FDn33

FDn33 – Northern Dry-Mesic Mixed Woodland

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Dry-Mesic Mixed Woodlands (FDn33) are a common pine-dominated community found on sandy habitats of the Northern Minnesota Drift and Lake Plains, Northern Minnesota and Ontario Peatlands, and Northern Superior Uplands ecological Sections of Minnesota (Figure 1). Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

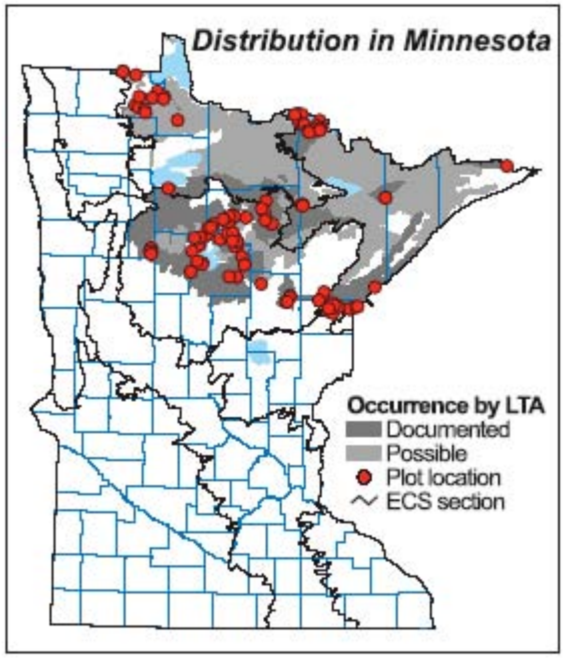


Figure 1. The range of FDn33 forests in Minnesota (shaded) and distribution of releve samples (red dots).

Commercial Trees and Management Opportunities

As a commercial forest, FDn33 sites offer a wide selection of crop trees and several possible structural conditions. Red pine, paper birch, white pine, quaking aspen, jack pine, and balsam fir are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on FDn33 sites (see Suitability Tables). Big-toothed aspen, red maple, and black spruce are ranked as good crop trees, and stands can be managed to perpetuate these trees as co-dominants, especially when present or with evidence of former presence (e.g. stumps) in a particular stand.

Among these species, quaking aspen, jack pine, red pine, paper birch, white spruce, black spruce, and white pine were the dominant native trees that have occupied FDn33 sites for a long time and have had the opportunity through successive generations to adapt to physical conditions typical of these sites **(PLS/FIA-1)**. Balsam fir was likewise native to FDn33 sites but occurred naturally at lower abundance. The consequence of fire suppression, commercial logging, and settlement in the past century has been to promote much more quaking aspen and fir than was usual. Past history and land use as also encouraged the ingress of species that were not significant in native FDn33 stands such as red maple. The increased abundance of red maple and aspen complicates our interpretations of conifer behavior, and the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

The historic FDn33 landscape presented a rather balanced and full successional spectrum of these forests. About 14% of these sites were young and recovering from stand-regenerating fire **(PLS-1)**. At this time, crown fires and severe surface fires left a rather clean, mineral-soil slate for tree establishment. Silvicultural systems such as clear-cutting or clear-cutting with reserves best matches best our impression of natural fires and skips. Quaking aspen, big-toothed aspen, and jack pine are the species with open regeneration strategies able to succeed following clear-cutting and variable seedbeds ranging from mineral (jack pine, big-toothed aspen) to rather undisturbed duff (quaking aspen).

About 27% of the historic FDn33 landscape were stands transitioning between the young and mature growth-stages. At this time the decline of initial-cohort quaking aspen and jack pine, and a burst of balsam fir regeneration were causing succession. Large-gap strategists like red pine, paper birch, and white pine did well recruiting beneath the disintegrating canopy. Seed-tree to variants of shelterwooding when accompanied by soil disturbance should create natural regeneration opportunities for red pine. Retaining slightly more cover for paper birch and white pine is required. Concepts like the group shelterwood system, especially when the gaps are expanded over 20-30 years (femelschlag) to accomplish canopy removal best fit the idea of a disintegrating canopy and regeneration opportunities for paper birch and white pine. Birch more than white pine needs some site preparation that mixes organics into the mineral soil. Natural shelterwooding is a reasonable match if adequate advance regeneration of white pine and birch is present. Group selection is a possible match as the patches of declining aspen and jack pine are fairly small and as long as red pine, white pine, and paper birch seed trees are present in the legacy matrix.

Most (44%) of the historic FDn33 landscape was mature FDn33 forest. This was a period of rather stable conditions where paper birch and red pine dominated these sites. Modest amounts of initial-cohort trees were dying and producing small-gaps, while late-successional species like white pine and spruce were building advance regeneration and starting to recruit tree-sized individuals. This episode was a period where these trees were vigorous and not likely to senesce until stands approached the 100-year age-class. 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 FDn33 stands. Because the red and white pines are so long-lived in comparison to the other trees, concepts aimed at two-story forest management could approximate mature woodlands, where we suspect that surface fires and perhaps spruce budworm cycled shorter-lived species below persistent pine standards. Coppicing aspen with red pine standards would seem to make some sense as aspen shows surprising shade-tolerance when beneath red pine on FDn33 sites (R-2). Cycling fir and spruce on short rotation below white pine standards would seem to be a promising strategy to approximate outbreaks of spruce budworm in mature woodlands. .

An considerable amount of FDn33 sites were estimated to be older than 125 years (15%). At this time the continued demise of paper birch and red pine created single-tree gaps that favored recruitment of white pine, balsam fir, and spruce. Variants of selective harvesting would be most appropriate for maintaining FDn33 stands in this condition. Initial selections would be species-oriented and aimed at final removal of paper birch and any declining large-diameter red pine. Depending upon the distribution of these trees, small-to-large gaps would be formed to release advance regeneration of white pine, spruce, or fir. Alternatively white pine, spruce, and maybe even some red pine could be planted in openings of appropriate size – large gaps for red pine, white pine or black spruce, and smaller gaps for white spruce. Following selections would be diameter oriented removal in order to create a pool of available advance regeneration, promote recruitment of well-formed poles, and removal from above of high-quality logs.

Management Concerns

FDn33 communities occur mostly on sandy soils where there is little concern of soil compaction or rutting. The most common situation is for FDn33 woodlands to be on outwash plains, which may or may not have been subsequently modified into dunes. In this setting, it is fairly safe to assume that the soil particles have been well-sorted and therefore are highly unlikely to compact. Rutting is a concern only when the soil is totally saturated in the spring and above frost. FDn33 woodlands can occur on scoured bedrock terrain, where surface textures can be just about anything, including loamy textures that might compact. However, the overall soil depth is very shallow (~1 foot) and the soil especially stony. Because of the skeletal strength that the stones provide, we doubt that these soils are especially susceptible to compaction or rutting regardless of the matrix soil texture. On stagnation moraines, this community consistently occurs on what are essentially included patches of sandy outwash or partially sorted flow-till. Under normal circumstances, the soil texture is coarse enough to not worry about compaction and rutting. However, in this setting, it is common for patches of compactable till to crop-out at the stand scale. Usually, these compactable areas are evident as patches of plants typical of mesic hardwood forests, especially lady fern. Normally, these sites are operable in any season (except spring breakup) as long as major skid trails and landings circumvent the mesic inclusions.

The landscape balance of growth-stages and stand ages for the FDn33 community is somewhat different than it was historically. Today, there is significantly more young FDn33 woodland, and old woodlands are now incredibly rare **(PLS/FIA-1)**. Otherwise, the amount of 35-135 year-old woodland is about the same. The consequence of this imbalance has been to lose late-successional, long-lived conifers like white pine and spruce on these sites. These species and older forests should be conserved or enhanced when opportunities arise. All of the pines have suffered considerable loss and are under-represented in all age-classes. Although our analysis did not automatically eliminate plantations, heavily stocked plantations were not included and this decision has affected our estimate of pine's peril. The real conservation issue is the lack of any attempt serious to naturally regenerate pine on these sites, and the overwhelming tendency to favor red pine over white and jack pine. It makes sense to us to work towards silvicultural strategies to regenerate naturally all of the pines. Aspen, paper birch, and red maple are the benefactors of modern conditions because logging does not selectively kill these trees as did natural processes. Aspen and paper birch were natural dominants, but red maple was not. Thus, management strategies aimed at reducing the abundance of red maple would move sites a little closer to their normal condition.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 6,807 corners within the primary range of the FDn33 community. At these corners, there were 17,310 bearing trees comprising the species that one commonly finds in FDn33 forests.

Natural Rotations of Disturbance in FDn33 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**220 years**
Catastrophic windthrow photograph	**1,130 years**
Partial Canopy Loss, photograph	**80 years**

The PLS field notes described about 7% of the FDn33 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands with some references to scattered timber and post-fire thickets. From these data, a rotation of 220 years was calculated for stand-replacing fire.

Elsewhere in the FDn33 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 1,130 years for windthrow.

