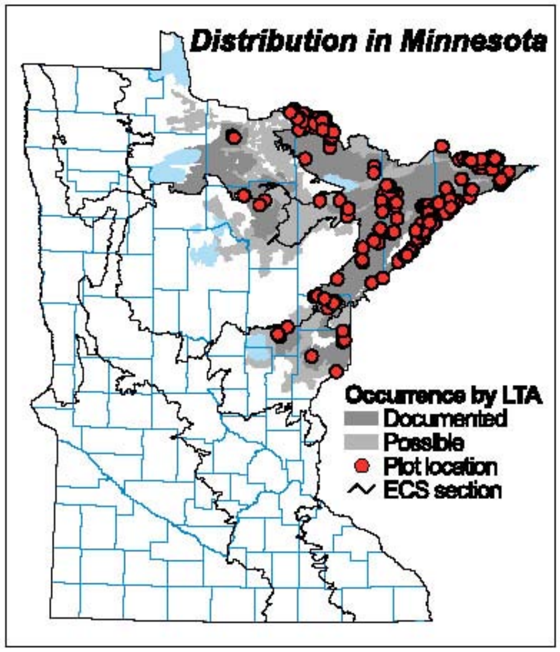
FDn43

FDn43 – Northern Mesic Mixed Forest

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Introduction and Management Highlights

Northern Mesic Mixed Forests (FDn43) are a widespread fire-dependent community found mostly within the Northern Superior Uplands and having outliers in the adjacent portions of the Minnesota Drift and Lake Plains, Western Superior Uplands, and Northern Minnesota & Ontario Peatlands ecological Sections of Minnesota. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.



The range of FDn43 forests in Minnesota (shaded) and distribution of releve samples (red dots).

Commercial Trees

As a commercial forest, FDn43 sites offer a wide selection of crop trees. Paper birch, white pine, quaking aspen, red pine, northern white cedar, balsam fir, and white spruce are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on FDn43 sites (see Suitability Tables). Red maple is ranked as a good crop tree, and stands could be managed to perpetuate red maple as a co-dominant.

Except for red maple, all of these species are native and have occupied FDn43 sites **(PLS/FIA-1)** for a long time. All were provided with the opportunity through successive generations to adapt to physical conditions typical of FDn43 sites. The consequence of fire suppression, commercial logging, and settlement in the past century has been to promote much more quaking aspen, and balsam fir than was usual. Past history and land use as also encouraged the ingress of species that were not significant in native FDn43 stands such as red maple. The increased abundance of red maple now complicates our interpretations and the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

The historic FDn43 landscape presented a rather balanced and full successional spectrum of these forests. About 17% of these sites were young and recovering from stand-regenerating fire. At this time, crown fires and severe surface fires left a rather clean, mineral-soil slate for tree establishment. Because of the topographic relief and soil variation typical of the FDn43 landscape, clear-cutting with reserves best matches best our impression of natural fires and skips. Jack pine, red pine, quaking aspen, and paper birch are the species with open regeneration strategies able to succeed following clear-cutting with reserves.

Nearly 30% of the historic FDn43 landscape were stands transitioning between the young and mature growth-stages. At this time the decline of initial-cohort quaking aspen and a burst of balsam fir regeneration were causing succession. Large-gap strategists like white pine and paper birch where the species to make the most of gaps in the canopy of initial-cohort aspen. Patch cutting and variants of shelterwooding would create similar canopy conditions where we would predict success for paper birch regeneration. Sheleterwooding and group selection would create the large-to-small gaps that were used by white pine. Alternatively, balsam fir totally occupied gaps in the aspen canopy. We do not understand the ecological significance of this event, yet it was common on FDn43 sites and characteristic of other communities located throughout the Northern Superior Uplands. Rarely did this event result in the production of fir timber as most died before reaching pole-size. Its indirect effect seems to be that of a natural herbicide, creating understory conditions that favored the ingress of white spruce and possibly white cedar and white pine. Fir “pulses” moved stands towards conifer domination. There are no removal systems that mimic this event, rather it might be an observable signal that underplantings of white spruce (white cedar and white pine?) might succeed with little or no further silvicultural manipulation.

Most, 31%, of the historic FDn43 landscape was mature FDn43 forest. This was a period of rather stable conditions where paper birch and perhaps red pine dominated these sites. This episode was a period where these trees were vigorous and not likely to senesce until stands approached the 100-year age-class. Silviculturally, the paper birch and red pine in these stands likely experienced some crown-release as the vestiges of initial-cohort aspen continued to die. For stands with vigorous, well-formed birch and red pine, this period might be an opportunity for crown release and production of large-diameter, high-quality trees. Also it is clear that in the groundlayer, white pine was the species to benefit most from the continued loss of initial-cohort aspen. Group selection and variants of shelterwooding would best approximate the small-to-large canopy gaps favoring establishment and recruitment of white pine in mature FDn43 stands.

The second transition, and second transitions in general, are hard to interpret because there is no reason to suppose synchronous mortality of one species and replacement by another. Most likely, they are caused by things like the gradual accumulation of duff, formation of secondary strata, or chronic disease rather than the more punctuated demise of an initial-cohort of short-lived trees. In the case of FDn43 forests, this transition is initiated by a pulse of northern white cedar recruitment, possibly in response to single-tree gaps as individual paper birch died at the start of the transition. Harvesting strategies aimed at capturing overmature paper birch and perhaps red pine would best fit the natural process. This seems to have been an extended event that created mostly small, individual-tree or several-tree gaps. Silvicultural systems most like this are the variants of selective harvesting, and trees with some small-gap ability like white spruce, white pine, northern white cedar, balsam fir, and red maple should respond positively.

An amazing amount of FDn43 sites were estimated to be older than 115 years (16%). At this time the continued demise of paper birch and individual mortality of some long-lived conifers created single-tree gaps that favored recruitment of white spruce, white pine, northern white cedar, balsam fir, and red maple. Variants of selective harvesting would be most appropriate for maintaining FDn43 stands in this condition.

Management Concerns
FDn43 communities occur mostly on stony, sandy loam till overlying the scoured bedrock terrain of northeastern Minnesota. Soil compaction is a concern; however, the stones can lend structural strength for heavy equipment. Because the till is dense and compact, it can perch water and may require long drying times in the spring and after storms. Rutting is less a concern because of the stones and generally good drainage. FDn43 forests are also common on stagnation moraines. In that setting, they occur on sandy loam till that is quite similar to that of the scoured bedrock landscape. The concern for compaction and rutting is similar. On the stagnation moraines, the soils are more variable spatially, and field investigation will generally reveal coarser-textured and better drained areas, which are the preferred skidding and landing. Occasionally, FDn43 forests occur on sandy and gravelly outwash. In that case, there is little risk of compaction or rutting.

The landscape balance of young and transitioning FDn43 forests <55 years old today is similar to its historic condition **(PLS/FIA-1)**. Mature stands 55-95 years old are a bit more common today than they were historically. Second transition and old FDn43 stands >95 years old have been lost to the mature growth-stage of modern forests. The primary reason for this is that the large-diameter, long-lived conifers that contributed most to survey corners older than 95 years are essentially gone from today’s forests. Most striking is the loss of white pine in the mature growth-stage where it once accounted for 24% of the trees 55-95 years old, and now it represents just 1% of the FIA trees. The even mixture of white pine and white spruce that characterized old native FDn43 forests accounted for 56% of all the bearing trees, and today they represent just 5%. Northern white cedar makes up a higher percentage of trees in today’s old forests, but there is much less old forest in general. Also, there is no evidence of young cedars on these sites as they are absent from FIA plots in stands younger than 95 years. Historically, jack pine was an important post-fire tree on these sites, and no jack pines were recorded on the FIA plots. We believe that the loss of these conifers is linked to their exploitation followed by poor regeneration and general lack of attention. Logging operations have not approximated the beneficial effects of intense fire for regenerating the pines. Severe fires are needed to prepare suitable pine seedbeds on sites this mesic. All of the pines would benefit from silvicultural attention and prescribed fire. Just getting some white pine seed trees back on the landscape would be a sensible, first-step to restore the natural composition of mature FDn43 forest. The link between fire and white spruce is less obvious. Our best guess is that the lack of fire has resulted in much greater abundance of balsam fir, especially in the young growth-stage. Historically fire eliminated balsam fir of all sizes. Fir had to invade 40-50 year-old native stands, whereas it is now it has constant presence as a tree. Fir trees come with an even larger bank of seedlings and saplings in the understory. The density of fir, much of it non-commercial, has reached population levels where spruce budworm outbreaks are common if not chronic. These outbreaks may explain the diminished success of white spruce. Silvicultural strategies aimed at the pines or white spruce should probably include a plan to kill or substantially reduce balsam fir on FDn43 sites. Commercial exploitation and lack of white cedar regeneration has long been a management concern across the FDn43 landscape. There is no obvious connection between cedar regeneration and the lack of fire; however, ring-counts often show punctuated cedar establishment as if responding to an event like fire. For now, we do not understand why cedar ingress tends to be rapid or why FDn43 stands about 80-100 years old are particularly receptive. Cedar pulses are an empirical phenomenon that the FDn43 community shares with other communities where cedar is a component. Understanding this is a research need for restoring white cedar.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 11,725 corners within the primary range of the FDn43 community. At these corners, there were 30,194 trees one commonly finds in FDn43 forests.

Natural Rotations of Disturbance in FDn43 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**220 years**
Catastrophic windthrow photograph	**2,790 years**
Partial Canopy Loss, photograph	**260 years**

The PLS field notes described about 7% of the FDn43 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands with some references to post-fire thickets. From these data, a rotation of 220 years was calculated for stand-replacing fire.

Elsewhere in the FDn43 landscape, the surveyors described lands as windthrown and lacking suitable-sized trees for scribing. Such corners were encountered at about 1% of the time, yielding an estimated rotation of 2,790 years for windthrow.

Far more common at FDn43 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, or scattered timber with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked pine-hardwood forests. About 2% of the survey corners were described as such, resulting in a calculated rotation of 260 years for disturbances that maintained early and mid-successional trees on FDn43 sites. That more corners were described as burned (710) compared to windthrown (63) suggests that surface fires were the more prevalent cause of partial canopy loss.

Compared to other northern fire-dependent communities (FDn) communities in Minnesota, FDn43 rotations of catastrophic disturbance are similar in that they exceed the longevity of most initial cohort species. This means that natural stand dynamics will usually involve a few generations of trees and a shift from large regeneration gaps to smaller ones. The rotation of 220 years for stand-replacement fire and the rotation of 260 years for maintenance surface fires are the longest for any FD community in Minnesota. This is also the only FD community in the state that we consider to be mesic by virtue of the moisture-demanding understory plants and loamy soils. Mesic site conditions, long winters, and persistent snowpack suggest to us that the probability of spring fires is significantly reduced and that contributed to our long estimates of fire rotation. The region though, supported mostly coniferous forest and is susceptible to summer and fall drought. These conditions allowed for extremely hot and damaging fire when it eventually occurred. The near absence of mesic trees like sugar maple and basswood throughout the range of FDn43 is testimony to the effectiveness of fire in this community.

Natural Stand Dynamics & Growth-stages

Views and Summaries for MHc26 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.

