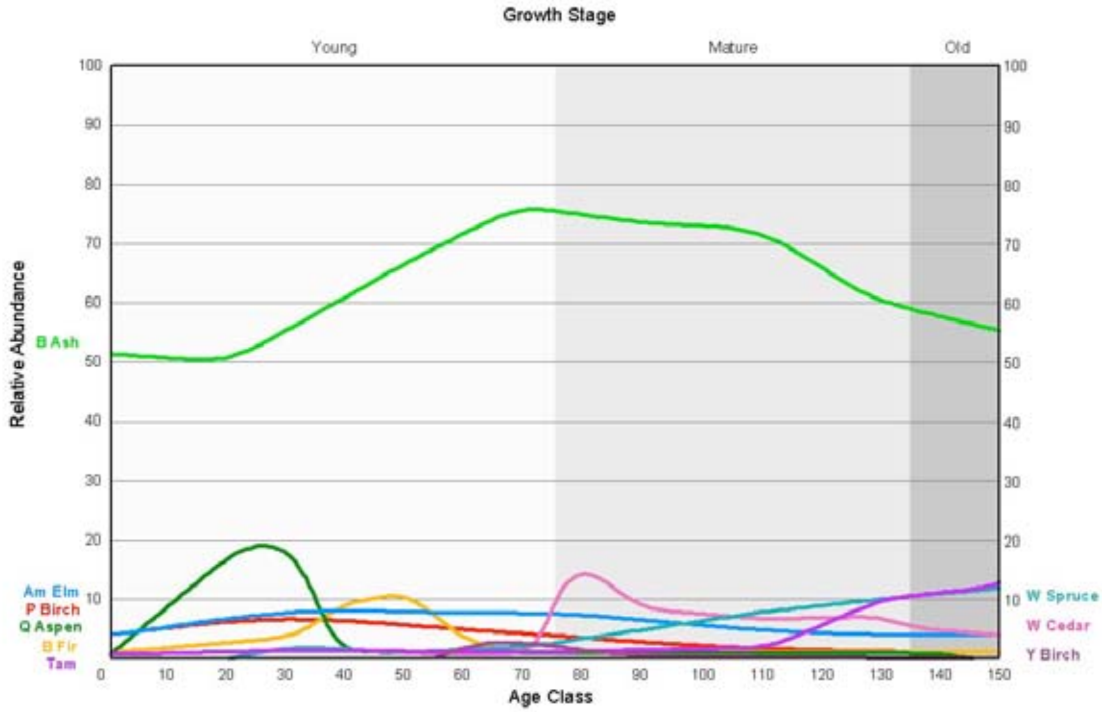
PLS-1

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 WFn64 forests, but were rare historically appear in Table **PLS/FIA-1**.

Public Land Survey linked text

(PLS-2) Abundance of trees throughout succession in WFn64

Caption: Graphed for the different species of WFn64 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 WFn64 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent WFn64 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	
Paper birch	4	11%	1	2%	2	2%	89	4%
Tamarack	3	8%	8	13%	1	1%	59	3%
White cedar	1	3%	5	8%	1	1%	118	5%
Red maple	0	0%	1	2%	0	0%	12	1%
Black ash	27	75%	46	73%	92	87%	1750	78%
Quaking aspen	0	0%	0	0%	4	4%	37	2%
American elm	1	3%	2	3%	6	6%	152	7%
Yellow birch	0	0%	0	0%	0	0%	20	1%
Total (% of grand total, 2442)	36	1%	63	3%	106	4%	2237	92%

PLS-3

Table PLS-3 includes only trees ranked as having excellent, good, or fair suitability for WFn64 sites. Tree sums will not match the totals in the Natural Disturbance Regime text, because trees of poorer suitability were included in that analysis.