More common at FDn33 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 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 forests. About 7% of the survey corners were described as such, resulting in a calculated rotation of 80 years for disturbances that maintained early and mid-successional trees on FDn33 sites. That more corners were described as burned (328) compared to windthrown (89) suggests that surface fires were the more prevalent cause of partial canopy loss.

Compared to other northern fire-dependent communities (FDn), FDn33 rotations of stand-regenerating disturbances are similar in that the fire rotation exceeds the longevity of most initial cohort species and windthrow was unimportant. The exception was red pine where its longevity roughly matches the rotation of catastrophic fire and it maintained a significant presence in all growth-stages that could be attributed to survival of initial-cohort trees. Otherwise, natural stand dynamics involved at least a couple of tree generations and succession of species. FDn33 shows the succession of jack to red to white pines commonly observed throughout northeastern Minnesota. Unlike most other FDn communities, the rotation of 80 years for surface fire is short and similar to fire-dependent communities of the central floristic region (FDc). The obvious connection between FDn33 and FDc communities is their affinity for deep, sandy/gravelly, somewhat excessively drained soils. These conditions must have promoted surface fire more so than the till-derived soils and rugged topography where we find most other FDn communities. Surface fires were apparently effective in maintaining pine and early-successional hardwoods as there is little evidence that FDn33 sites commonly escaped disturbance long enough for shade-tolerant species to exert dominance.

Natural Stand Dynamics & Growth-stages

Following stand-regenerating fire or rarely windstorms, the overall pattern of compositional change in FDn33 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 FDn33, quaking aspen, jack pine, red pine, and paper birch are the species that benefit greatly from fire because they compete poorly with later-successional species – first losing ground to white pine and ultimately to fire-sensitive species like spruce and balsam fir.

The FDn33 community is floristically woodland in that some light-loving plants occur in the groundlayer. However, with regard to tree density, FDn33 behaves like forest. Early in its development it achieves high tree densities comparable to any forest of the northern floristic region. From their inception through the mature growth-stage, the mean distances to FDn33 bearing trees increases from 23 feet to 34 feet. This is the usual pattern of forest succession where stands are initially dense and thin as trees and their crowns get larger. Distances of about 20 feet are typical of forests unaffected by surface fire. Distances of about 30 feet are typical of northern communities influenced by surface fires that favor survival of the older, larger, thicker-barked trees. The variances of these means are initially small, but increase relative to their means as the classes get older. This means that not only did tree density decline in old age, but their distribution became patchier. This too is consistent with the idea of surface fires influencing tree density.

Young Growth-stage: approximately 0-35 years
About 13% of the FDn33 landscape in pre-settlement times was covered by forests estimated to be under 35 years old **(PLS-1)**. At that time, it was about twice as likely for stands to be mixed as it was for them to be monotypic. Monotypic conditions were represented mostly by survey corners where all bearing trees were aspen, but some corners attended by all paper birch or red pine. At survey corners with mixed composition, jack pine and aspen were the most cited species, but paper birch and red pine were also common. In describing young, burned stands the surveyors indicated that in addition to aspen, jack pine, red pine, and paper birch, white pine was present as well **(PLS-3)**. These were almost all large-diameter survivors and therefore, not part of the initial-cohort.

All of the initial-cohort species are well adapted to re-colonizing after catastrophic fire. The vegetative strategies of aspen and paper birch are as evident as the seeding strategies of the pines on FDn33 sites. The substantially higher density of trees in the young growth-stage is due in part to vigorous suckering of aspen. Paper birch sprout well from the root collar, but tend to regenerate at spacing limited by the wider distribution of their parent trees in the pre-disturbance forest. The good success of jack and red pine is probably an indication that stand-regenerating fires were hot and duff-consuming. Both species establish, and we believe compete with aspen, better on mineral soil. In modern forests, both hard pines show almost no inclination to establish seedlings beneath the canopy or on duff typical of mature FDn33 woodlands **(R-2)**. Within the range of the FDn33 community, jack pines tend to have serotinous cones and depend upon hot, canopy-removing fires to open most of their cones.

The ability of the initial-cohort trees to dominate young FDn33 woodlands is a consequence of their persistence in the mature and old growth-stages. With the possible exception of jack pine, all of the initial-cohort trees persist at substantial abundance in old woodlands. 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. Big-toothed aspen is far less capable of persisting in mature forests by filling canopy gaps. White pine is similar to quaking aspen in that it shows excellent ability to establish seedlings in mature forests. It would seem however, that the effects of catastrophic fires were to cleanse FDn33 sites of advance regeneration of white pine as it tended to not often be present at burned survey corners as small-diameter trees. Red pine and paper birch, also maintained a significant presence in older stands and were prepared to re-colonize following fires. Surface fires must have helped to maintain these species and possibly jack pine as white pine exerted dominance in old forests.

A common hypothesis for hardwood dominance (56% of all trees, PLS-1) in regenerating patches of FDn33 habitat is that these patches were burned at least twice in short succession. Catastrophic fires may have usually resulted in good regeneration of jack and red pine, but if burned again before the pines reach sexual maturity, the seed source is lost thus favoring colonization of trees capable of long-distance seeding like quaking aspen, big-toothed aspen, and paper birch. Double burning probably wasn't the usual cause of hardwood dominance in young FDn33 forests, but it could have played a role in the initial establishment of some FDn33 patches.

Transitional Stage: approximately 35-55 years

About 27% of the historic FDn33 landscape was forest undergoing considerable compositional change as stands approached maturity (PLS-1). Stands in this stage were more often mixed (76%) than monotypic (24%). Monotypic conditions were represented by survey corners where all attending trees were aspen, but it was also common for all trees to be red pine. Mixed conditions involved mostly aspen and jack pine, with paper birch, red pine, and white pine contributing less often. Even at this young age, fire-sensitive fir had ingressed and achieved enough diameter to serve as a bearing tree. Fir bearing trees attended 7% of the transitioning corners, which is surprising as we believe that there was almost no fir in the usual, post-fire stand (1%, PLS-3).

The transition stage is driven mostly by the behavior of jack pine and quaking aspen. Initial-cohort jack pine and aspen decline throughout the period (PLS-2). Aspen was the first species to decline, falling sharply from a peak of about 50% relative abundance in the 20-year age class to just about 10% in the 50-year age class. This is amazingly rapid decline. We tend to believe it because it occurs over a span of age classes where data are plentiful and adjacent samples consistent with the idea of a 30-year collapse of the population. In contrast, the decline of jack pine is steady throughout the period, falling gradually from about 16% to 8% relative abundance in the transition and continuing to decline at about the same rate into the mature growth-stage. White pine and paper birch were the immediate benefactors of the loss of aspen and jack pine.

Balsam fir also contributed significantly to the compositional movement during the transition. Fir was not an important initial-cohort tree, rather it had a pulse of recruitment that resulted in peak abundance in the 40-50 year age-classes at about 15% (PLS-2). Curiously, just as it seems that 50-year old FDn33 stands were well on their way to the "spruce-fir climax," the relative abundance of fir collapses to lower levels (~5% relative abundance) that we 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). Several have proposed the idea that balsam fir is a nurse-crop for long-lived conifers. The notion that balsam fir in any way "prepares" sites for 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, black spruce, or white pine rather than sugar maple. On FDn33 sites the effect of the fir pulse is to promote recruitment and regeneration opportunities for white pine and spruce. The rise in spruce abundance during the transition mirrors the decline of pulsing fir more so than the loss of aspen and jack pine. The role of balsam fir certainly wasn't that of a cover crop for spruce, as smaller-diameter spruce almost never (<3%) occurred in the presence of larger firs. If the fir pulse was in any way preparatory for ingress of spruce, the effect was indirect and probably soil-mediated.

Mature Growth-stage: approximately 55-125 years

About 18% of the historic FDn33 landscape was mature forest where the rate of successional change slowed significantly and appears to have been more stable (PLS-4). About 81% of the stands in this stage were mixed. Red pine, white pine, paper birch, aspen, and jack pine were the species most mentioned, but there were many minor species beginning to contribute to the local flora. The surveyors mentioned an amazing 22 different species of trees at survey corners that we modeled to be FDn33 woodland. Fire-sensitive, mesic taxa like maple, yellow-birch, ash, elm, and cedar added to the variety of the mature woodland. The stable composition during the mature growth-stage, and the arrival of fire-sensitive species is rather good evidence that mature FDn33 forests probably were patches of habitat that had escaped fire for some time. Quaking aspen, balsam fir, and white pine have excellent ability to establish and recruit seedlings under the typical FDn33 canopy (R-2), and these species could easily maintain their populations in mature woodlands without disturbance. The persistence and dominance of red pine during this period is attributed to good survival and its longevity. Jack pine show little ability to establish and recruit seedlings under a canopy, and consequently its populations decline during the mature growth-stage.