Following stand-regenerating fire or very rarely windstorms, the overall pattern of compositional change in FDn43 communities is for lots if initial change, which then decelerates as the stand becomes older **(PLS-4)**. This pattern is common for communities where fire favors one or two pioneer species and is capable of eliminating late-successional species sensitive to fire. For FDn43, jack pine and quaking aspen are the species that benefit greatly from fire because they compete poorly with later-successional species ... first losing ground to paper birch and white pine and ultimately to fire-sensitive species like white spruce, northern white cedar, and balsam fir.

The FDn43 community is true forest. Early in its development it achieves high tree densities that vary little throughout the course of stand maturation. From their inception through the old growth-stage, the mean distances to bearing trees are between 20 and 22 feet for any growth-stage. The variances of these means are small, meaning that the FDn43 community was not at all patchy or showed much spatial difference in structure.

Young Growth-stage: approximately 0-35 years

About 17% of the FDn43 landscape in pre-settlement times was covered by forests estimated to be under 35 years old **(PLS-1)**. Stands in this stage were more often mixed than monotypic, which is typical of fire-dependent communities like FDn43 that occur on rugged topography. Monotypic conditions were represented mostly by survey corners where all bearing trees were quaking aspen. At survey corners with mixed composition, aspen was still the most cited species, but jack pine and paper birch were common as well. In describing young, burned stands the surveyors indicated that in addition to quaking aspen, jack pine, and paper birch, the initial-cohort included white and red pine as well.

Surprisingly, the surveyors used some fire-sensitive trees such as balsam fir, white spruce, and northern white cedar as bearing trees at corners they described as burned. Together these species accounted for 13% of the bearing trees at "burned" corners **(PLS-3)**. This suggests rather strongly that fires left an unexpected amount of legacy conifers. It is probably significant that these conifers tend to have higher presence in wetter habitats that occur throughout the bedrock-controlled FDn43 landscape as included drains, basins, and lakeshores. If wetter habitat was responsible for skips within burns, then one expects survey corners to pick up at least a few of these trees.

Young stands recovering from windthrow were negligible and wind had no differential effect on composition in comparison to fire that can't be attributed to chance **(PLS-3)**.

The ability of quaking aspen to dominate young FDn43 forests is a consequence of its persistence in the mature and old growth-stages. For a pioneer species, quaking aspen shows surprisingly good success in maintaining a presence in older forests by establishing seedlings or suckers and recruiting some to mid- and full-canopy heights **(R-2)**. Apparently quaking aspen was successful enough at maintaining clone rootstocks and scattered seed trees so that they could rapidly repopulate burned areas, even if the burned stand had reached the older growth-stages.

Other initial-cohort trees like jack pine, red pine, white pine, and paper birch also maintained a significant presence in older stands and were prepared to re-colonize following fires. White pine and paper birch are similar to quaking aspen in that regeneration and recruitment in the older growth-stages seems possible. For red and especially jack pine, which show little establishment in mature stands **(R-2)**, their persistence in older forests must be attributed to their longevity on FDn43 sites.

Transitional Stage: approximately 35-55 years

About 30% of the historic FDn43 landscape was forest undergoing considerable compositional change as stands approached maturity **(PLS-1)**. Stands in this stage were more often mixed than monotypic. Monotypic conditions were represented mostly by survey corners where all bearing trees were quaking aspen, and much less often by paper birch and balsam fir. At survey corners with mixed composition, quaking aspen was still the most cited species and it was mixed most often with paper birch, balsam fir, and jack pine.

The transition stage is driven almost entirely by the behavior of quaking aspen and balsam fir. Initial-cohort quaking aspen decline throughout the period **(PLS-2)**. Aspen's plummet of 42% relative abundance between the 30- and 40-year age classes is nearly mirrored by a 29% rise in balsam fir. Because quaking aspen are not short-lived or senescent at 30 years on mesic habitats, it is exceeding tempting to suspect that balsam fir in some way was the causal agent in aspen decline rather than a benign benefactor of openings beneath dead aspen. Curiously, just as it seems that 50-year old FDn43 stands were well on their way to the "spruce-fir climax," the relative abundance of fir collapses to lower levels (~10% relative abundance) that we often see maintained into old-growth. It is highly unusual for trees to peak strongly and decline within compositional transitions, creating significant movement within the ordination **(PLS-4)** but not across growth-stages **(PLS-1)**. The notion that balsam fir in any way "prepares" sites for paper birch and long-lived conifers, only to altruistically "step aside" has no basis in ecological theory. Nonetheless, the pulse of fir abundance in the first transition stage is observed in most terrestrial forests of the northern floristic region of the state where succession is towards white spruce, white cedar, or white pine rather than sugar maple. On FDn43 sites the effect of the fir pulse is to promote recruitment and regeneration opportunities for paper birch and white pine. It seems also that this event is tied to the initial ingress of white spruce and white cedar as well.

Mature Growth-stage: approximately 55-95 years

About 31% of the historic FDn43 landscape was mature forest where the rate of successional change slowed slightly **(PLS-4)**. Stands in this stage were far more likely to be mixed than monotypic. Patches of pure aspen or pure paper birch were most common, but there were patches of solid red and white pine as well. About 60% of the mixed corners were combinations of quaking aspen, paper birch, balsam fir, or white pine.

The mature growth-stage of FDn43 forests represents an extended, mid-successional period. It is perceived as a stable episode mostly because the dominant, paper birch, shows little change in relative abundance **(PLS-2)**. There was considerable change going on, but it occurred mostly in the understory. In general, this period marks the end of significant regeneration opportunities for most early-successional trees and marks the beginning of white spruce and white cedar regeneration starting roughly in the 60-year age-class of the G-1 window **(PLS-5)**.

For the initial-cohort of quaking aspen, jack pine, paper birch, and red pine, the best opportunity for establishment was immediately after a fire. However, young individuals were observed until the beginning (~60 years) of the mature growth-stage. For red and jack pine, we believe that individuals established at this late time were the ones to persist into the older growth-stages and it is testimony to their longevity on FDn43 sites. For paper birch, white pine, and balsam fir the first years of the mature growth-stage offered good opportunities for regeneration, but that opportunity seemed to end by about 80 years. For white pine, we believe that this was the conclusion of good regeneration opportunities and that longevity carried it through the older growth-stages. Birch and fir, however, carry through older growth-stages most often as smaller trees, that just didn't meet our half-diameter rule for considering them as regeneration beyond 60-70 years (PLS-5). We believe these trees persisted due to modest regeneration throughout the mature growth-stage and into older stages.

Second Transition Stage: approximately 95-115 years
About 6% of the historic FDn43 landscape was forest undergoing considerable compositional change as it approached old age (PLS-1). Stands in this stage were almost always of mixed composition. Monotypic conditions were represented mostly by survey corners where all bearing trees were paper birch, and sometimes white or red pine. At this time, most of the FDn43 trees could occur at mixed survey corners. The combinations included remaining initial cohort-trees as well as the late-successional species like white spruce, white pine, white cedar, and balsam fir.

The second transition was driven mostly by the behavior of paper birch, because it was the most abundant tree. Paper birch that peaked during the mature growth-stage were in decline throughout the period (PLS-2). Conifers with at least some shade tolerance benefited most from the decline of birch. From a landscape perspective, white spruce seems to be the species with the strongest response, increasing in relative abundance from just 4% in the mature growth-stage to 28% in the old growth-stage. When one looks at individual survey corners though, spruce was making most progress coming through pine and aspen more so than under declining birch. White pine, balsam fir, and even some young paper birch were the species making the most of the birch decline at the scale of individual survey corners. A pulse of white cedar abundance at about 80-100 years also contributed to compositional movement in the ordination (PLS-4). This pulse is much like that of balsam fir in the first transition, but shorter and at lower abundance. Such pulses, peaking at about age 90, are observed in other northern forests where cedar is an important late-successional tree.

Old Growth-stage: approximately >115 years
About 16% of the historic FDn43 landscape was old forest (PLS-1). Because FDn43 is common and widespread in northeastern Minnesota, 16% in the old growth-stage represented extensive acreage. Stands in this stage were rarely monotypic. Monotypic conditions were represented mostly by survey corners where all trees were white pine. Mixtures of paper birch, white pine, and white spruce were most common, but even at this late stage there were still some corners that were mixtures of early-successional trees such as jack pine, quaking aspen, and red pine.

Succession to the point where pines are replaced with fire-sensitive white spruce, balsam fir, and white cedar is a property of northern fire-dependent forests (FDn) in contrast to those of the central floristic region (FDc) which share the same pine cover-types but not the fire-sensitive species. Although it is true that FDn forest have longer rotations of catastrophic fires, it was the relentless frequency of surface fires in FDc forests that eliminated the possibility of succession to white spruce, balsam fir, and white cedar. The direct, detrimental effect of fire on these species is well known, but we believe that elimination of organic seedbeds was equally important as it seems to effectively stop regeneration of these species. This was especially important on FDn43 sites as they were the most mesic of FDn communities. The thickness of the mor humus typical of old FDn43 sites is commonly 5" to as much as 10" thick on islands and other sites naturally protected from fire. Our interpretation is that the accumulation of duff and perhaps nurse logs played an important role in promoting succession on FDn43 sites and such humus layers characterize the old growth-stage.

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?

Paper Birch

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

Suitability

FDn43 sites provide ***excellent habitat*** for paper birch trees. The ***suitability rating*** of 4.8 for paper birch is influenced mostly by its high presence (69%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is an important co-dominant and sometimes dominant tree, contributing 18% mean cover in mature stands. The ranking is nearly perfect, tied with white pine on FDn43 sites as sampled by releves. Except for FDn12, northern fire-dependent forests offer good-to-excellent habitat for paper birch (see Suitability Tables). Among these, the richer and moister FDn33 and FDn43 communities provide the best commercial opportunities for paper birch.

Young Growth-stage: 0-35 years

Historically, paper birch was an occasional tree in young FDn43 stands recovering from fire **(PLS-1)**. Young paper birch represented 21% of the trees at survey corners described as burned, second only to quaking aspen and white pine **(PLS-3)**. Our interpretation is that this percentage is too high if birch was relying solely on stump sprouts for regeneration. It seems likely that sprouting and seeding were both viable regeneration strategies for paper birch in the post-fire environment. Young birch trees responded similarly to windthrow, representing 25% of the trees at windthrown survey corners. Windthrow, however, was rare and not an important means of regenerating trees on FDn43 sites. Because paper birch increases during the young growth-stage **(PLS-2)** we believe that it had some ability to recruit into under-stocked areas of burned stands. Small-diameter paper birch regeneration was abundant following disturbance until the 40-year age-class **(PLS-5)**. Because paper birch was clearly an important initial-cohort tree and because its primary window of establishment was immediate after disturbance, we believe that it was able to function as an ***early-successional*** tree on FDn43 sites.

Transition: 35-55 years

As stands transitioned to mature conditions paper birch increased in abundance, presumably because of its ability to outlive initial cohort aspen **(PLS-1, PLS-2)**. More likely is the idea that paper birch survived, more so than aspen, the pulse of balsam fir regeneration during the transition stage (see Stand Dynamics). Throughout northern Minnesota, paper birch was historically more associated with conifers than with other hardwoods. In contrast, aspen was positively associated with hardwoods, especially oak. Paper birch had good recruitment in the G-1 gap window that spans the transition stage **(PLS-5)**. More than half of the bearing tree regeneration coming in below larger trees during the transition were paper birch, suggesting some increase in abundance due to recruitment. It is most likely that paper birch was reacting to openings created as the initial-cohort died. This is supported by the fact that nearly all of the smaller birch were coming in under aspen, jack pine, and other birch. The fir pulse might have helped create opportunities for paper birch regeneration, but it was not the role of a nurse crop as birch mostly overtopped fir at corners where they were both present.