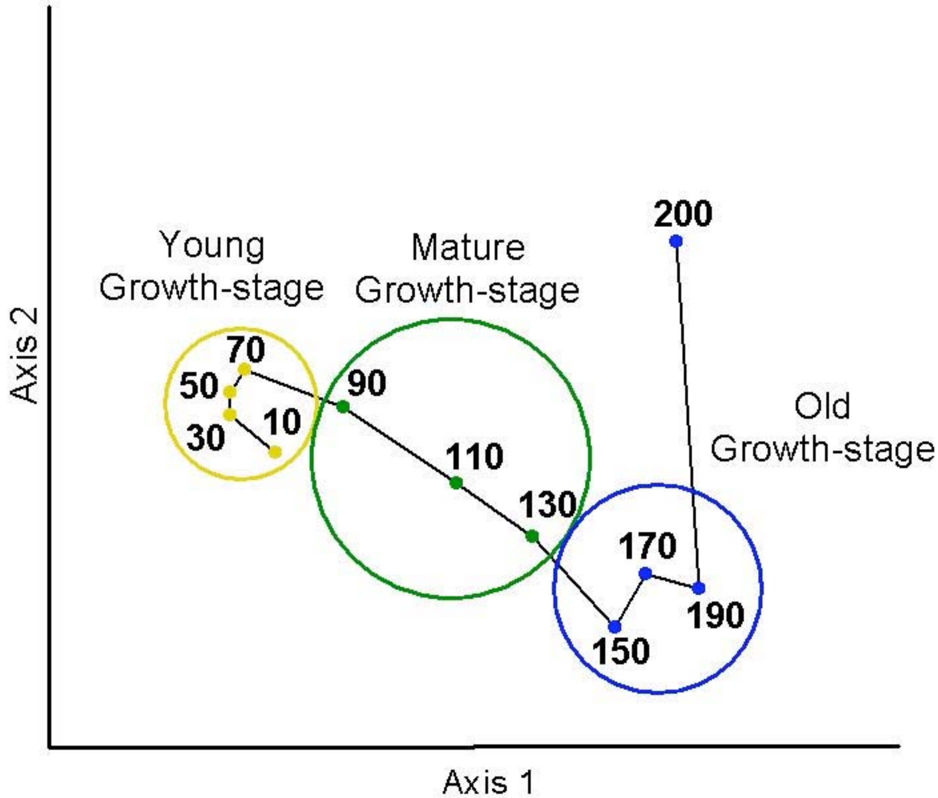
PLS survey corners were assigned to four disturbance categories:

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 WFn64 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 WFn64 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 0-70 years	G-1 70-150 years	I-1 150-190 years	G-2 >190 years
Minor	Tamarack	0-20	Good	Poor to 100	--	--
Yes	Quaking Aspen[1]	0-30	Excellent	--	--	--
Yes	Paper Birch	0-30	Good to 50	--	--	--
Yes	Balsam Fir	0-40	Good to 50	--	--	--
Yes	American Elm	0-50	Good to 60	--	--	--
Yes	Black Ash	0-70	Excellent	Fair to 100	--	--
Yes	Red Maple	30-40	Fair 30-40	--	--	--
No	Yellow Birch[2]	70	--	Poor	--	--
No	White Cedar	80	--	Fair at 80	--	--
No	White Spruce	80-120	Fair	Fair	--	--

Recruitment windows from ordination PLS-4:

- **P-D:** post-disturbance filling of understocked areas, 10-70 years
- **G-1:** gap filling during very modest decline of initial-cohort black ash, paper birch, balsam fir, and American elm, 70-150 years
- **I-1:** ingress of seedlings under canopy of black ash, white cedar, and American elm, 150-190 years
- **G-2:** gap filling during decline of black ash and some white cedar, about 190 years

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

Shading: light yellow = trees with peak regeneration immediately after disturbance; **light green** = trees with peak regeneration in gaps formed during the decline of the initial cohort

1. Quaking aspen subordinate bearing trees are extremely sparse and the data unreliable.
2. Yellow birch was not present as subordinate trees in the PLS data. The interpretation presented here is based upon FIA data for just a few trees and is unreliable.