The big puzzle is the behavior of spruce during the mature growth stage. The historic data clearly show that this period was especially favorable for its establishment and recruitment to the point to where it was an important tree in the following old growth-stage (PLS-1). There is really very little spruce in modern, mature FDn33 woodlands. White spruce was not included in this discussion (R-1, R-2) because of its low suitability (1.8, see Suitability Tables). Not shown in Table R-2 is white spruce's good regeneration indices (3.2-3.3) indicating its ability to establish and recruit seedlings beneath a canopy – which is entirely consistent with spruce invading and rising to importance in the mature growth-stage. However, black spruce had the higher suitability (3.7) due almost entirely to very high mean cover-when-present (46%) and thus, is the species included in this discussion. Black spruce shows almost no ability to establish and recruit seedlings beneath a canopy – which means it is not a good candidate for explaining the rise of spruce importance historically. The poor regenerant and seedling indices (R-2) are surprising given its substantially better performance in similar communities like FDn32. The big difference between mature FDn32 and FDn33 woodlands is the tendency of FDn32 woodlands to offer a mossy seedbed, which would seem to be advantageous to the establishment of black spruce. It is possible that a consequence of modern land management is the loss the historic, mossy seedbeds typical of mature woodlands due to a substantial increase in shade from aspen, birch, and red maple (PLS/FIA-1). If this is the case, then black spruce might well have been the species to experience great success in mature FDn33 woodlands in the past. Alternatively, white spruce could have been the species to succeed historically, and it no longer does because of our inclination to establish red pine plantations on these sites and not reserve white spruce seed trees. We favor this latter hypothesis because when seed trees are present in releves, so is white spruce regeneration.

Old Growth-stage: approximately >125 years
About 15% of the historic FDn33 landscape was old forest (PLS-1). Because FDn33 is common and widespread in north-central Minnesota, 15% in the old growth-stage represented extensive acreage. At this stage, 91% of all survey corners were of mixed composition. White pine, spruce, birch, and red pines were mixed with each other and a very long list of other species that includes a substantial component of fire-sensitive trees. Nearly all monotypic survey corners were ones where white pine or red pine represented all attending trees.

Spruce and white pine are the late-successional trees on FDn33 sites and balsam fir dominated the understory and sub-canopy. Balsam fir and white pine are clearly adept at establishing and recruiting seedlings beneath a canopy (R-2), and were able to rely on that ability to perpetuate their local populations until old stands were re-cycled by fire. White spruce is also capable of persisting in old woodlands by establishment and recruitment, but black spruce is not. Paper birch had modest recruitment abilities in old woodlands, but we believe that enough mineral-soil seedbeds were created by fine-scale disturbances (e.g. tip-ups, slope erosion) to allow birch to persist at low abundance. Red pine was a component of old forests because of its longevity.

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. The thickness of the mor humus typical of old FDn33 sites is commonly 3" or more. Also important is the tendency of FDn communities to develop mossy groundlayers. Many of the late-successional conifers on FDn sites (but absent from FDc communities) are adept at establishing seedlings on mossy substrates. The FDn33 community tends to do this less often than FDn communities farther to the northeast, but still patches of mosses are common in older woodlands. Our interpretation is that the accumulation of duff and perhaps nurse logs played an important role in promoting succession on FDn33 sites and such humus layers characterize the old growth-stage.

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?

Red Pine

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

Suitability

FDn33 sites provide ***excellent habitat*** for red pine trees. The ***suitability rating*** of 4.9 for red pine is influenced mostly by its presence (49%) as trees on these sites in modern forests **(R-1)**. When present, red pine is an important co-dominant or dominant tree, contributing 35% mean cover in mature stands. This ranking is first among trees common on FDn33 sites as sampled by releves. Northern fire-dependent forests in general offer excellent habitat for red pine trees (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically, at 17% relative abundance red pine was an important tree in young FDn33 stands recovering mostly from fire **(PLS-1)**. Young red pines represented 44% of the trees at survey corners described as burned, which is by far the most common tree **(PLS-3)**. Our interpretation is that red pines were important initial-cohort trees on FDn33 sites, because seed trees were usually present in old woodlands. Red pine was also the most abundant tree at windthrown corners (28%), but the lower percentage suggests that fire presented a much better opportunity for establishment. Also, windthrow was such an infrequent event that it wasn't an important means of establishing red pine on FDn33 sites. Small-diameter red pine regeneration is most abundant in the post-disturbance window and was continuously present until the 70-year age-class **(PLS-5, PLS-2)**. Because red pines seemed to recruit throughout the young growth-stage we believe that it had some ability to fill understocked areas of burned stands for several years. In young woodlands, red pine regeneration was mostly coming in under larger red pines.

Transition: 35-55 years

As stands transitioned to mature conditions red pine increased in abundance, presumably because of it was outliving initial cohort aspen and jack pine **(PLS-1, PLS-2)**. Most likely the decline of the initial-cohort trees released some red pine seedlings established during the young growth-stage. At this time, it was about as likely for red pines to be the largest tree at a survey corner as it was to be the smallest one. We believe that this is a consequence of a long window of recruitment from stand-initiation through the transition. Small-diameter red pine regeneration is present at fair levels in the 40-60 year age-classes **(PLS-5)**. We believe that there was limited establishment and recruitment of red pine in response to the breakup of the initial aspen and jack pine canopy. At this time, young red pines were mostly coming in among larger red pines, but there were numerous examples of red pines replacing aspen and jack pine.

Mature Growth-stage: 55-125 years

Red pine had peak abundance as a co-dominant or dominant tree in mature stands, which is why we consider red pine a ***mid-successional*** species – able to replace initial cohort trees but dropping in relative abundance as stands became old **(PLS-1)**. Red pines represented nearly 50% of all bearing trees in the 90- and 100-year age classes **(PLS-2)**. Although most mature survey corners with red pines were of mixed composition, the proportion of pure red pine corners actually increased to about a third of all such corners during the transition. Our interpretation is that patches of FDn33 habitat tended to be more monotypic as aspen and jack pine died, leaving only the longer-lived red pines. Small-diameter red pine regeneration was detectable until the 70-year age-class **(PLS-5)**. We believe that this limited establishment was in response to large gaps in the canopy as some initial-cohort aspen and jack pine finally died. This was important to red pine in that it assured that some seed-trees would carry into the old growth-stage. When red pines were the smaller tree at a corner, they now are almost always under larger red pines. Starting in the transition stage, but most evident in the mature stage is the tendency of red pines to be the larger diameter tree at survey corners. It seems possible that at about this time, red pines reached a stature, where they became rather impervious to surface fires and that the selective pressure of surface fires was to kill shorter trees beneath them, including their own advance regeneration.

Old Growth-stage: >125 years

Rather commonly (13%) stands reached old age **(PLS-1)**. The relative abundance of red pine in old forests declined throughout the period, but did so rather slowly **(PLS-2)**. At this time it was about three times as likely for red pines to be the largest tree at a survey corner as it was for them to be the smallest. When red pine was the smallest tree, it was mostly among larger red pines or sometimes white pines. Our interpretation is that old woodlands had rather pure patches of red pine and that it had limited ability to replace itself, even though we did not detect small-diameter regeneration beyond the 70-year age-class **(PLS-5)**. The long initial window of establishment and recruitment coupled with red pine's longevity is the primary reason FDn33 sites were dominated by red pine throughout succession, which according to our calculations was terminated by catastrophic fires about every 200 years (see Natural Disturbance Regime). We believe that surface fires on a much shorter rotation (80 years) must have provided some regeneration opportunities for red pines in old woodlands, but on the average red pine was losing ground to fire-sensitive species like spruce and even some mesic hardwoods.

Regeneration Strategy

Red pine's primary regenerative strategy on FDn33 sites is to seed into ***open habitat*** after stand-regenerating disturbance. It was substantially better at doing so after fire than following windthrow **(PLS-3)**. In the historic PLS data this interpretation is supported by: (1) red pine's substantial abundance in young FDn33 stands **(PLS-1)**, (2) it was the most abundant tree at burned or windthrown corners **(PLS-3)**, and (3) its peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class **(PLS-2)**. The high percent of red pine as poles in pole stands (situation 22) in the FIA data **(FIA-1)** is also characteristic of species that regenerate effectively in the open. The releve sampling of mature FDn33 woodlands suggests also that red pine needs open habitat to reproduce because it has poor ability to establish seedlings beneath a canopy **(R-2)**.

Historic Change in Abundance

Today, red pine is in peril on FDn33 sites. The low percentage of sapling stands versus the high percentage of pole stands of red pine in the FIA data would suggest less success or effort regenerating FDn33 stands with red pine over the past 30 years **(FIA-1)**. Historically, the relative abundance of red pine in young FDn33 forests was 17% compared to just 1% today **(PLS/FIA-1)**. Equally startling, is the loss of red pine in mature stands where its modern abundance of 1% is dwarfed by its historic dominance at 27% relative abundance. We attribute this decline to logging and stand re-initiation without using fire as a management tool, which can favor aspen on FDn33 sites. Essentially all young red pine on FDn33 sites is now in plantation.