Mature Growth-stage: 55-95 years

Paper birch had peak abundance as a co-dominant in mixed mature stands, which is why we consider birch a ***mid-successional*** species – able to replace initial cohort trees but dropping in relative abundance as stands aged **(PLS-1, PLS-2)**. Subordinate birch were present at the beginning of the mature growth-stage, but occurred only rarely after age 70 **(PLS-5)**. We interpret this as modest, but continued success of recruiting seed-origin trees under declining initial-cohort trees. At this stage paper birch occurred mostly at survey corners with mixed composition, and it still was more often the subordinate tree when mixed with initial-cohort quaking aspen, jack pine, and red pine. About 7% of the mature survey corners had all paper birch bearing trees, and the diameter variation among those trees would suggest that it could replace itself.

Second Transition: 95-115 years
As stands transitioned to old conditions paper birch decreased in abundance, more so than other species **(PLS-1, PLS-2)**. We interpret this as the natural senescence of initial-cohort paper birch and probably the trees that were established in the young growth-stage. Because paper birch had some success recruiting young trees during the mature growth-stage, it still was an important tree. This transition marks the point though where birch is no longer dominant. There was no small-diameter paper birch regeneration beyond the 70-year age-class **(PLS-5)**, which is why we believe there was limited recruitment during the second transition. During this stage birch was more often the largest tree at survey corners, but it was still common at subordinate diameters. When the smaller tree, it was mostly replacing itself in what must have been old pockets of pure birch.

Old Growth-stage: >115 years
Paper birch persisted in the old growth-stage **(PLS-1, PLS-2)**. If persistence requires regeneration and recruitment, then we must assume that paper birch has secondary strategies that make it able to respond to fine-scale or maintenance disturbances. The ability of paper birch to establish and recruit seedlings through all height strata in modern FDn43 forests suggests that it can persist under a regime of fine-scale disturbance on such sites **(R-2)**. However, the indices for germinants and seedlings are more in line with species that require somewhat larger openings. Surface fires might also explain the persistence of paper birch into the old growth-stage because it did well after stand regenerating fire. This seems highly unlikely though because the common condition in the old-growth stage was for paper birch to co-occur with fire-sensitive species like fir and white spruce. We suspect that other maintenance disturbances such as pocket-diseases created the few-tree gaps where paper birch is successful in modern forests.

Regeneration Strategies
FDn43 sites are such good habitat for paper birch that it is an important or dominant tree throughout the course of a long succession. It is clear that birch has multiple strategies for regeneration and survival, and that those strategies were successful in all growth-stages. Birch achieved dominance by using it's primary regenerative strategy of filling ***large-gaps***. It was most successful at this when the gaps were forming within a declining canopy of quaking aspen and to some extent jack pine and other paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that paper birch abundance peaks in response to the decline of the initial cohort species **(PLS-1, PLS-2)**, (2) it is abundant at survey corners showing partial canopy loss **(PLS-3)**, and it has good establishment in a gap window **(PLS-5)**. The high percent of paper birch poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate best in large gaps. In the releve data paper birch has high presence in the understory and shows good ability to establish and recruit seedlings **(R-2)**. The index values of 3.3 to 4.5 in the regenerating layer are most in line with species that do well in large-gaps.

Paper birch was also able regenerate and sometimes dominate ***open habitat*** after stand-regenerating fires. We believe that the initial cohort of young birch was composed of both stump sprouts and seed-origin trees. Birch's regenerative ability after fire is evident in the PLS data by: (1) its high relative abundance in young stands **(PLS-1)**, its high presence at burned survey corners **(PLS-3)**, and its peak regeneration in the post-disturbance window and with it's absolute peak being the initial age-class **(PLS-5)**. Paper birch also has high presence in the canopy of young, post-logging pole stands (situation 22), which is typical of trees that do well in the open **(FIA-1)**.

Historic Change in Abundance
Today, paper birch remains an important and often dominant tree on FDn43 sites **(PLS/FIA-1)**. Modern stands have significantly less paper birch than they did historically. Most likely, this is the consequence of logging not providing the seeding opportunities for birch as did fire. The lack of paper birch regeneration in the young growth-stage is probably the reason that mature forests are no longer dominated by paper birch. Aspen, now plays a much greater role. Modern old forests have birch in similar abundance as they did in the past.

White Pine

- ***excellent habitat suitability rating***
- ***mid- (late) successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 20-50 years***

Suitability

FDn43 sites provide ***excellent habitat*** for white pine trees. The ***suitability rating*** of 4.8 for white pine is influenced mostly by its presence (39%) as trees on these sites in modern forests **(R-1)**. When present, white pine is an important co-dominant and sometimes dominant tree, contributing 26% mean cover in mature stands. The ranking is nearly perfect, tied with paper birch on FDn43 sites as sampled by releves. Except for FDn12, northern fire-dependent forests offer excellent habitat for white pine (see Suitability Tables). Among these FDn43 provides the best commercial opportunity for white pine.

Young Growth-stage: 0-35 years

Historically, white pine was a minor tree in young FDn43 stands **(PLS-1, PLS-2)**. Young white pines represented 25% of the trees at survey corners described as burned, second only to quaking aspen **(PLS-3)**. Our interpretation is that some white pines got their start on FDn43 sites by seeding on mineral soil exposed by hot fires. White pines represented 17% of the trees at corners affected by stand-regenerating wind. Windthrow, however, was very infrequent and was not an important means of regenerating white pine. White pine regeneration coming in among larger trees was detectable throughout the 0-30 year post-fire window **(PLS-5)**. We interpret this as white pine having fair success filling under-stocked areas of the regenerating stand. Because the abundance of white pine regeneration and trees increase substantially in the 40-year age class, it also seems likely that white pine had some success building a seedling bank under young aspen.

Transition: 35-55 years

As stands transitioned to mature conditions white pine increased in abundance **(PLS-1)**. We estimate that this increase started at low abundance following disturbance and continued throughout the successional cycle into old-growth conditions **(PLS-2)**. Small-diameter, white pine regeneration coming in among larger trees was consistently present in the 20-50 year age-classes, peaking in the first gap window **(PLS-5)**. In most cases, white pine regeneration was coming in under other white pines, meaning that fires on FDn43 sites must have provided habitat patches particularly suited to white pine that led to monotypic pockets. It was almost as common for white pine regeneration to be coming through quaking aspen. We interpret this as good success at establishment and recruitment of seed-origin white pines under a partial canopy of initial-cohort trees. Also, it seems likely that the collapse of the initial-cohort aspen released white pine seedlings established during the young growth-stage.

Mature Growth-stage: 55-95 years

In the mature growth-stage white pine becomes about as abundant as it will ever be in the course of stand maturation. Its relative abundance of 24% is second only to paper birch **(PLS-1)**. White pine's ability to decisively replace the initial-cohort trees is why we consider white pine to be a ***mid-successional*** species, although it remains important in the older growth-stages. White pine's increase in relative abundance is mostly the result of good establishment and recruitment until about age 50 **(PLS-5)** followed by high survivorship. Regeneration and recruitment following the 50-year age-class was modest, and was not detected at all beyond 80 years. In most cases, white pine regeneration was coming in under older white or red pines. Less often, young white pines were coming in beneath quaking aspen or paper birch. We interpret this as modest, but continued success of recruiting seed-origin trees under the remnants of the initial-cohort canopy and beneath trees that are less shade-tolerant than white pine.

Second Transition: 95-115 years

As stands transitioned to old conditions white pine increased slightly in abundance, presumably because of its ability to outlive the paper birch that was dominant in the mature growth-stage **(PLS-**

1). Small-diameter, white pine regeneration coming in among larger trees was not detected during this second transition stage. When white pines were the smallest tree at a survey corner, they were almost always beneath other white pines, red pines, or paper birch. It seems that there was some white pine regeneration during this transition, but only under itself or under trees less tolerant of shade than white pine.

Old Growth-stage: >115 years
In the old growth-stage white pine was and important co-dominant, occurring almost always at survey corners of mixed composition. At 28% relative abundance, it was tied with white spruce as the most common tree on old FDn43 sites (PLS-1). Normally, a tree of this importance in the old growth-stage would be considered ***late-successional***. However, we believe that white pine's presence in old stands was mostly a consequence of its longevity, as regeneration opportunities were scarce. Small-diameter, white pine regeneration coming in among larger trees was not detected during the old growth-stage. When white pines were the smallest tree at a survey corner, they were still mostly coming in only beneath other white pines or less-tolerant trees such as red pines and paper birch. Infrequently, white pine was subordinate to the obvious climax species, white spruce. In modern forests, white pine shows good ability to recruit under a canopy (R-2). Our interpretation is that white pine had some regeneration success in patches of FDn43 habitat that were not yet invaded by white spruce.

Regeneration Strategies
White pine's primary regenerative strategy on FDn43 sites is to fill ***large-gaps***. It is most successful at this beneath other white pines, but also did well when gaps formed within the declining canopy of initial-cohort quaking aspen. In the historic PLS data this interpretation is supported by: (1) the fact that white pine abundance rises sharply in response to the decline of the initial cohort species (PLS-1, PLS-2), (2) it has high abundance at survey corners showing partial canopy loss (PLS-3), and (3) it shows peak establishment in a gap window rather than post-disturbance or ingress windows (PLS-5). The high percent of white pine poles under trees (situation 23) in the FIA data (FIA-1) is also a characteristic of species that tend to regenerate best in large gaps.

The releve sampling of mature FDn43 forests suggests, however, that white pine can function to a limited extent as a ***small-gap strategist*** with good establishment and recruitment in understory strata (R-2). It is significant that the regeneration indices (3.2-3.7) are more typical of large-gap species. The lowest index was for saplings, suggesting that recruiting white pine seedlings to heights taller than 2m is a regenerative bottleneck for white pine under a canopy.

Historic Change in Abundance
Today, white pine is mostly gone from the FDn43 landscape, accounting for less than 3% of the trees at FIA subplots in any growth-stage (PLS/FIA-1). Young FIA plots recorded no white pine in a naturally regenerated forest. The releve sampling paints a slightly better picture of white pine's current status. White pine has fairly high presence as a tree (39%, R-1)) and higher presence (44%, R-2) in the understory. The releve sampling is biased, favoring ecologically intact remnants of FDn43 forests. However, the presence of white pine was not a deciding factor in plot location and most of the 203 releve plots were on sites previously logged and still available for commercial interests. Regardless of the data source, it is widely accepted that white pine populations on FDn43 sites have declined to the point where restoration efforts are warranted.

Quaking Aspen

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

Suitability
FDn43 sites provide ***excellent habitat*** for quaking aspen trees. The ***suitability rating*** of 4.7 for quaking aspen is influenced mostly by its high presence (46%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is an important co-dominant and sometimes dominant tree, contributing 21% mean cover in mature stands. The ranking is third, following paper birch and white pine on FDn43 sites as sampled by releves. As long as the soils are fairly deep (not FDn22), northern fire-dependent forests provide good-to-excellent habitat for quaking aspen (see Suitability Tables). Among these, FDn43 offers the best commercial opportunities for quaking aspen.