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 WFn64 sites

This table presents an index of suitability for trees in WFn64 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 WFn64			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Black ash (Fraxinus nigra)	**78**	**44**	**5.0**
Tamarack (Larix laricina)	**9**	**21**	**4.0**
Quaking aspen (Populus tremuloides)	**12**	**16**	**4.0**
White cedar (Thuja occidentalis)	**15**	**12**	**3.9**
Yellow birch (Betula alleghaniensis)	**14**	**8**	**3.2**
Red maple (Acer rubrum)	**10**	**11**	**3.1**
Paper birch (Betula papyrifera)	**15**	**4**	**2.6**
American elm (Ulmus americana)	**7**	**8**	**2.1**
			*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 WFn64 Stands

This table presents an index of regeneration for WFn64 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 WFn64 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 Very Wet Ash Swamp – WFn64

Trees in understory	% presence R, SE, SA	R-index	SE-index	SA-index	T-index
Black ash (Fraxinus nigra)	88	5.0	5.0	5.0	5.0
Red maple (Acer rubrum)	46	3.8	3.8	3.5	2.5
American elm (Ulmus americana)	37	3.7	3.7	3.7	2.0
Paper birch (Betula papyrifera)	28	2.0	2.0	2.8	3.0
White cedar (Thuja occidentalis)	25	3.3	3.0	3.7	3.3
Yellow birch (Betula alleghaniensis)	23	3.5	3.5	4.0	3.0
Quaking aspen (Populus tremuloides)	16	2.7	2.5	3.3	3.5
Tamarack (Larix laricina)	7	2.3	1.8	1.7	3.5

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

% presence: the percent of 123 WFn64 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 WFn64 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples WFn64 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
Tamarack	3		33%		33%		33%
Paper birch	84	48%	5%	2%	11%	5%	30%
White cedar	271	2%	19%	5%	20%	4%	51%
Quaking aspen	134	9%	25%	8%	8%	10%	40%
Red maple	21		14%	14%	24%	19%	29%
Black ash	1424	8%	20%	15%	22%	19%	16%
Yellow birch	11			18%		18%	64%
American elm	37	8%	11%	38%	8%	22%	14%

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 WFn64 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 WFn64 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 - 75		~75	75 - 135		~135	> 135	
	Young			Mature			Old	
Balsam Fir	6%	16%		1%	12%		2%	16%
Paper Birch	4%	4%		3%	5%		3%	4%
American Elm	6%	6%		5%	7%		6%	4%
Black Ash	72%	55%		71%	56%		56%	36%
White Cedar	1%	1%		8%	7%		4%	31%
Tamarack	1%	0%		2%	0%		12%	0%
White Spruce	1%	1%		5%	1%		13%	1%
Balsam Poplar	1%	8%		--	4%		0%	1%
Quaking Aspen	2%	6%		1%	4%		--	3%
Yellow Birch	1%	0%		1%	1%		--	1%
Red Maple	1%	1%		1%	--		1%	0%
Miscellaneous	6%	3%		4%	4%		4%	4%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	55%	51%		35%	40%		10%	9%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 1,113 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 1,831 FIA subplots that were modeled to be WFn64 sites.

Public Land Survey linked text
FIA linked text

Silviculture Systems for WFn64: 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										
Black Ash	Large-gap (small-gap)										
Tamarack	Open (large-gap)										
Quaking Aspen	Open										
N. White Cedar	Large-gap										
Yellow Birch	Large-gap										
Red Maple	Large-gap (small-gap)										

Forest Health

Tamarack

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Water table fluctuations	"	Predispose to mortality
Larch casebearer	Seedlings and saplings	"
Larch sawfly	Saplings and larger	"
E. Larch beetle	Pole-sized and larger	Mortality
Stem decay	"	Volume loss

WATCHOUTS!

∞ Natural or induced water table fluctuations can predispose tamaracks to mortality, usually caused by larch beetle.

∞ Prolonged defoliation by larch casebearer or larch sawfly can also predispose tamarack to mortality.

∞ Presalvage/ salvage stands if larch beetles are causing mortality because, once established, they rapidly spread to both weakened and healthy trees.

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

Quaking Aspen

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

WATCHOUTS!

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

∞ Harvest during the winter to ensure adequate regeneration.

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

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

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

Northern 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.

Yellow Birch

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

WATCHOUTS!

∞ Encourage and preserve all yellow birch regeneration. Consider retaining yellow birch during partial harvests to ensure a local seed source.

∞ 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.

∞ 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.

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.

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