Paper Birch

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

Suitability

FDn33 sites provide ***excellent habitat*** for paper birch trees. The ***suitability rating*** of 4.7 for paper birch is influenced mostly by its high presence (47%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is an important co-dominant and sometimes dominant tree, contributing 19% mean cover in mature stands. The ranking is second, following red pine on FDn33 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 FDn33 communities provide the best commercial opportunities for paper birch.

Young Growth-stage: 0-35 years

Historically, at 16% relative abundance paper birch was an important tree in young FDn33 stands **(PLS-1, PLS-2)**. Young paper birch represented just 6% of the trees at survey corners described as burned, well behind red pine, white pine, aspen, and jack pine **(PLS-3)**. Our interpretation is that immediately after a fire, birch regeneration was almost entirely stump sprouts. Young birch trees responded more favorably to windthrow, representing 14% of the trees at windthrown survey corners, but still behind the common fire-followers. Its better representation at windthrown corners could be from release of advance regeneration as paper birch has fair ability to establish and recruit seedlings beneath a canopy **(R-2)**. Small-diameter paper birch regeneration started low, but increases to peak in the 30- and 40-year age-classes **(PLS-5)**. During this time, paper birch was almost always at mixed survey corners and was almost always the smaller diameter bearing tree. Our interpretation is that paper birch was very good at filling-in among faster-growing aspen and pine in open conditions. Because paper birch was clearly an important initial-cohort tree and because its primary window of establishment was in the young growth-stage, we believe that it was able to function as an ***early-successional*** tree on FDn33 sites.

Transition: 35-55 years

As stands transitioned to mature conditions paper birch increased in abundance, presumably because of continuous recruitment in the young growth-stage and its ability to outlive initial cohort aspen and jack pine **(PLS-1, PLS-2)**. Paper birch had good recruitment in the G-1 gap window that spans the transition stage **(PLS-5)**. Similar to the young growth-stage, most (~70%) of the birch occurred as smaller-diameter trees among larger ones. Most often, it occurred among larger jack pine, aspen, or larger paper birch. It seems clear that birch was doing well beneath itself and was filling canopy gaps as mortality started to affect overstory aspen and jack pine.

Mature Growth-stage: 55-125 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)**. The absolute peak in birch abundance was at about 30% in the 60-80 year age-classes **(PLS-2)**. Beyond that, birch abundance declines, resulting in an average abundance of 19% across the whole growth-stage. Small-diameter birch regeneration was reasonably abundant up until the 80-year age-class, and was detectable up to the 100-year age-class **(PLS-5)**. At this time, smaller diameter birch occurred mostly among larger birch, red pine, white pine, and aspen. Our interpretation is that birch had some success replacing itself and recruiting beneath pine. The losses of birch were mostly in pockets where spruce and fir achieved dominance. It is possible that patches with a fair amount of birch and little spruce and fir, were places where surface fires had burned through older FDn33 woodlands.

Old Growth-stage: >125 years

Paper birch persisted in the old growth-stage at about 14% relative abundance **(PLS-1, PLS-2)**. If persistence requires regeneration and recruitment, then we must assume that paper birch has secondary strategies that make it able to respond to fine-scale or maintenance disturbances. The ability of paper birch to establish and recruit seedlings through all height strata in modern FDn33 woodlands is just fair, suggesting that it can persist at low abundance under a regime of fine-scale disturbance on such sites **(R-2)**. The indices for germinants and seedlings (2.5) are more in line with species that require quite large openings. Surface fires might explain the persistence of paper birch into the old growth-stage because it did well after stand regenerating fire. This seems highly likely because during the old growth-stage it tends to co-occur with other species that did well in the initial-cohort. Alternatively, other maintenance disturbances such as pocket-diseases could have created the few-tree gaps where paper birch enjoys modest success in modern forests. Some birch occurred with larger-diameter spruce, but not balsam fir. This might point more towards *Armillaria* pockets than spruce budworm as the agent creating regenerative opportunities for birch in old woodlands.

Regeneration Strategies

FDn33 sites are such good habitat for paper birch that it is an important or dominant tree throughout the course of succession. It is clear that birch has multiple strategies for regeneration and survival, and that those strategies were successful in all growth-stages. By any of our measures, birch was successful any time light made it to the ground. 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 in mature forest where we suspect rather small gaps **(PLS-3)**, (3) and it has good establishment in a gap window where we presume large gaps **(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 fair ability to establish and recruit seedlings **(R-2)**. The index values of 2.5 to 4.2 in the regenerating layer are most in line with species that do well in very large-gaps.

Paper birch was also able regenerate and sometimes dominate ***open habitat*** after stand-regenerating events. It was successful after fire, but was more so after windthrow. We believe that the initial cohort of young birch was composed of both stump sprouts and some 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 fair at burned survey corners **(PLS-3)**, and its peak regeneration in the post-disturbance window **(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 can perform in the open **(FIA-1)**.

Historic Change in Abundance

Today, paper birch remains an important co-dominant tree on FDn33 sites **(PLS/FIA-1)**. In young forests there is considerably less paper birch today (5%) than there was historically (16%). Most likely, this is the consequence of logging not providing the mineral-soil seedbeds for birch as did fire. Today, logging favors coppiced aspen far more than birch, but birch has held its own far better than the pines. In the older growth-stages, birch is slightly more abundant than it was historically. Because of birch's plastic abilities to regenerate on FDn33 sites, it should continue to be an important co-dominant regardless of management strategy.

White Pine

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

Suitability
FDn33 sites provide ***excellent habitat*** for white pine trees. The ***suitability rating*** of 4.7 for white pine is the result of rather balanced presence (31%) and mean cover-when-present (27%) as trees on these sites in modern forests **(R-1)**. When present, white pine is an important co-dominant and sometimes dominant tree. The ranking is third, behind red pine and just barely behind paper birch on FDn33 sites as sampled by releves. Except for FDn12, northern fire-dependent forests offer excellent habitat for white pine (see Suitability Tables). Among these FDn33 is about as good as any in providing commercial opportunity for white pine.

Young Growth-stage: 0-35 years
Historically, white pine was a minor tree in young FDn33 stands **(PLS-1, PLS-2)**. Young white pines represented 24% of the trees at survey corners described as burned, second only to red pine **(PLS-3)**. Our interpretation is that some white pines got their start on FDn33 sites by seeding on mineral soil exposed by hot fires. White pines represented 20% 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. No white pine regeneration coming in among larger trees was detectable throughout the 0-30 year post-fire window **(PLS-5)**. Apparently, white pine bearing trees at burned survey corners were all large diameter trees that survived the fire and caused us to assign the corner to an older growth-stage.

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 in the later age-classes of young woodlands and continued throughout the remainder of the successional cycle **(PLS-2)**. Small-diameter, white pine regeneration coming in among larger trees was consistently present throughout the transition **(PLS-5)**. At this time it was about equally likely for white pines to be the largest tree at a survey corner as it was for it to be the smallest one. This is the signature of a species with steady recruitment over several years. In most cases, white pine regeneration was coming in under other white pines, meaning that fires on FDn33 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 red pine or paper birch. We interpret this as good success at establishment and recruitment of seed-origin white pines under a canopy of initial-cohort trees. White pine has excellent ability to establish seedlings and good success recruiting to saplings under a canopy in modern FDn33 woodlands **(R-2)**.

Mature Growth-stage: 55-125 years
In the mature growth-stage the relative abundance of white pine continues to steadily increase as the woodland matures **(PLS-1, PLS-2)**. 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 not detected using our stringent half-diameter rule, but its ability to develop advance regeneration in modern forests is quite good **(R-2)** and we suspect that white pines were able to sustain or increase their local populations by establishment and recruitment. In the mature growth-stage white pines occurred mostly at survey corners of mixed composition and it was the largest or smallest tree about equally often. Our interpretation is that white pine continued to establish seedlings, recruit to taller strata, and replace other species throughout the period.

Old Growth-stage: >125 years
In the old growth-stage white pine was and important co-dominant, occurring almost always at survey corners of mixed composition. At 30% relative abundance, it was the most common tree on old FDn33 sites **(PLS-1)**. Because of its dominance in the old growth-stage, we consider white pine to be ***late-successional*** on these sites. However, we believe that white pine's presence in old stands was largely a consequence of its longevity, as most of its regeneration opportunities occurred in the transition and early age-classes of the mature growth-stage. Small-diameter, white pine regeneration coming in among larger trees was not detected during the old growth-stage **(PLS-5)**. By the old growth-stage, it became far more common for white pine to be the largest tree at the survey corners. This supports the idea white pine dominance by longevity more so than by continued establishment and recruitment. 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. 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 in old woodlands, white pine had some regeneration success in patches of FDn33 habitat that were not yet invaded by white spruce.