Young Growth-stage: 0-35 years
Historically, quaking aspen was the overwhelming dominant in young FDn43 stands recovering mostly from stand-regenerating fire **(PLS-1, PLS-2)**. Young aspen represented 26% of the trees at survey corners described as burned, which is more than any other tree **(PLS-3)**. Aspen was also the leading species following windthrow, representing 28% of the trees at such survey corners. Young FDn43 corners with quaking aspen trees present were mostly mixed in composition (73%), but often (27%) all of the bearing trees were quaking aspen. Its dominance in the young growth-stage and its leading abundance following fire and windthrow is why we consider quaking aspen to be an ***early successional*** species on FDn43 sites. Small-diameter, quaking aspen regeneration was most often observed coming in among larger trees in the 0-30 year post-disturbance window **(PLS-5)**. This is typical of early successional species, and we interpret this as quaking aspen showing excellent ability to recruit into under-stocked areas of burned stands. The presence of smaller diameter aspen could be due natural variation among suckers that are more-or-less connected to parent rootstocks, but it is more likely that seed-origin trees were the smaller ones filling in among the suckers.

Transition: 35-55 years
Transitioning of young FDn43 forests was driven in-part by the steady loss of initial-cohort quaking aspen leaving longer-lived paper birch and red pine **(PLS-1)**. We estimate that this decline started immediately due to self-thinning, and continued during the entire process of stand maturation as it was out-competed in older growth-stages **(PLS-2)**. Small-diameter aspen regeneration was detectable throughout the transition up until age 60 **(PLS-5)**. In most cases quaking aspen regeneration was coming in under older aspen, but there was also some regeneration beneath jack pine. We interpret this as limited replacement of itself in large-gaps as some of the initial-cohort aspen started to senesce. During the transition period, aspen was present at most survey corners and about 16% were still pure aspen. It is possible that some quaking aspen establishment and recruitment to bearing-tree size (~4" dbh) was the consequence of it being the only species present in monotypic pockets.

Mature Growth-stage: 55-95 years
In mature FDn43 stands the relative abundance of aspen was just 12% and was continuing to decline **(PLS-1, PLS-2)**. We attribute most of the presence of quaking aspen in the mature growth-stage to longevity of initial-cohort trees in a mesic habitat. Small-diameter quaking aspen regeneration coming in among larger trees was detected only in the 60-year age-class of the mature growth-stage **(PLS-5)**. When present, quaking aspen regeneration was mostly coming in under older aspen, but there was also limited regeneration under jack, red, and white pine. The ability of aspen to recruit seedlings or suckers through all height strata in modern FDn43 forests is surprising, suggesting that it can persist under a regime of fine-scale disturbance on FDn43 sites **(R-2)**. Its regeneration indices (4.2-4.3) are quite in line with species able to regenerate in ***small gaps***. Apparently modern forests are somehow different and quaking aspen is now able to

express some behavior typical of small-gap strategists. Most obvious is the fact that modern stands in the mature growth-stage are 52% quaking aspen compared to just 12% in the historic data **(PLS/FIA-1)**. Our interpretation is that quaking aspen is successful replacing itself in response to fine-scale disturbance, especially when other species are not present on the site.

Second Transition: 95-115 years
As stands transitioned to old conditions the relative abundance of quaking aspen continued to decline **(PLS-1, PLS-2)**. At this stage, most aspen bearing trees were at survey corners of mixed composition, and for the first time it was often mixed with balsam fir and white spruce. Our interpretation is that quaking aspen was declining because it was being replaced by more competitive shade-tolerant conifers. Small-diameter quaking aspen regeneration coming in among larger trees was not detected during this second transition stage **(PLS-5)**. When aspen were the smallest trees at survey corners, they were almost always beneath older aspen or white pine. It seems to us that there was some aspen regeneration during this transition, but only under itself or under trees less tolerant of shade than quaking aspen.

Old Growth-stage: >115 years
In the old growth-stage quaking aspen was a minor co-dominant **(PLS-1,PLS-2)**, occurring almost always at survey corners of mixed composition. At this stage quaking aspen was most often mixed with white spruce or other shade-tolerant trees likely to replace it, including some mesic hardwoods. There is little evidence that the persistence of quaking aspen in the old growth-stage was the result of regeneration and recruitment. Small-diameter quaking aspen regeneration coming in among larger trees was not detected during the old growth-stage **(PLS-5)**. When aspen were the smallest trees at survey corners, they were mostly overtopped by white spruce or white pine. There were still a few situations where smaller-diameter aspen were present with other aspen and the last remnants of initial-cohort jack pine. Our interpretation is that the fires characteristic of FDn43 sites must have created some severely burned patches where early-successional trees were dominant and could replace themselves until the sites were ultimately invaded by shade-tolerant trees like balsam fir and white spruce.

Regeneration Strategies
Quaking aspen's primary regenerative strategy on MHc26 sites is to dominate ***open habitat*** after stand-regenerating fires. In the historic PLS data this interpretation is supported by: (1) the fact that 60% of the bearing trees in young stands were quaking aspen **(PLS-1)**, (2) aspen represented the largest proportion of bearing trees at burned and windthrown corners **(PLS-3)**, and (3) aspen's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. The high percent of quaking aspen as initial-cohort trees in young forests (situations 11 and 22) in the FIA data **(FIA-1)** is also characteristic of species that regenerate effectively in the open. Because quaking aspen was infrequent in older FDn43 forests, we believe that following fires, a significant component of initial-cohort aspen were seed-origin trees.

The releve sampling of mature FDn43 forests suggests, however, that quaking aspen is able to function also as a ***small-gap strategist*** with excellent establishment and recruitment in the understory strata **(R-2)**. Its regeneration indices (4.2-4.3) are most in line with small-gap strategists. Modest abundance of quaking aspen in subordinate situations (12, 23, 13) at FIA subplots support also the idea that aspen can regenerate in small gaps **(FIA-1)**. Our interpretation is that quaking aspen is so overwhelmingly abundant in modern stands, that we often see aspen replacing itself in small gaps because it is the only tree present. This is consistent with the historic data in that aspen regeneration throughout stand maturation was mostly beneath older aspen.

Historic Change in Abundance
Today, quaking aspen remains an important and often dominant tree on FDn43 sites **(PLS/FIA-1)**. Most (76%) young FDn43 stands are dominated by aspen, which is a significant increase over the historic condition where aspen accounted for 60% of the trees in young stands. The most significant departure from historic times is the overwhelming abundance of quaking aspen in the mature growth-stage where it now has 52% relative abundance compared to just 12% in the pre-settlement forest. Equally surprising is the abundance of aspen in the old growth-stage (23%) in

comparison its low abundance (5%) historically. Our interpretation is that quaking aspen has benefited greatly from logging on rotations much shorter than the natural fire cycle and the general loss of conifers on the FDn43 landscape.

Red Pine

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

Suitability
FDn43 sites provide ***excellent habitat*** for red pine trees. The ***suitability rating*** of 4.5 for red pine is a consequence of roughly equal presence (22%) and mean cover when present (26%) as trees on these sites in modern forests **(R-1)**. 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 fourth, behind paper birch, white pine, and quaking aspen. All of the northern fire-dependent forest communities offer excellent habitat for red pine (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, red pine was an occasional tree in young FDn43 stands recovering mostly from fire **(PLS-1, PLS-2)**. Young red pines represented 7% of the trees at survey corners described as burned, well behind white pine and the fire-tolerant hardwoods **(PLS-3)**. Our interpretation is that red pines were well-established after fire, but that their stem-counts were low in comparison to quaking aspen and paper birch seeding in after severe fires. Although windthrow was infrequent, red pines represented 5% of the trees at corners affected by stand-regenerating wind. This percentage is slightly less than that after fire, and it seems that windthrow offered similar opportunities for red pine regeneration in an open environment. Small-diameter red pine regeneration was most common in the post-disturbance window **(PLS-5)**, and continues well into the following transition. For this reason and because the abundance of red pine increases during the young growth-stage, we believe that it was able to recruit into under-stocked areas of burned stands and possibly establish some seedlings among initial-cohort aspen.

Transition: 35-55 years
As stands transitioned to mature conditions red pine increased in abundance, presumably because of its ability to outlive initial cohort aspen and jack pine **(PLS-1)**. We estimate that this increase started at low abundance following disturbance until it peaked at about age 90 **(PLS-2)**. Some small-diameter red pine regeneration was coming in among larger trees during the transition until about age 60 **(PLS-5)**. In most cases, red pine regeneration was coming in under other red pines and sometimes under quaking aspen or jack pine. We interpret this as fair success at establishment and recruitment of seed-origin red pines under a partial canopy of initial-cohort trees less tolerant of shade than red pine. Also, it seems likely that the collapse of the initial-cohort aspen released a suppressed bank of red pine seedlings established during the young growth-stage.

Mature Growth-stage: 55-95 years
Red pine had peak presence as a co-dominant in mixed mature stands, which is why we consider red pine a ***mid-successional*** species – able to replace or outlive initial cohort trees but dropping in relative abundance as stands aged **(PLS-1, PLS-2)**. The peak in relative abundance is mostly the result of good establishment during the young growth-stage **(PLS-5)** and excellent survival in the transition and mature growth-stage. Regeneration during the mature growth-stage was modest. Small-diameter red pine regeneration was detected only in the 60-year age-class of the mature growth-stage **(PLS-5)**. Red pine regeneration was coming in mostly under older red pines, and sometimes coming in under jack and white pine. We interpret this as modest success of recruiting seed-origin trees within distinct patches of FDn43 habitat where the post-fire environment strongly favored pines over aspen or paper birch.

Second Transition: 95-115 years
As stands transitioned to old conditions red pine decreased in abundance, presumably because initial-cohort red pines were starting to senesce **(PLS-1)**. Small-diameter red pine regeneration

coming in among larger trees was not detected during this second transition stage (PLS-5). Rarely red pines were the smallest tree at survey corners and when so, they were almost always subordinate to other red pines or paper birch. It seems to us that there was little or no regeneration of red pine during this transition, and that it persisted into during this transition and into the old growth-stage only because of its longevity.

Old Growth-stage: >115 years

In the old growth-stage red pine was a minor co-dominant, occurring almost always at survey corners of mixed composition. At 5% relative abundance, it was well behind shade tolerant trees like white spruce and balsam fir, as well mid-tolerant trees like paper birch and white pine (PLS-1). Normally, trees even of modest importance in the old growth-stage would be considered to have some properties of late-successional species. However, we believe that red pine's presence in old stands was entirely a consequence of its longevity, as regeneration opportunities were scarce. Small-diameter, red pine regeneration coming in among larger trees was not detected during the old growth-stage (PLS-5). When red pines were the smallest tree at a survey corner, they were still mostly coming in only beneath other red pines or sometimes white pine. There were no examples of smaller-diameter red pines under more shade-tolerant trees. In modern forests, red pine shows no significant ability to recruit under a canopy (R-2), strengthening further the argument that old stands would ultimately lose their red pines without disturbance.

Regeneration Strategies

Red pine's primary regenerative strategy on FDn43 sites is to establish seedlings in ***open habitat*** after stand-regenerating fire. In the historic PLS data this interpretation is supported by: (1) the fact that red pine was present as an initial-cohort tree (PLS-1), (2) red pine was among the trees at burned and windthrown corners (PLS-3), and (3) red pine'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 red pine in young modern stands (situations 11 and 22) in the FIA data is also characteristic of species that regenerate effectively in the open (FIA-1).