Regeneration Strategies
White pine's primary regenerative strategy on FDn33 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 red pine and paper birch. 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 where we presume the formation of large canopy-gaps **(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 the G-1 gap window rather than post-disturbance or ingress windows **(PLS-5)**. The releve sampling of mature FDn33 forests also suggests that white pine is favored in large gaps. The regenerant and seedling indices are excellent (4.0), meaning that establishment beneath a canopy is not a problem for white pine **(R-2)**. The lowest index was for white pine saplings (3.5), suggesting that recruiting white pine seedlings to heights taller than 2m is a regenerative bottleneck for white pine under a canopy. This bottleneck is typical of species that need a bit more light than is offered by single- or few-tree gaps in the undisturbed FDn33 forests that were sampled by releves.

Historic Change in Abundance
Today, white pine is mostly gone from the FDn33 landscape. It accounted for just 1% of the FIA trees in any forest estimated to be younger than 125 years **(PLS/FIA-1)**. Historically, mature FDn33 woodland represented the most common landscape condition, and 19% of the trees in stands that age were white pines. Today white pine is common only in old FDn33 woodlands (19% relative abundance), which in general cover far less of the landscape than they once did. The releve sampling paints a substantially brighter picture of white pine's current status. White pine has fairly high presence as a tree (31%, **R-1**)) and higher presence (43%, **R-2**) in the understory. The releve sampling is biased, favoring ecologically intact remnants of FDn33 forests. However, the presence of white pine was not a deciding factor in plot location and most of the 124 releve plots were on sites previously logged and still available for commercial interests. Our interpretation is that white pine is doing just fine in stands where there are several old seed trees. The issue would seem to be the general lack of old white pines in the landscape, and just establishing seed trees on sites that lack them, would probably ensure the future of white pine in FDn33 woodlands.

Quaking & Big-toothed Aspen

- ***excellent habitat suitability rating for quaking aspen***
- ***good habitat suitability rating for big-toothed aspen***
- ***early successional***
- ***open (large-gap) regeneration strategists***
- ***regeneration window at 0-30 years***

Identification Problems

The PLS surveyors did not distinguish between quaking and big-toothed aspen. Thus, interpretations of PLS data for the more common quaking aspen should always be done knowing that some of these trees were likely big-toothed aspen. FDn33 releve samples show that for plots with aspen present: 15% have both species present; 18% are big-toothed aspen without quaking aspen; 67% are quaking aspen without big-toothed aspen. We consider quaking and big-toothed aspen to be ecologically equivalent for most silvicultural considerations.

Suitability

FDn33 sites provide ***excellent habitat*** for **quaking aspen** trees. The ***suitability rating*** of 4.5 for quaking aspen is influenced mostly by its very high presence (35%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is an important co-dominant and sometimes dominant tree, contributing 20% mean cover in mature stands. This ranking is fourth, behind red pine, paper birch, and white pine on FDn33 sites. In general, the richer FDn communities, FDn32, FDn33, and FDn43 offer excellent habitat for quaking aspen (see Suitability Tables).

FDn33 sites offer ***good habitat*** for **big-toothed aspen**. The ***suitability rating*** of 3.8 for big-toothed aspen is based upon its 15% presence and 19% mean cover when present. This ranking is seventh among trees common on FDn33 sites. FDn33, and FDn22 communities are the only FDn communities that provide opportunities to grow big-toothed aspen (see Suitability Tables).

Young Growth-stage: 0-35 years

Historically at 40% relative abundance, aspen was a dominant tree in young FDn33 stands recovering mostly from stand-regenerating fire **(PLS-1, PLS-2)**. Young aspen represented 13% of the trees at survey corners described as burned, which follows the pines **(PLS-3)**. Aspen was a leading species following windthrow, representing 26% of the trees at such survey corners. Young FDn33 corners with quaking aspen trees present were mostly mixed in composition (68%), but often (22%) all of the bearing trees were aspen. Its dominance in the young growth-stage and its peak abundance following fire and windthrow is why we consider aspen to be an ***early successional*** species on FDn33 sites. Small-diameter, 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 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 FDn33 forests was driven in-part by rapid loss of initial-cohort aspen leaving longer-lived paper birch and red pine **(PLS-2)**. We estimate that this decline started at about age 30, with aspen declining from about 50% relative abundance to about 10% by the 40-year age-class to initiate compositional changes in the following transition. Small-diameter aspen regeneration was detectable throughout the transition to the 60-year age-class **(PLS-5)**, but is was insignificant in comparison to the abundant regeneration in the post-disturbance environment. When aspen was the smaller tree at a survey corner, it was sometimes beneath initial-cohort jack pines, but most was beneath larger aspen. In fact, 11% of all transitioning survey corners were pure aspen. We interpret this as modest replacement of itself in large gaps within monotypic patches of aspen.

Mature and Old Growth-stages: 55-125 years, and older
By the time FDn33 stands reached the mature growth-stage the relative abundance of aspen held steady between 5-10% of the bearing trees **(PLS-1)**. From this point forward, aspen played no significant role in stand dynamics. Except for the 60-year age-class, small-diameter quaking aspen regeneration coming in among larger trees was not detected in the older growth-stages **(PLS-5)**. When present as the smaller tree at a survey corner, aspen was among other initial-cohort trees such as red pine, white pine, jack pine, or itself. Our interpretation is that the pines cast only partial shade giving aspen some chances at recruitment, and that there were still a few patches of FDn33 habitat that were mostly aspen. The ability of aspen to recruit seedlings or suckers through all height strata in modern FDn33 forests is surprising, its excellent performance suggests that it can persist under a regime of fine-scale disturbance on FDn33 sites **(R-2)**. Its regeneration indices (4.2-4.3) are quite in line with species able to regenerate in small-to-large gaps. Historically, this ability must have allowed aspen to persist into the older growth stages and allowed it to dominate young forests after fire.

Regeneration Strategies
Quaking aspen's primary regenerative strategy on FDn33 sites is to dominate ***open habitat*** after stand-regenerating fires. In the historic PLS data this interpretation is supported by: (1) the fact that 40% of the bearing trees in young stands were aspen **(PLS-1)**, (2) aspen represented a significant 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 **(PLS-2)**. The high percent of quaking or big-toothed 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. Big-toothed aspen has much less regenerative ability than quaking aspen under a canopy with regeneration indices of just 1.8-3.3 **(R-2)**, suggesting that it is strictly an open regeneration strategist.

The releve sampling of mature FDn33 forests suggests, however, that quaking aspen is able to function also as a ***large-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 species that can use either small or large gaps. Significant abundance of quaking aspen in subordinate situations (12, 23, 13) at FIA subplots support also the idea that aspen can regenerate in large or 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.

Historic Change in Abundance
Today, aspen is an important and often dominant tree on FDn33 sites **(PLS/FIA-1)**. Most (74%) young FDn33 stands are dominated by aspen, which is a significant increase over the historic condition where aspen accounted for 40% of the trees in young stands. Aspen also shows considerable gains in the mature growth-stage where it now has 48% relative abundance compared to just 9% in the pre-settlement forest. Our interpretation is that aspen has benefited greatly from logging on rotations that are much shorter than the natural fire cycle and also benefited from the general loss of conifers on the FDn33 landscape.

Jack Pine

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

Suitability
FDn33 sites provide ***excellent habitat*** for jack pine trees. The ***suitability rating*** of 4.0 for jack pine is a consequence of balanced presence (18%) and mean cover-when-present (18%) on these sites in modern forests **(R-1)**. The ranking is fifth, following red pine, paper birch, white pine, and quaking aspen on FDn33 sites as sampled by releves. Northern fire-dependent forests in general offer fair-to-excellent habitat for jack pine trees (see Suitability Tables). Among the FDn communities, jack pine is favored on sites poorer and drier than FDn33.

Young Growth-stage: 0-35 years
Historically, at 15% relative abundance jack pine was an important co-dominant in young FDn33 stands recovering from any disturbance, but especially after fire **(PLS-1, PLS-2)**. Young jack pines represented 10% of the trees at survey corners described as burned which surprisingly, is considerably less than red pine, white pine and aspen **(PLS-3)**. Normally, jack pine is favored over these species where fires burn hot and to the mineral soil. Perhaps the deciduous component of FDn33 woodlands helped to mute the effects of fire on the ground or helped to create a patchier exposure of mineral soil. Jack pine was not especially important (5% relative abundance) following windthrow, which further suggests that the mineral soil seedbed was important to regenerating jack pine. Jack pine's peak abundance in the young growth-stage and its importance following fire is why we consider it to be an ***early successional*** species on FDn33 sites. In contrast to most communities where jack pine is initially important, we recorded no survey corners where all bearing trees were jack pine. Rather, it was mixed with regenerating aspen. Small-diameter jack pine regeneration coming in among larger trees was abundant for the throughout the young growth-stage **(PLS-5)**, and jack pine regeneration was common until about the 60-year age-class.

Transition: 35-55 years
Natural succession, or transitioning of young FDn33 forests was driven in-part by the steady loss of initial-cohort jack pine leaving longer-lived red pine and some paper birch **(PLS-1)**. We estimate that this decline started in the young growth-stage and continued at a steady pace throughout the transition and into the mature growth-stage **(PLS-2)**. The jack pine establishment window lasted throughout the transition **(PLS-5)**. We believe that this allowed for jack pine to persist at low abundance, but second-cohorts of jack pine probably didn't develop without further disturbance. During the transition period, jack pine remained an important tree, but still it occurred only in mixture with other species. Most often it was the largest tree at a survey corner, which is typical of initial-cohort trees. When it was the smaller tree at a corner, it was among larger jack pine, red pine, or aspen. Trees beneath aspen were probably just suppressed initial-cohort jack pines. Trees beneath jack pine or red pine could be younger trees that regenerated and recruited in the young growth-stage.

Mature and Old Growth-stages: 55-125 years and older
In mature FDn33 stands the relative abundance of jack pine stabilizes at about 5-10% and it had little influence on stand dynamics **(PLS-1)**. Although much diminished from earlier growth-stages, jack pine somehow managed to persist in old woodlands. If jack pine's continued dominance required regeneration and recruitment, then we must assume that jack pine has secondary strategies for behaving like a mid-successional species able to respond to fine-scale or maintenance disturbances. Jack pine's poor ability to establish and recruit seedlings in modern FDn33 forests diminishes the possibility of it responding to fine-scale disturbance **(R-2)**. Most likely, the primary limitation to establishing seedlings is the tendency of jack pine to have mostly closed, serotinous cones in on FDn33 sites. Unusually warm weather can open some cones,

especially on older, senescent branches; however, seedfall followed by establishment, and recruitment was inadequate to sustain ~7% relative abundance of jack pine in older forests. This leaves only the likelihood that jack pine responded very favorably to surface fires, which is obvious in its reaction to burned over lands and high presence (14%) at survey corners affected by maintenance disturbance **(PLS-3)**. Unlike the transition stage, jack pine in mature forests was coming in mostly under red pine, which could have easily survived surface fires. Our best guess is that surface fires tended to favor the persistence of both jack and red pine in older woodlands and positioned them to do well in the initial cohort when stand-regenerating fires eventually occurred.

Regeneration Strategy

Jack pine's primary regenerative strategy on FDn33 sites is to dominate ***open habitat*** after stand-regenerating fire. In the historic PLS data this interpretation is supported by: (1) the fact jack pine has peak relative abundance in the young growth-stage **(PLS-1)**, (2) jack pine was important at burned corners **(PLS-3)**, and (3) jack pine's peak regeneration was in the post-disturbance window with it's absolute peak being the initial age-class **(PLS-5)**. The limited ability of jack pine to regenerate under a canopy in modern forests **(R-2)** supports strongly the idea that surface fires, mineral soil seedbeds, and rather open conditions are required for second-cohorts of jack pine to form beneath red pine.

Historic Change in Abundance

Today, jack pine is in peril on FDn33 sites. The low percentage of sapling stands versus the higher percentage of pole stands of jack pine in the FIA data would suggest less success or effort regenerating FDn33 stands with jack pine over the past 30 years **(FIA-1)**. Historically, the relative abundance of jack pine in young FDn33 forests was 15% compared to something lower than a full percent today **(PLS/FIA-1)**. Equally startling, is the loss of jack pine in mature stands where its modern abundance of <1% is substantially lower than its historic abundance at 7%. We attribute this decline to logging and stand re-initiation without using fire as a management tool, which tends to favor aspen on FDn33 sites. Essentially all young jack pine on FDn33 sites is now in plantation.

Balsam Fir

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

Suitability
FDn33 sites provide ***excellent habitat*** for balsam fir trees. The ***suitability rating*** of 4.0 for balsam fir is influenced mostly by its presence (20%) as trees on these sites in modern forests **(R-1)**. When present, balsam fir is often a co-dominant tree, contributing 14% mean cover in mature stands. The ranking is sixth, behind red pine, paper birch, white pine, quaking aspen, and jack pine on FDn33 sites as sampled by releves. As long as the soils are fairly deep (not FDn22), northern fire-dependent forests (FDn) offer good-to-excellent habitat for balsam fir (see Suitability Tables). Balsam fir is favored on the richer or moister FDn43 sites over sandy sites like FDn33 and FDn12.

Young Growth-stage: 0-35 years
Historically, balsam fir was a minor tree in young FDn33 stands **(PLS-1, PLS-2)**. Young firs were barely present at survey corners described as burned, windthrown, or having suffered partial canopy loss due to maintenance disturbances **(PLS-3)**. Fire was by far the most frequent disturbance in FDn33 forests, and we believe that it was extremely effective in eliminating fir trees and all advance regeneration. Because of balsam fir's affinity for wetter habitats included in the FDn33 landscape, we believe that seed sources were usually present, and that fir was able to start re-colonizing burned FDn33 sites fairly soon after fires. Small-diameter balsam fir regeneration was first detected in the 30-year age class and it increased dramatically to peak at 40 years **(PLS-5, PLS-2)**. In fact, the presence of fir in the young growth-stage was entirely as small-diameter regeneration, which is typical of an invading species. When present, it was most often coming in among larger jack pines. Post-fire thickets of pine and quaking aspen were probably fine habitat for young seed-origin firs, particularly at the stage where the groundlayer is suppressed and the initial-cohort trees start to self-thin. Supporting this argument is the excellent performance of balsam fir seedlings under a canopy in modern FDn33 forests **(R-2)**. The closing years of the young growth-stage and early years of the transition offered the best window of opportunity for initial ingress and recruitment of balsam fir.

Transition: 35-55 years
The transition to mature conditions is mostly the consequence of the steady loss of initial-cohort aspen and jack pine leaving longer-lived trees like red pine **(PLS-1)**. The transition is characterized by a pulse of fir abundance, which was a major contributor to movement in ordination space **(PLS-4)** and definition of the transition period. Fir was essentially absent in the post-disturbance years but rises to nearly 15% of the trees in the 40-year age-class – only to have the local populations collapse to just 4% relative abundance by the start of the mature growth-stage **(PLS-2)**. The pulse of fir regeneration **(PLS-2)** resulted in recruitment of very few trees. For most of the transition stage, balsam fir was small-diameter regeneration. It was more than ten-times as likely to be the smallest bearing tree at a survey corner than it was for it to be the larger tree. It seems to us that balsam fir was little more than a mid-canopy tree similar to ironwood in northern hardwood stands. The inability of fir to reach tree heights is common on droughty sites throughout northern Minnesota, and recruitment doesn't improve until water tables are within reach of their roots (~10 feet). We are uncertain if fir played an ecological role in transitioning FDn33 forests. As often observed, ingress of spruce and white pine followed the fir pulse; however, the benefit to these trees must have been indirect as no spruce regeneration was observed coming in among fir bearing trees. It is possible that the rapid demise of fir to close the transition period was due to the density-dependent reaction of spruce budworm to abundant fir.

Mature and Old Growth-stages: 55-125 years, and older

In the mature growth-stage balsam fir abundance stabilized at about 4-5%, and it played no further important role in stand dynamics **(PLS-1)**. Balsam fir's relative abundance in the mature growth-stage is the result of ingress and recruitment between the 30 and 60-years age-classes **(PLS-5)**. Continued small-diameter regeneration was not observed in the mature growth-stage. However, almost all fir bearing trees in the older growth-stages were the smallest tree at the survey corners, suggesting renewed attempts at recruitment. In modern forests, balsam fir is second only to red maple in its ability to establish and recruit seedlings beneath a canopy **(R-2)**. It excellent ability to do this must have allowed for it to persist indefinitely in older woodlands that were unaffected by surface fires. In fact, the rather low abundance of fir in older woodlands is probably good evidence that most older stands had been affected by surface fires.

Regeneration Strategies

Balsam fir's primary regenerative strategy on FDn33 sites is to build a bank of seedlings in the groundlayer and to then recruit saplings in gaps. We believe that the ingress of balsam fir happened early during aspen and jack pine self-thinning, and that they persisted in suppression until gaps opened above them to create the pulse of fir recruitment. Balsam fir's ***large-gap*** abilities is evident in the historic PLS data by: (1) the their immediate increase in abundance in response to the decline of initial-cohort aspen **(PLS-1, PLS-2)** and, (2) its peak recruitment in the G-1 gap window rather than the post-disturbance or ingress windows **(PLS-5)**.

In the modern data, it is clear that balsam fir is an able competitor in filling ***small-gaps***. The high percentage of balsam in subordinate situations in the FIA data (situations 12 and 13) is especially characteristic of species successful in small gaps **(FIA-1)**. Most significant though, is its excellent ability to establish and recruit seedlings under a canopy in modern stands **(R-2)**. Its historic persistence in older woodlands **(PLS-1)** and at undisturbed survey corners **(PLS-3)** is further testimony to its small-gap abilities.