Nearly equal are behavioral traits that suggest red pine regenerated effectively in ***large canopy gaps***. In the historic PLS data this interpretation is supported by: (1) the fact that red pine increases in abundance as a reaction to the decline of initial-cohort aspen and jack pine (PLS-1, PLS-2), and (2) its peak presence was at survey corners showing partial canopy loss due to maintenance disturbances (PLS-3). A high percentage of red pine poles beneath trees (situation 23) is also consistent with species that do well regenerating in large gaps (FIA-1). Most detrimental to this argument is the fact that red pine shows incredibly poor ability to establish seedlings in stands sampled by releves, many of which did not show full crown closure (R-2).

Historic Change in Abundance

Today, red pine is mostly gone from the FDn43 landscape, accounting for less than 1% of the trees at FIA subplots in any growth-stage (PLS/FIA-1). Young FIA plots recorded no red pine in a naturally regenerated forest. The releve sampling paints a slightly better picture of red pine's current status. Red pine is present as a tree in 22% of the releves (R-1). The releve sampling is biased, favoring ecologically intact remnants of FDn43 forests. Its presence as regeneration in just 4% of the releves (R-2) is alarming and quite consistent with the FIA data. It is widely accepted that red pine populations on FDn43 sites have declined to the point where restoration efforts are warranted.

Northern White Cedar

- ***excellent habitat suitability ranking***
- ***mid- (late-) successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 80-100 years***

Suitability
FDn43 sites provide ***excellent habitat*** for white cedar trees. The ***suitability rating*** of 4.4 for white cedar is influenced mostly by its high mean cover when present (27%) as trees on these sites in modern forests **(R-1)**. White cedar can be an important co-dominant when present. White cedar's presence is 20% 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 fifth, following paper birch, white pine, quaking aspen, and red pine on FDn43 sites as sampled by releves. FDn43 is the only northern fire-dependent community that provides habitat for white cedar (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, white cedar was nearly absent in young FDn43 stands **(PLS-1, PLS-2)**. Young cedars represented 2% of the trees at survey corners described as burned, well behind most other species **(PLS-3)**. Similarly, young cedars represented just 1% of the trees at survey corners described as windthrown. Although white cedar does well as a cultivar in open environments, it seems that disturbed, open FDn43 habitat was not particularly favorable. Small-diameter, white cedar regeneration coming in among larger trees was not detected in the post-disturbance window **(PLS-5)**. Because of white cedar's affinity for wetter habitats included in the FDn43 landscape, we believe that the few, small-diameter cedars showing up in post-burn situations were coming from unburned wetlands near burned survey corners.

Transition: 35-55 years
As stands transitioned to mature conditions white cedars were essentially absent **(PLS-1)**. Small-diameter white cedar regeneration was not detected in the age-classes that match the transition period **(PLS-5)**. Again, it seems most likely that the few cedar trees recorded at corners estimated to fall within the transition stage were probably in nearby wetlands within forests older than we assigned to the FDn43 corner.

Mature Growth-stage: 55-95 years
In the mature growth-stage white cedar reaches its peak abundance as a bearing tree at 3%, which is why we must consider white cedar a ***mid-successional*** species – able to replace initial-cohort trees but dropping (slightly) in relative abundance as stands aged **(PLS-1, PLS-2)**. White cedar's increase in relative abundance as a tree is mysterious in that we detected almost no regeneration in younger FDn43 forests. Regeneration during the mature growth-stage was surprisingly good. Young cedars were often coming in among larger trees in stands estimated to be 80-100 years old **(PLS-5)**. In most cases, cedar regeneration was coming in under older paper birch and white pine. We interpret this as successful establishment and recruitment under the canopy of declining paper birch in mature FDn43 forests. This is substantiated by cedar's good ability to recruit under the canopy of modern examples of this community **(R-2)**. The delay of ingress to about 80 years is interesting and not understood. Most obvious is that its increase matches the start of paper birch decline, suggesting that cedars were replacing senescent birch. Another possible explanation is that white cedar was waiting for the development of organic seedbeds composed of duff, mosses, or nurse logs, which could possibly take about 80 years to form after a catastrophic fire. Given the spatial heterogeneity of fire removing all duff, the variety of trees and plants contributing to humus, and the gradual nature of duff accumulation, it just seems too unlikely that we would see the sharply defined initiation of white cedar regeneration at 80 years if seedbed formation were the real cause of cedar ingress in mature forests. Cedar regeneration and recruitment was a definite "pulse" very much like that of balsam fir during the first transition in this community. For now, the timing of cedar ingress remains an unexplained

empirical fact that is not unique to the FDn43 community, suggesting that we might be confusing landscape events with stand dynamics.

Second Transition: 95-115 years

As stands transitioned to old conditions (95-115 years) white cedar decreased, but just slightly in abundance **(PLS-1)**. Small-diameter white cedar regeneration coming in among larger trees continued until about age 100, but there are very few records of this compared to more abundant species **(PLS-5)**. The few white cedar records at corners estimated to be in the second transition showed no instances of it being the largest or smallest tree at a corner, suggesting that the cedars established in the mature growth stage were somewhere in the mid-canopy. Our interpretation is that cedar establishment was essentially over by the beginning of the second transition and that trees established earlier were surviving but not as tall or large-diametered as other species.

Old Growth-stage: >115 years

In the old growth-stage white cedar was a minor co-dominant, occurring always at survey corners of mixed composition **(PLS-1)**. We believe that white cedar's presence in old stands was mostly a consequence of its longevity, and that trees established during the mature growth-stage would persist until the next catastrophic fire. For this reason, we consider white cedar to be secondarily a ***late-successional species***. Small-diameter white cedar regeneration coming in among larger trees was not detected during in age-classes contributing to the second transition **(PLS-5)**. When white cedars were the smallest tree at a survey corner, they were present only beneath white pines. But in modern forests, white cedar shows good ability to recruit under a canopy that is usually not white pine **(R-2)**. Our interpretation is that white cedar had limited success regenerating in old patches of FDn43 habitat that were not yet invaded by white spruce, because there were almost no examples of white cedar and white spruce at the same survey corners.

Regeneration Strategies

White cedar's primary regenerative strategy on FDn43 sites is to fill ***large-gaps***. It is most successful at this when gaps are forming within a declining canopy of paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that white cedar abundance responds to the decline of paper birch in the mature growth-stage **(PLS-1, PLS-2)** and (2) it is present at survey corners showing partial canopy loss **(PLS-3)**. 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 FDn43 forests suggests, however, that white cedar is able to function also as a ***small-gap*** strategist with good-to-excellent establishment and recruitment in all height strata **(R-2)**. It is significant that the regenerant and seedling indices for white cedar (3.3-3.5) are more in line with trees that rely on larger canopy gaps, but recruitment of established seedlings to saplings is excellent. This suggests that getting white cedar to germinate is the main bottleneck in white cedar regeneration under a canopy.

Historic Change in Abundance

Today, white cedar is in peril on FDn43 sites. It is essentially absent from stands younger than about 100 years old **(PLS/FIA-1)**. It is substantially more abundant in old FDn43 stands than it was historically, but such stands represent only 2% of the landscape condition. From FIA data, one would conclude that regeneration on FDn43 sites is a major obstacle. The releve sampling paints a slightly better picture of white cedar's current status. It has fairly high presence as a tree (20%, **R-1**) and higher presence in the understory (29%, **R-2**) in our releve samples, suggesting that there is consequential regeneration when seed trees are present. Conserving and establishing seed trees would provide a start in restoring white cedar to FDn43 sites.

Balsam Fir

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

Suitability

FDn43 sites provide ***excellent habitat*** for balsam fir trees. The ***suitability rating*** of 4.4 for balsam fir is influenced mostly by its high presence (46%) as trees on these sites in modern forests **(R-1)**. When present, balsam fir is a common co-dominant tree, contributing 11% mean cover in mature stands. The ranking is sixth, following paper birch, white pine, quaking aspen, red pine, and northern white cedar on FDn43 sites as sampled by releves. As long as the soils are fairly deep (not FDn22), northern fire-dependent forests offer good-to-excellent habitat for balsam fir (see Suitability Tables). Among these, FDn43 offers the best commercial opportunity for balsam fir.

Young Growth-stage: 0-35 years

Historically, balsam fir was a minor tree in young FDn43 stands **(PLS-1, PLS-2)**. Balsam firs represented 7% of the trees at survey corners described as burned, well behind fire-tolerant species like aspen, paper birch, and white pine **(PLS-3)**. Nonetheless, the presence of any balsam fir on burned lands is surprising given its well-known sensitivity to fire. One would also guess that fire-sensitive trees like balsam fir would be substantially more abundant at windthrown corners, but this wasn't the case as fir represented just 5% of the trees at windthrown survey corners. Because of balsam fir's affinity for wetter habitats included in the FDn43 landscape, we believe that the few, small-diameter firs showing up in post-burn situations were coming from unburned wetlands near burned survey corners. Small-diameter balsam fir regeneration was rarely observed coming in among larger trees after fires. Balsam fir regeneration fir first appears in the 30-year age-class at the close of the young growth-stage **(PLS-5)**. Our interpretation is that young firs were absent from the actual burned patches of FDn43, but its widespread presence in habitats less likely to burn, assured local seed sources. Post-fire thickets of quaking aspen were probably fine habitat for young seed-origin firs, particularly at the stage where the groundlayer is suppressed and aspen starts to self-thin. Supporting this argument is the phenomenal performance of balsam fir under a canopy in modern stands, with perfect indices of regeneration **(R-2)**.

Transition: 35-55 years

The transition to mature conditions is characterized by a burst of balsam fir recruitment that is coincident with the decline of initial-cohort quaking aspen **(PLS-2)**. About 12% of all bearing trees in the 40-year age-class were recruiting fir, contributing to its excellent ranking in the gap window **(PLS-5)**. At the beginning of the transition, the abundance of fir rises dramatically to peak abundance exceeding 30% in the 40 and 50 year age-classes. The zenith is short-lived as the relative abundance of fir plummets to about 10% relative abundance to close the transition period. It is hard to visualize the rise from 4% relative abundance at age 30 to 33% relative abundance at age 40 without a pre-existing, pervasive bank of fir seedlings under 20-30 year old aspen. Young aspen stands must have offered especially good habitat for establishing balsam fir, because this pulse of fir regeneration is a feature common to many northern forest communities where the initial stages are aspen-dominated and fir is important in later growth-stages. Equally impressive is the collapse of fir populations before the transition stage concludes. Between age classes 50 and 60 years, the relative abundance of fir drops 24%. Balsam fir is short-lived, however, the rapid collapse of the transitional cohort must have involved mortality well short of fir's normal life span. The destructive agent, perhaps spruce budworm, must have been density-dependent as fir populations never again approach those of the transition stage or show such rapid decline.

Mature Growth-stage: 55-95 years
In the mature growth-stage balsam fir abundance stabilized at about 10% and it persisted at similar abundance throughout the older growth-stages. **(PLS-1, PLS-2)**. Balsam fir's ability to decisively replace the initial-cohort trees and reach peak abundance during the transition stage is why we consider fir somewhat of a ***mid-successional*** species, although its behavior in the older growth-stages is quite typical of a late-successional species. Balsam fir's relative abundance in the mature growth-stage is certainly the result of ingress and recruitment in the G-1 gap window **(PLS-5)**. Regeneration during the mature growth-stage was modest. Balsam fir regeneration was often observed coming in among larger trees at the beginning of the growth-stage but not at all beyond 60 years. At this time, fir regeneration was coming in under older paper birch, quaking aspen, white pine, and sometimes other firs. We interpret this as modest, but continued success of recruiting seed-origin trees under the remnants of the initial-cohort canopy and beneath trees that are less shade-tolerant than balsam fir.

Second Transition: 95-115 years
As stands transitioned to old conditions balsam fir increased slightly in abundance **(PLS-1, PLS-2)**. Using the half-diameter rule, small-diameter balsam fir regeneration coming in among larger trees was not detected during this second transition stage **(PLS-5)**. Firs were, however, quite common occurring almost always at survey corners of mixed composition (~99%) and almost always as the smallest tree at the corner (~90%). When firs were the smallest tree at a survey corner, they were beneath almost any other species, especially paper birch, white pine, white cedar, and white spruce. Our interpretation is that balsam fir populations were maintained by recruitment during the second transition, and that very small diameter firs just weren't selected as bearing trees given the variety of diameters and species available to the surveyors. This argument is supported mostly by the fact that fir populations were increasing and the tree is not particularly long-lived.

Old Growth-stage: >115 years
In the old growth-stage balsam fir was an important tree, occurring almost always at survey corners of mixed composition. At 13% relative abundance, it was behind white spruce, white pine, and paper birch as the most common trees on old FDn43 sites **(PLS-1)**. Small-diameter balsam fir regeneration coming in among larger trees was not detected in recruitment windows of the old growth-stage **(PLS-5)**. Firs bearing trees were usually the smallest tree at old survey corners, and they could occur beneath any other species. Most often, smaller diameter firs were beneath white spruce, white pine, paper birch, and white cedar. In modern forests, balsam fir is unequalled in the ability to establish and recruit seedlings under a canopy **(R-2)**. For this reason, we believe that fir populations in the old growth-stage were maintained by establishment and recruitment. Other than the curious burst of fir abundance in the first transition, its persistence and regenerative abilities under a canopy are our reasons for considering balsam fir to be mostly a ***late-successional*** tree in FDn43 forests. The level of subordination in both the second transition and the old growth-stage is incredibly high. Our interpretation is that balsam fir was most successful at filling the subcanopy in old forests, never achieving the height, diameter, or age of the surrounding white spruce and white pine.

Regeneration Strategies
Balsam fir's primary regenerative strategy on Fdn43 sites is to satiate the groundlayer with seedlings and to then recruit saplings in ***small-gaps***. It was successful at doing this under any other tree, but most often it was under paper birch or long-lived conifers. In the historic PLS data this interpretation is supported by: (1) the fact that balsam fir abundance is steady throughout the older growth-stages **(PLS-1, PLS-2)** and, (2) it is most abundant at survey corners in mature, undisturbed conditions **(PLS-3)**. The high percentage of balsam fir seedlings in the FIA data (situations 12 and 13) is also characteristic of species successful in small gaps **(FIA-1)**. Most significant though, is its incredible ability to establish and recruit seedlings under a canopy in modern stands **(R-2)**.

The fir "pulse" described in the first transition would suggest that balsam fir can function to some extent as a ***large-gap*** regeneration strategist. This argument is supported mostly by: (1) the fact that fir, more than any other species, responded strongly to the decline of the initial-cohort aspen

(PLS-2), and (2) fir's primary regeneration window was a gap window rather than ingress windows (PLS-5). Also, the high percentage of balsam fir poles beneath trees (situation 23) is also typical of trees that are successful at filling large canopy gaps (FIA-1). Impressed by fir's ability to recruit under a canopy (R-2), we have discounted the idea that large gaps are in any way required for fir germination and establishment. In fact, we believe that fir's competitive advantage is under full shade and probably most obvious under the proximal canopy of quaking aspen. However, fir's response to release in large gaps was excellent and similar to other species that we have described as large-gap strategists.

Historic Change in Abundance

Today populations of balsam fir are considerably higher in FDn43 forests than they were historically (PLS/FIA-1). We believe that this is a consequence of fire suppression and fir's obvious abilities to function as a shade-tolerant, small-gap strategist. The increase in fir is most evident in the young growth-stage where it now represents 7% of the young trees in FIA samples. We believe that historically, post-fire FDn43 stands started with almost no balsam fir, whereas now they have significant initial presence after logging. Fir abundance has also doubled since historic times in old forests, but old forests now represent just 2% of the FDn43 landscape. The ratio of fir regeneration to actual trees is very high (R-1,R-2). Thus, the increase in tree abundance in modern stands brings with it substantial amounts of understory fir, perhaps because stands no longer start from "scratch" as they did after intense fires. Fir abundance in the understory now offers a competitive challenge for less tolerant crop trees.

White Spruce

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

Identification Problems

The PLS surveyors did not distinguish between white and black spruce. Thus, interpretations of PLS data for the more common white spruce should always be done knowing that some of these trees were likely black spruce. FDn43 releve samples show that for plots with spruce present: 3% have both species present; 21% are black spruce without white spruce; 76% are white spruce without black spruce. White spruce and black spruce are not at all alike in their ecology on FDn43 sites. Black spruce is far more like jack pine in these environments, and the following account was interpreted with bias to white spruce.

Suitability Ratings

FDn43 sites provide ***excellent habitat*** for white spruce trees. The ***suitability rating*** of 4.1 for white spruce is influenced mostly by its high presence (36%) as trees on these sites in modern forests **(R-1)**. When present, white spruce is an important co-dominant tree, contributing 10% mean cover in mature stands. This ranking is seventh, following paper birch, white pine, quaking aspen, red pine, northern white cedar, and balsam fir on FDn43 sites. Northern fire-dependent communities in general are not good habitat for white spruce (see Suitability Tables). FDn43 provides excellent habitat for white spruce because it is the most mesic of the northern fire-dependent forests.

The ***suitability rating*** of 2.6 for black spruce is based upon its 11% presence and 8% mean cover when present **(R-1)**. This ranking is ninth highest among trees common on FDn43 sites. Among the northern fire-dependent communities, black spruce is favored on the moister and poorer communities, especially FDn32. Black spruce is important on FDn43 sites because they are moist, but it is limited because these are rather rich sites.

Young Growth-stage: 0-35 years

Historically, white spruce was a minor tree in young FDn43 stands **(PLS-1, PLS-2)**. Young spruce represented 4% of the trees at survey corners described as burned, well behind fire-tolerant species like aspen, paper birch, and white pine **(PLS-3)**. Nonetheless, the presence of any white spruce on burned lands is surprising given its sensitivity to fire. One would guess that fire-sensitive trees like spruce would be substantially more abundant at windthrown corners, and this is the case for white spruce as it represented 8% of the trees at windthrown survey corners. Because of spruce's affinity for wetter habitats included in the FDn43 landscape, we believe that the few, small-diameter spruce showing up in post-burn situations were coming from unburned wetlands near burned survey corners. White spruce regeneration was rarely observed in the post-disturbance recruitment window **(PLS-5)**. Our interpretation is that white spruce were absent from the actual burned patches of FDn43, but could be important in stands originating after windthrow or perhaps following disease outbreaks.

Transition: 35-55 years

As stands transitioned to mature conditions white spruce increased ever so slightly in abundance **(PLS-1)**. This increase is very modest, but it is the beginning of a trend that will continue through old-growth where white spruce is the dominant tree **(PLS-2)**. Small-diameter white spruce regeneration coming in among larger trees was first significant in the G-1 gap window belonging to the transition **(PLS-5)**. Surprisingly, most regenerating spruce was coming in under jack pine and to a lesser extent under paper birch, quaking aspen, and fir. A common anecdote among Minnesota foresters is that balsam fir serves as a nurse crop for white spruce. This comes mostly from observations in modern forests where it is far more common (2-3 times in our releves) to have fir in stands without spruce than to have white spruce without any fir. Remarkably, this seems even more true in the historic data where ingress of spruce always follows an initial pulse of fir abundance as it did in FDn43 forests. Our interpretation is that it seems plausible that ingress of white spruce in the transition stage was the consequence of balsam fir altering the habitat in some way that promotes seed-origin white spruce. Alternatively, it is possible that the decline of initial-cohort tree like jack pine and aspen created partially shaded gaps in the canopy where we see spruce regeneration do well in managed forests. This hypothesis is favored by the fact that spruce was more often recorded as subordinate to jack pine and aspen than balsam fir.

Mature Growth-stage: 55-95 years

In the mature growth-stage white spruce abundance was slowly increasing but at abundances near just 4% **(PLS-1, PLS-2)**. All mature survey corners with spruce were of mixed composition, and spruce was always the smallest tree. This is the profile of a true, ingressing species. White spruce regeneration was coming in among larger trees throughout the mature growth-stage at levels suggesting fair establishment and recruitment in the I-1 ingress window **(PLS-5)**. At this time, spruce regeneration was coming in mostly under older paper birch, quaking aspen, and pines more so that fir. This favors the idea that spruce was responding more to gaps in the canopy than being nursed by balsam fir.

Second Transition: 95-115 years

As stands transitioned to old conditions white spruce increased greatly in abundance **(PLS-1, PLS-2)**. For the first time, white spruce bearing trees were occasionally the largest tree at a survey corner. Small-diameter, white spruce regeneration was abundant following the 100-year age-class **(PLS-5)**. In nearly all cases white spruce was coming in below less tolerant trees, especially jack pine, white pine, quaking aspen, paper birch, and red pine. Our interpretation is that white spruce populations increased greatly during this stage because they were able to replace initial-cohort pines and paper birch established during the first transition that were reaching the end of their lives.

Old Growth-stage: >115 years

In the old growth-stage white spruce was an important co-dominant and sometimes dominant tree, occurring almost always at survey corners of mixed composition. At 28% relative abundance, it was tied with white pine as the most common tree on old FDn43 sites **(PLS-1)**. White spruce's importance in the old growth-stage is the main reason that we consider it to be a ***late-successional*** species on FDn43 sites. Small-diameter, white spruce regeneration coming in among larger trees was at its peak in the I-2 ingress window of the old growth-stage, representing about 11% of all spruce bearing trees **(PLS-5)**. When white spruce were the smallest tree at a survey corner, they were still mostly coming in under less tolerant trees such as paper birch, white pine, quaking aspen, and red pine. For the first time though, there was significant regeneration under itself. Our interpretation is that old FDn43 sites would eventually be dominated by white spruce as the climax species. These spruce though were competing with some very long-lived species like white pine, white cedar, and red pine. It was highly unusual for FDn43 sites to escape catastrophic fire long enough to form rather pure stands of white spruce.

Regeneration Strategy

White spruce's primary regenerative strategy on Fdn43 sites is to satiate the groundlayer with seedlings and to then recruit saplings in ***small-gaps***. It was successful at doing this under any other tree, but most often it was coming in other trees less tolerant of shade. In the historic PLS data this interpretation is supported by: (1) the fact that white spruce abundance peaks in the old growth-stage when we assume a full canopy and lower strata **(PLS-1, PLS-2)**, (2) it is most abundant at survey corners in a mature, undisturbed condition **(PLS-3)**, and (3) its best recruitment window is an ingress window **(PLS-5)**. The fairly high percentage of white spruce seedlings in the FIA data (situations 12 and 13) is also characteristic of species successful in small gaps **(FIA-1)**. Its high abundance in sapling stands and pole stands (situations 11 and 22) is believed to be plantation spruce. More significant though, is spruce's good ability to establish and recruit seedlings under a canopy in modern stands **(R-2)**. It is important though that the regenerant and seedling indices (3.5-3.8) are more in line with species that do well in ***larger canopy gaps***. The bottleneck seems to be germination as spruce's recruitment indices rise steadily with height. Our interpretation is that white spruce functions well as a small-gap strategist, but seeding opportunities were better in large-gaps.