Historic Change in Abundance

Today populations of balsam fir have increased substantially in FDn33 forests compared to its historic abundance **(PLS/FIA-1)**. We believe that this is a consequence of fire suppression and fir's obvious abilities to function as a shade-tolerant, gap strategist. The increase in fir is obvious in the young growth-stage where it now represents 7% of the young trees in FIA samples compared to just 1% historically. We believe that post-fire FDn33 stands started naturally with almost no balsam fir, whereas now they have significant initial presence after logging. The disparity in fir abundance is similar in mature FDn33 forests where historically it was just 4% of the trees, but now is 11% of the FIA trees. In these older forests though, tree-sized firs are usually smaller than other species and do not contribute much to stand volumes. In the releve samples of mature forests, balsam fir had peak cover in the understory or subcanopy in 93% of the cases. This is evident also in Tables **R-1** and **R-2**, where it has far greater presence as regeneration (65%) compared to its presence as a tree (20%). 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.

Red Maple

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

Suitability
FDn33 sites provide ***good habitat*** for red maple trees. The ***suitability rating*** of 3.8 for red maple is influenced mostly by its presence (27%) 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 FDn33 sites. Only the FDn33 and FDn43 offer good habitat and commercial opportunities for red maple among FDn communities (see Suitability Tables).

Young Growth-stage: 0-35 years
Historically, red maple was present in just trace amounts in young FDn33 stands recovering mostly from fire **(PLS-1, PLS-2, PLS-3)**. Small-diameter red maple regeneration was present at low abundance in the post-disturbance window, but was increasing at the close of the period **(PLS-5)**. Our interpretation is that fire effectively eliminated red maple from FDn33 sites. Like balsam fir, red maple is sufficiently shade-tolerant to invade the thicket-like growth of quaking aspen common in young FDn33 woodlands **(R-2)**.

Transition: 35-55 years
As stands transitioned to mature conditions red maple abundance peaks at 3% relative abundance in the 40-year age-class **(PLS-2)**. 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 40year age-class 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 aspen, red pine, or white pine. Our interpretation is that red maple was able to seed into young FDn33 stands and that it enjoyed limited success recruiting seedlings to tree status beneath pines or as the initial-cohort canopy of quaking aspen disintegrated.

Mature and Old Growth-stage: 55-125 years and older
In the mature and old growth-stages the abundance of red maple had steady presence and abundance at about 2% **(PLS/FIA-1)**. Small-diameter red maple regeneration was present until the 80-year age-class **(PLS-5)**. At this time, red maple showed a clear preference for replacing less tolerant trees, especially paper birch, but also red pine, white pine, and quaking aspen. 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.

Regeneration Strategies
Red maple's primary regenerative strategy on FDn33 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 the G-1 gap window rather than post-disturbance or ingress windows **(PLS-5)**. The FIA data show red maple to be successful in any regenerative situation (situations 12,13, and 23; **FIA-1)**, but it was most abundant in situation 23, which we associate with large-gap species. Red maple's regeneration and recruitment indices are excellent (4.3-4.7) and most in line with ***small-gap*** strategists that are good at banking seedlings under a canopy **(R-2)** and then recruiting them to sapling size, even in single-tree gaps.

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 FDn33 forests where it has increased from trace relative abundance to about 4-9% 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" FDn33 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 94% 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 FDn33 sites may be a hindrance to managing these sites for the gap and open regeneration strategists that were more common historically.

Black & White Spruce

- ***good habitat suitability rating for black spruce***
- ***poor habitat suitability rating for white spruce***
- ***late-successional***
- ***large-gap (small-gap) regeneration strategists***
- ***regeneration window at >70 years***

Identification Problems

The PLS surveyors did not distinguish between black and white spruce. This presents a major difficulty in interpreting the historic data. FDn33 releve samples show that for plots with spruce present: there were no plots with both species present as trees; 69% are white spruce without black spruce; 31% are black spruce without white spruce. The lack of any releves with both species in the canopy suggests that these trees are not at all alike. About 14% of the releves have both species in the understory. These species do share the tendency to be ***late-successional*** on FDn33 sites. Spruce of any kind was infrequent at PLS survey corners younger than 70 years, but it increases thereafter. In the FIA data, where the spruce are distinguished, both white and black spruce are largely absent from subplots estimated to be 70 years or younger and both species increase steadily as stands age – just as we see in the historic data. The rate of increase is about twice as fast for white spruce as it is for black spruce, which seems consistent with the 2:1 ratio of white spruce to black spruce in our releves. Thus, the discussion of generic spruce's historic role during succession is probably valid and applicable to either species. We will, however, rely more on the modern data to explain stand dynamics in cases where their silvics and suitability seem to differ.

Suitability

FDn33 sites provide ***good habitat*** for black spruce trees. The ***suitability ranking*** of 3.7 for black spruce is influenced mostly by its very high presence (46%) mean cover-when-present **(R-1)**. Black spruce though is quite infrequent, occurring in just 6% of the 124 FDn33 releves. This ranking is ninth among trees common on FDn33 sites. Of the FDn communities, only FDn33 and FDn32 offer any real commercial opportunities for black spruce (see Suitability Tables).

The ***poor habitat suitability ranking*** of 1.8 for white spruce is based upon its 12% presence and very low mean abundance of just 4% when present. In general, we don't consider FDn33 sites as suitable for white spruce.

Young Growth-stage: 0-35 years

Historically, spruce was present in just trace amounts in young FDn33 stands **(PLS-1)**. Young spruce represented just 1% of the trees at survey corners described as burned, well behind fire-tolerant species like the pines, quaking aspen, and paper birch **(PLS-3)**. Small-diameter spruce was detected as early as the 30-year age-class at the close of the young growth-stage **(PLS-5)**, but it never reached 1% relative abundance of recruiting bearing trees throughout the growth-stage. All occurrences of spruce in the young growth-stage were as the smallest tree at the corner, and it was always in mixture with other species. Our interpretation is that spruce played no important role in regenerating FDn33 woodlands.

Transition: 35-55 years

As stands transitioned to mature conditions spruce slightly in abundance **(PLS-1)**. At this time spruce represented just 2% of the bearing trees. Small-diameter, spruce regeneration coming in among larger trees was detected throughout the transition **(PLS-5)**. In fact, all of the spruce detected during the transition were the smaller-diameter trees at survey corners, which is typical of new colonization. It is clear that the transition was a period of limited establishment of spruce, but neither species is particularly good at establishment under a canopy **(R-2)**. Our interpretation is that spruce establishment was limited to scattered microhabitats where both seedbed and light conditions just happened to be right. Most likely, these opportunities were tied to the decline of some canopy aspen and early pulses of fir, which seems to prepare sites for successful recruitment of spruce.

Mature Growth-stage: 55-125 years

In the mature growth-stage, spruce abundance increases dramatically on a trajectory that continued to increase in old FDn33 woodlands **(PLS-1, PLS-2)**. Throughout this episode, spruce occurred only at survey corners of mixed composition. It was about twice as likely for spruce to be the smallest tree at survey corners rather than the largest tree. This is typical of a species continuing to ingress by developing a bank of understory seedlings and saplings. Small-diameter spruce regeneration was commonly coming in among larger trees in age-classes spanning the mature growth-stage, suggesting continuously improving chances for establishment and recruitment **(PLS-5)**. At this time, spruce regeneration was coming in beneath almost any less tolerant species such as white pine, red pine, aspen, paper birch, and jack pine.

In the modern data both black and white spruce show substantially less ability establish and recruit seedlings under a canopy **(R-2)**. White spruce show fair ability in all height strata, which might account for the modest abundance of spruce in historic woodlands. Black spruce has poor ability to establish seedlings, but good ability to recruit them to heights over 2m. Our impression is that poor establishment is related to the lack of mossy seedbeds, because in similar communities with such seedbeds (e.g. FDn32) black spruce has much better regenerant and seedling index values. We believe that the conversion of FDn33 sites from predominantly coniferous forest to predominantly hardwood forests of aspen and birch **(PLS/FIA-1)**, had reduced the likelihood of a mossy forest floor and diminished regeneration opportunities for black spruce. In the FIA data, both species have peak abundance as poles beneath trees **(FIA-1)**, which we associate with species filling large-gaps. Our best guess is that banks of spruce seedlings gradually accumulate on the forest floor, survive well in suppression, and are capable of filling gaps as initial-cohort pines, aspen, and birch die.

FDn33 woodlands were no exception to the general rule that spruce ingress follows the pulse of fir abundance in the transition. As usual, spruce bearing trees were not coming in among larger firs, which means that the effect of fir was indirect. Dense understory fir have the effect of killing shrubs and groundlayer plants, and greatly acidifying the soil surface. Apparently, this effect is good for spruce establishment. Silviculturally, this suggests that underplanting of spruce should be postponed until the fir pulse is completed at about 60 years.