Historic Change in Abundance

Today white spruce is considerably less abundant than it was historically **(PLS/FIA-1)**. It never was especially abundant in young and mature FDn43 forests, rather its forte was to dominate old stands. For a fire-dependent community, FDn43 was unusual in that a lot of those forests actually reached old age. Because FDn43 is such a common northern forest community, this means that old, mixed spruce and pine FDn43 forests were extensive on the pre-settlement landscape. Our interpretation is that there is significantly less white spruce on the FDn43 landscape because there are very few old stands.

Red Maple

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

Identification Problems

The PLS surveyors did not distinguish between red and sugar maple. Thus, interpretations of PLS data for the more common red maple should always be done knowing that some of these trees were possibly sugar maple. FDn43 releve samples show that for plots with maples present: 3% have both species present; 6% are sugar maple without red maple; 91% are red maple without sugar maple. We consider red and sugar maple to be ecologically equivalent for most silvicultural considerations on these sites.

Suitability

FDn43 sites provide ***good habitat*** for red maple trees. The ***suitability rating*** of 3.4 for red maple is influenced mostly by its presence (16%) as trees on these sites in modern forests **(R-1)**. When present, red maple is a minor co-dominant tree, contributing 10% mean cover in mature stands. This ranking is eighth among trees common on FDn43 sites. Only the FDn33 and FDn43 offer good habitat and commercial opportunities for red maple (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, red maple was present in just trace amounts in young FDn43 stands recovering mostly from fire **(PLS-1, PLS-2, PLS-3)**. Red maple did not appear as a bearing tree often enough at young survey corners to evaluate its historic ecological behavior in the post-fire years. Small-diameter red maple regeneration was present at low abundance in the post-disturbance window **(PLS-5)**. Our interpretation is that such trees were advance regeneration in fire skips. Alternatively they were individuals that invaded FDn43 sites under a thicket-like growth of quaking aspen. We believe that fire, the more common stand-regenerating event, eliminated most red maple from young FDn43 sites.

Transition: 35-55 years

As stands transitioned to mature conditions red maple abundance peaks at 2% relative abundance in the 40- and 50-year age-classes. This short-lived peak is the main evidence that red maple was a ***mid-successional*** tree – able to replace initial-cohort aspen and declining in abundance in later growth-stages. Small-diameter red maple regeneration coming in among larger trees had its peak abundance in the 40-50 year age-classes as well **(PLS-5)**. At this time red maples were always the smallest tree at survey corners, which is typical of a species colonizing a site well after the stand-regenerating event. Though the sample size is small, it seems that small-diameter red maples were mostly coming in under quaking aspen. Our interpretation is that red maple was able to seed into young FDn43 stands and that it enjoyed limited success recruiting seedlings to tree status as the initial-cohort canopy of quaking aspen disintegrated.

Mature Growth-stage: 55-95 years

In the mature growth-stage the abundance of red maple steadily declines from its 2% peak, averaging just 1% relative abundance in the whole growth-stage **(PLS-FIA-1)**. Small-diameter red maple regeneration was present until the 70-year age-class **(PLS-5)**. At this time, red maple showed a clear preference for replacing less tolerant trees, especially quaking aspen but also paper birch and white pine. We interpret this as red maple having some recruitment success in gaps as initial-cohort trees aspen and birch continued to die, but its abundance declines because there weren't many initial-cohort trees left.

Second Transition and Old Growth-stage: 95-115 years and older

During the second transition and old growth-stage the relative abundance of red maple stabilized at just less than 1% relative abundance **(PLS/FIA-1)**. Though we did not detect small-diameter red maple regeneration beyond the 70-year age-class **(PLS-5)**, there must have been some regeneration in order to sustain its constant presence. At this time, most red maple bearing trees were still the smaller tree at the corner. In those cases it was far more common for red maples to be subordinate to less-tolerant paper birch or white pine. Our interpretation is that red maples had limited success sustaining a small population of trees by establishment and recruitment in patches of FDn43 habitat that had yet to be invaded by white spruce and balsam fir.

Regeneration Strategies
Red maple's primary regenerative strategy on FDn43 sites is to fill ***large-gaps***. It was most successful at this when gaps formed within the canopy of declining initial-cohort quaking aspen. In the historic PLS data the large-gap strategy of red maple is supported by: (1) the fact that red maple abundance peaks in response to the decline of the initial-cohort **(PLS/FIA-1)**, and (2) it shows peak recruitment in a gap window rather than post-disturbance or ingress windows **(PLS-5)**. The FIA data show red maple to be successful in any regenerative situation, and not necessarily pre-disposed to large gap situations (situation 23, **FIA-1**). The releve sampling also supports the idea that red maple is a large-gap strategist. Red maple's regenerant and seedling indices (4.3) are excellent and in line with small-gap strategists that are good at banking seedlings under a canopy **(R-2)**. Red maple's sapling index (3.5) is just good, suggesting a recruitment bottleneck at getting seedlings over 2m tall. The sapling index and the bottleneck are typical of large-gap strategists.

Historic Change in Abundance
Populations of red maple have been expanding in Minnesota. Red maple abundance has at least doubled since pre-settlement times and is most evident in the young and mature growth-stages of FDn43 forests where it has increased from trace relative abundance to about 3-4% of the trees today **(PLS/FIA-1)**. Our interpretation is that this is the consequence of fire-suppression, in particular the lack of surface fires that periodically "cleansed" FDn43 stands of maple regeneration. Logging doesn't eradicate maple as did fire, and modern regeneration harvests simply release advance regeneration of red maple. An amazing fact is that 93% of all the red maple references in the FIA data were in regenerating situations (not situation 33, **FIA-1**). It would seem that in spruce-climax communities, red maple seems to play a subcanopy role similar to that of ironwood in hardwood stands that will climax with sugar maple. The abnormal abundance of red maple on some FDn43 sites may be a hindrance to managing these sites for the gap and open regeneration strategists that were more common historically.

(PLS-1) Historic Abundance of FDn43 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the FDn43 community by growth-stage. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow, green, and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

Dominant Trees	Forest Growth Stages in Years				
	0 - 35	35 - 55	55 - 95	95 - 115	> 115
	Young	T1	Mature	T2	Old
Quaking Aspen	60%		12%		5%
Jack Pine	19%		3%		3%
Red Pine	3%		9%		5%
Paper Birch	15%		31%		18%
Balsam Fir	1%		10%		13%
White Pine	2%		24%		28%
White Cedar	–		3%		2%
White Spruce	–		4%		28%
Miscellaneous	–		7%		–
Percent of Community in Growth Stage in Presettlement Landscape	17%	30%	31%	6%	16%

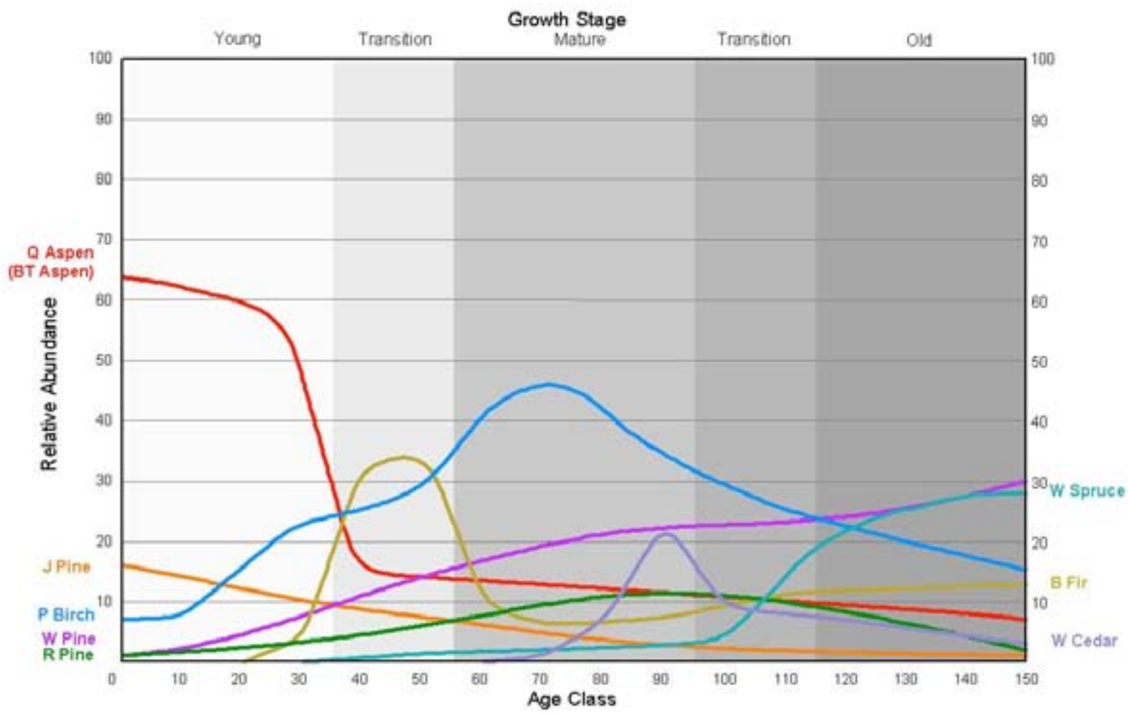
PLS-1

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 FDn43 forests, but were rare historically appear in Table **PLS/FIA-1**.

Public Land Survey linked text

(PLS-2) Abundance of trees throughout succession in FDn43

Caption: Graphed for the different species of FDn43 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 FDn43 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent FDn43 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	
White pine	**401**	**25%**	**24**	**17%**	**120**	**24%**	**4512**	**16%**
Quaking aspen	**411**	**26%**	**40**	**28%**	**117**	**23%**	**4735**	**17%**
Red maple	**4**	**0%**	**3**	**2%**	**2**	**0%**	**258**	**1%**
Red pine	**116**	**7%**	**7**	**5%**	**72**	**14%**	**1626**	**6%**
Jack pine	**118**	**7%**	**11**	**8%**	**38**	**8%**	**1563**	**6%**
Paper birch	**330**	**21%**	**36**	**25%**	**91**	**18%**	**7188**	**26%**
White cedar	**36**	**2%**	**2**	**1%**	**8**	**2%**	**648**	**2%**
Balsam fir	**116**	**7%**	**7**	**5%**	**25**	**5%**	**4108**	**15%**
White (Black) spruce	**70**	**4%**	**12**	**8%**	**33**	**7%**	**2983**	**11%**
Total (% of grand total, 29871)	**1602**	**5%**	**142**	**0.5%**	**506**	**2%**	**27621**	**92%**

PLS-3

Table PLS-3 includes only trees ranked as having excellent, good, or fair suitability for FDn43 sites. Tree sums will not match the totals in the Natural Disturbance Regime text, because trees of poorer suitability were included in that analysis.

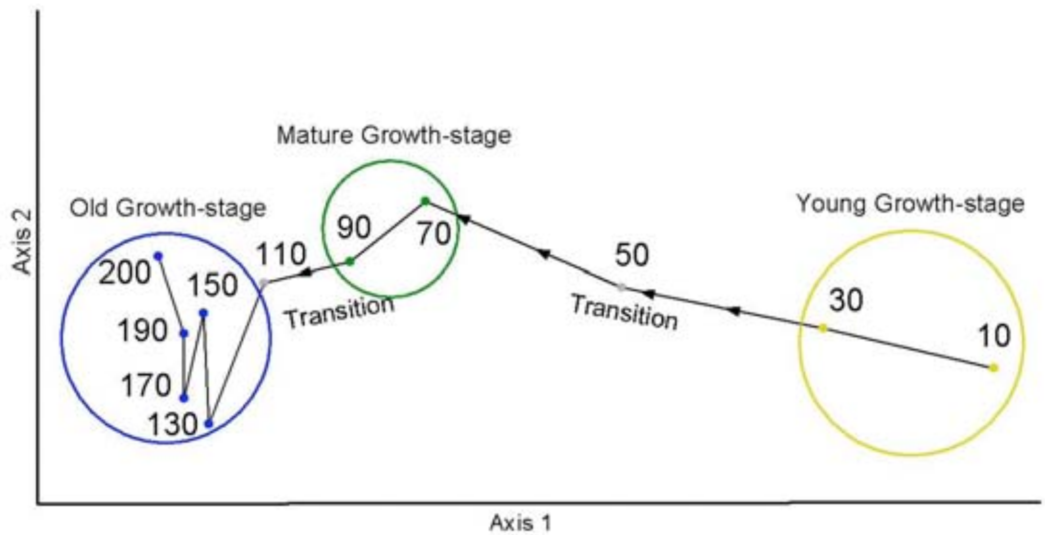
PLS survey corners were assigned to four disturbance categories:

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 FDn43 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 FDn43 Trees

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

Initial Cohort	Species	Peak Years	P-D 0-30 years	G-1 30-70 years	I-1 70-90 years	G-2 90-110 years	I-2 >110 years
Yes	Quaking Aspen	0-30	Excellent	Poor to 60	--	--	--
Yes	Jack Pine	0-20	Good	Fair to 60	--	--	--
Yes	Paper Birch	0-40	Good	Good to 70	--	--	--
Minor	Red Pine	0-40	Fair	Fair to 60	--	--	--
Minor	White Pine	20-50	Fair	Good to 50	Poor to 80	--	--
No	Red Maple	40-50	Poor after 20	Fair to 70	--	--	--
No	Balsam Fir	30-50	Fair after 30	Excel. to 60	--	--	--
No	White Cedar	80-100	--	Almost none	Good	Fair to 100	--
No	White Spruce[1]	>120	Almost none	Fair	Fair	Good	Excel.

Recruitment windows from ordination PLS-4:

- P-D: post-disturbance filling of understocked areas, 10-30 years
- G-1: gap filling during decline of initial-cohort quaking aspen and jack pine, 30-70 years
- I-1: ingress of seedlings under canopy of paper birch, white pine, and some quaking aspen, red pine and balsam fir, 70-90 years
- G-2: gap filling during decline of paper birch and quaking aspen, 90-110 years
- I-2: ingress of seedlings under white pine, white spruce and some paper birch

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

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

1. White spruce bearing trees couldn't be segregated from black spruce in the PLS notes for this community. A small fraction of spruce records are probably black spruce, which we believe would show establishment patterns more like jack pine than white spruce.

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 FDn43 sites

This table presents an index of suitability for trees in FDn43 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 FDn43			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Paper birch (Betula papyrifera)	**69**	**18**	**4.8**
White pine (Pinus strobus)	**39**	**26**	**4.8**
Quaking aspen (Populus tremuloides)	**46**	**21**	**4.7**
Red pine (Pinus resinosa)	**22**	**26**	**4.5**
White cedar (Thuja occidentalis)	**20**	**27**	**4.4**
Balsam fir (Abies balsamea)	**46**	**11**	**4.4**
White spruce (Picea glauca)	**36**	**10**	**4.1**
Red maple (Acer rubrum)	**16**	**10**	**3.4**
Black spruce (Picea mariana)	**11**	**8**	**2.6**
Jack pine (Pinus banksiana)	**5**	**9**	**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 8^{th} 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 FDn43 Stands

This table presents an index of regeneration for FDn43 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 FDn43 communities. Changes in the index values from one stratum to another can be used to estimate regenerative bottlenecks, whether establishment (R-index) or recruitment (SE-, SA-, or T-indices).

Natural regeneration indices for germinants, seedlings, saplings, and trees common in the canopy of Northern Mesic Mixed Forest – FDn43					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Balsam fir (Abies balsamea)	**93**	**5.0**	**5.0**	**5.0**	**4.0**
Paper birch (Betula papyrifera)	**72**	**3.3**	**3.3**	**4.5**	**4.8**
White spruce (Picea glauca)	**59**	**3.5**	**3.8**	**4.0**	**4.0**
Quaking aspen (Populus	**58**	**4.2**	**4.3**	**4.3**	**4.5**
White pine (Pinus strobus)	**44**	**3.7**	**3.7**	**3.2**	**4.5**
Red maple (Acer rubrum)	**43**	**4.3**	**4.3**	**3.8**	**3.3**
White cedar (Thuja occidentalis)	**29**	**3.5**	**3.3**	**4.0**	**4.0**
Black spruce (Picea mariana)	**20**	**2.7**	**2.7**	**3.3**	**3.0**
Red pine (Pinus resinosa)	**4**	**0.7**	**0.7**	**1.0**	**4.3**
Jack pine (Pinus banksiana)	**2**	**0.3**	**0.7**	**1.7**	**3.0**

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

% presence: the percent of 201 FDn43 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 FDn43 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples FDn43 forests. The purpose of the table is to provide a general impression of how often a species is seen certain regenerative situations: canopy of a regenerating forest (situations 11, 22), in the subcanopy (situations 12, 23), or in the seedling bank below a remote canopy (situation 13). The situation of trees in older stands at tree height (33) provide no insight about regeneration. Species are ordered by the sum of their percents in 12 and 13 situations, which generally ranks them as would shade-tolerance ratings. The total number of trees counted for each species is presented to provide a sense of reliability.

Species	Tree Count	Structural Situations					
		11	22	12	23	13	33
White pine	102		5%		11%	2%	82%
Jack pine	78	5%	22%	5%	12%	3%	54%
Red pine	105	9%	12%	5%	11%	4%	59%
White cedar	110		22%	14%	16%		49%
Paper birch	2575	5%	29%	9%	28%	6%	22%
Quaking aspen	9203	35%	15%	16%	8%	9%	17%
White spruce	278	8%	25%	13%	12%	12%	31%
Black spruce	115	7%	25%	24%	33%	8%	4%
Red maple	634	15%	18%	18%	19%	23%	7%
Balsam fir	1798	6%	18%	23%	22%	23%	8%

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 FDn43 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 FDn43 community and estimated to fall within the young, mature, and old growth-stages. Arrows indicate increase or decrease between historic growth-stages only and for the more common trees. Green shading and text was used for the historic PLS data and blue was used for the FIA data. Percents on the bottom row allow comparison of the balance of growth-stages across the pre-settlement landscape (*ca.* 1846-1908 AD) and the modern landscape (*ca.* 1990 AD).

Dominant Trees	Forest Growth Stages in Years									
	0 - 35		35 - 55		55 - 95		95 - 115		> 115	
	Young		T1		Mature		T2		Old	
Quaking Aspen	60%	76%			12%	52%			5%	23%
Jack Pine	19%	0%			3%	0%			3%	0%
Red Pine	3%	0%			9%	1%			5%	1%
Paper Birch	15%	5%			31%	20%			18%	18%
Balsam Fir	1%	7%			10%	13%			13%	25%
White Pine	2%	0%			24%	1%			28%	3%
White Spruce	–	1%			4%	2%			28%	2%
White Cedar	–	0%			3%	0%			2%	14%
Red Maple	–	3%			1%	4%			–	1%
Black Spruce	0%	0%			0%	1%			0%	6%
Balsam Poplar	–	4%			–	2%			–	2%
Miscellaneous	0%	4%			3%	4%			0%	5%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	17%	20%	30%	26%	31%	48%	6%	3%	16%	2%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 11,725 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 10,785 FIA subplots that were modeled to be FDn43 sites.

Public Land Survey linked text
FIA linked text

Silviculture Systems for FDn43: 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										
Paper Birch	large-gap (open)										
White Pine	large-gap (small-gap)										
Quaking Aspen	open (small-gap)										
Red Pine	open (large-gap)										
N. White Cedar	large-gap (small-gap)										
Balsam Fir	small-gap (Large-gap)										
White Spruce	small-gap Large-gap										
Red Maple	large-gap										

Forest Health

Paper Birch

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

WATCHOUTS!

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

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

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

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

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

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

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

White Pine

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

WATCHOUTS!

∞ Protect seedlings and saplings from browse damage.

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

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

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

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

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

Quaking Aspen

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

WATCHOUTS!

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

∞ Harvest during the winter to ensure adequate regeneration.

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

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

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

Red Pine

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Diplodia blight & canker	Regeneration	Mortality
Sirococcus shoot blight	"	"
Bark beetles	Pole-sized and larger	Mortality
Red pine pocket mortality	"	"
Stem decay	"	Volume loss

WATCHOUTS!

∞ Avoid creating pine slash and storing fresh cut products inside or adjacent to red and jack pine stands from February 1 to September 1 in order to prevent the buildup of bark beetle populations and mortality losses due to their subsequent attack of residual pines.

∞ 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.

∞ Natural and artificial regeneration growing below red pine overstory trees may not survive due to the accumulation of *Diplodia* and *Sirococcus* infections. Seedlings and saplings within 1 chain of red pine overstory trees are also likely to be heavily infected.

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.

Balsam Fir

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

WATCHOUTS!

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

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

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

White Spruce

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

WATCHOUTS!

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

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

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

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

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

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

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.

FDn43 Acceptable Operating Season to Minimize Compaction and Rutting

Primary Soils	Secondary Soils	Not Applicable

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

Plants below indicate wetter inclusions of FDn43 that are more susceptible to compaction.

Mountain maple (*Acer spicatum*)
Balsam fir (C) (*Abies balsamea*)
Common oak fern (*Gymnocarpium dryopteris*)
Lady fern (*Athyrium filix-femina*)

White cedar (*Thuja occidentalis*)
Palmate sweet coltsfoot (*Petasities frigidus*)
Swamp red currant (*Ribes triste*)
Black ash (U) (*Fraxinus nigra*

(U) – understory (C) – canopy

Footnotes on back

Foot Notes

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

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

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

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

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

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

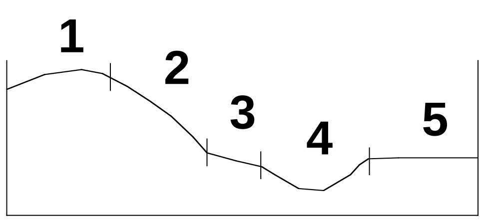
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

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

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

4. Landscape Position

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



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

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

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

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

   W Winter – the ground is snow covered or partially frozen

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

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

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

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

Public Land Survey linked text

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

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

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

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

Modern Forest linked text

Releve Samples

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

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

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

For more information on the releve method and NPC Classification:

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

FIA Samples

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

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

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

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

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

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

Link to the USFS website, north central