Old Growth-stage: >125

In the mature growth-stage, spruce abundance plateauedl or slightly increased **(PLS-2)**. Throughout this episode, spruce occurred only at survey corners of mixed composition. For the first time it was common for spruce to be the largest tree as survey corners (~7% of all corners). However, it was still about three-times more likely for them to be the smallest tree at a corner (20% of all corners). Small-diameter spruce regeneration coming in among larger trees was abundant in this growth-stage **(PLS-5)**. At this time, spruce regeneration was still most common beneath less tolerant species, but now a fair amount was beneath larger spruce. This suggests that patches of pure spruce started to form in woodlands this old. Old FDn33 woodlands were characterized by spruce-dominated mid- and sub-canopies beneath aging red pine, white pine, and younger, emergent white spruce. Our interpretation is that spruce is a climax species on FDn33 sites and could maintain its populations indefinitely until catastrophic fire would regenerate the woodland.

Regeneration Strategies

White spruce's primary regenerative strategy on FDn33 sites was to develop a bank of seedlings and to then recruit saplings in ***small-gaps***. It was successful at doing this under any other tree, but it was especially successful replacing red pine, white pine, jack pine, aspen, and paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that spruce abundance peaks in the mature 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) it has fair recruitment in the I-1 ingress window **(PLS-5)**. In modern forests, white spruce shows just fair ability to establish seedlings under a canopy **(R-2)**. White spruce's indices are more in line with species needing ***large-gaps***. It's peak abundance as poles in tree stands is also consistent with the need for large-gaps **(FIA-1)**.

Because the surveyors did not distinguish spruce, we are forced to conclude also that **black spruce's** historic preference was to also recruit in small-gaps. In releves, it is clear that black spruce is having difficulty establishing seedlings beneath a canopy and has indices that suggest it needs far more light than is offered in small gaps **(R-2)**. It's peak abundance as poles in tree stands (situation 23) is most consistent with ***large-gap*** species **(FIA-1)**. However, its abundance in young sapling and pole stands (situations 11 and 22) is more indicative of open regeneration strategists. When compared to white spruce in either the FIA or releve data, it seems that black spruce needs substantially more light than white spruce for successful recruitment.

For spruce, we are forced to make some guesses about their light requirements because of some disparity in the data sets. All data sources suggest that spruce establishment and recruitment is hindered by hardwoods, whether naturally in young, aspen-dominated FDn33 woodlands – or less-naturally in modern, older stands where management has favored greater abundance of hardwoods. We are committed to the idea that the natural pattern was for both species to build seedling banks as stands became increasingly coniferous and poor, and to then recruit in gaps. In today's practice, the existing cover-type will alter any strategy for establishing spruce through partial harvesting. In hardwood cover-types, it would seem that ***large-gaps*** are essential and that artificial establishment would be required. For stands that seem to be on the natural course of succession and are predominantly coniferous, the presence advance regeneration and recruitment success in ***small-gaps*** seems a safe strategy.

Historic Change in Abundance

Today spruce is in some peril in FDn33 woodlands. It musters no more than 1% relative abundance in any growth-stage in forests sampled by FIA plots **(PLS/FIA-1)**. This is most evident in the mature and old growth-stages where it once accounted for 5-13% of all trees. In part, we blame this situation on the tendency for FDn33 woodlands to have far more deciduous trees in older growth-stages today. This seems to effectively diminish establishment and recruitment of spruce. Also significant, it the fact that there just aren't a lot (1%) of old FDn33 woodlands on the landscape in comparison to historic times (15%). It would seem to us that some restorative effort should be aimed at improving the presence of spruce as seed trees on FDn33 sites, and at allowing some stands to achieve old age.

(PLS-1) Historic Abundance of FDn33 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the FDn33 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.

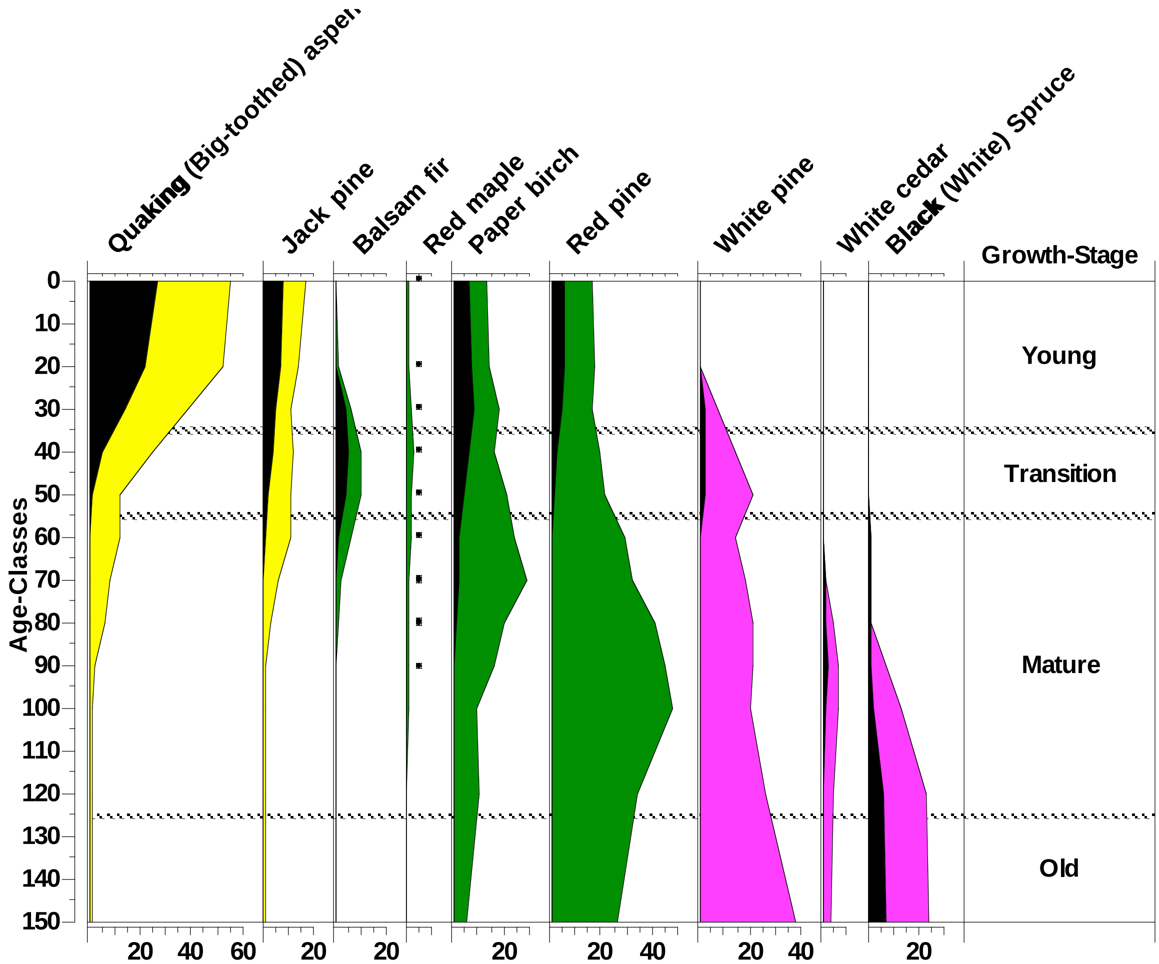
Dominant Trees	**Forest Growth Stages in Years**				
	0 - 35	**35 - 55**	**55 - 125**	**~125**	**> 125**
	Young	**T1**	**Mature**	**T2**	**Old**
Quaking (Big-toothed) Aspen[1]	**40%**	||	**9%**	|	**7%**
Jack Pine	**15%**	|	**7%**	|	**2%**
Red Pine	**17%**	⌉	**27%**	||	**16%**
Paper Birch	**16%**	⌉	**19%**	|	**14%**
Balsam Fir	**1%**	⌉	**4%**	⌉	**5%**
White (Black) Spruce[1]	**–**	⌉	**5%**	⌉	**13%**
White Pine	**–**	⌉⌉	**19%**	⌉⌉	**30%**
Miscellaneous	**11%**		**10%**		**13%**
Percent of Community in Growth Stage in Presettlement Landscape	**14%**	**27%**	**44%**		**15%**

1. The PLS surveyors did not consistently distinguish the more prevalent quaking aspen from big-toothed aspen nor did they distinguish the more prevalent white spruce from black spruce on FDn33 sites.

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

(PLS-2) Abundance of trees throughout succession in FDn33

Graphed for the individual species of FDn33 trees is their relative abundance (%) as PLS bearing trees by age class. Species with good-to-excellent suitability have colored graphs as follows: early successional (yellow); mid-successional (green); late-successional (magenta). The data were smoothed from adjacent classes (3-sample moving average). Not shown is the very old growth-stage because of sparse data (see PLS-1). Black insets show the proportion of bearing trees that were small-diameter trees that were presumably recruiting to bearing tree size (~4" dbh, see PLS-5). For infrequent trees, the presence of small-diameter trees is indicated by black dots rather than insets.



FDn33, J.C. Almendinger, April 2008

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

(PLS-3) Historic Abundance of FDn33 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent FDn33 forests. The columns represent our interpretation of disturbance at the survey corners. Trees in parentheses are minor species that occur in modern forests but couldn't be separated from more common trees because the surveyors did not distinguish them in their field notes. Shading associates trees that peak in the same disturbance category.

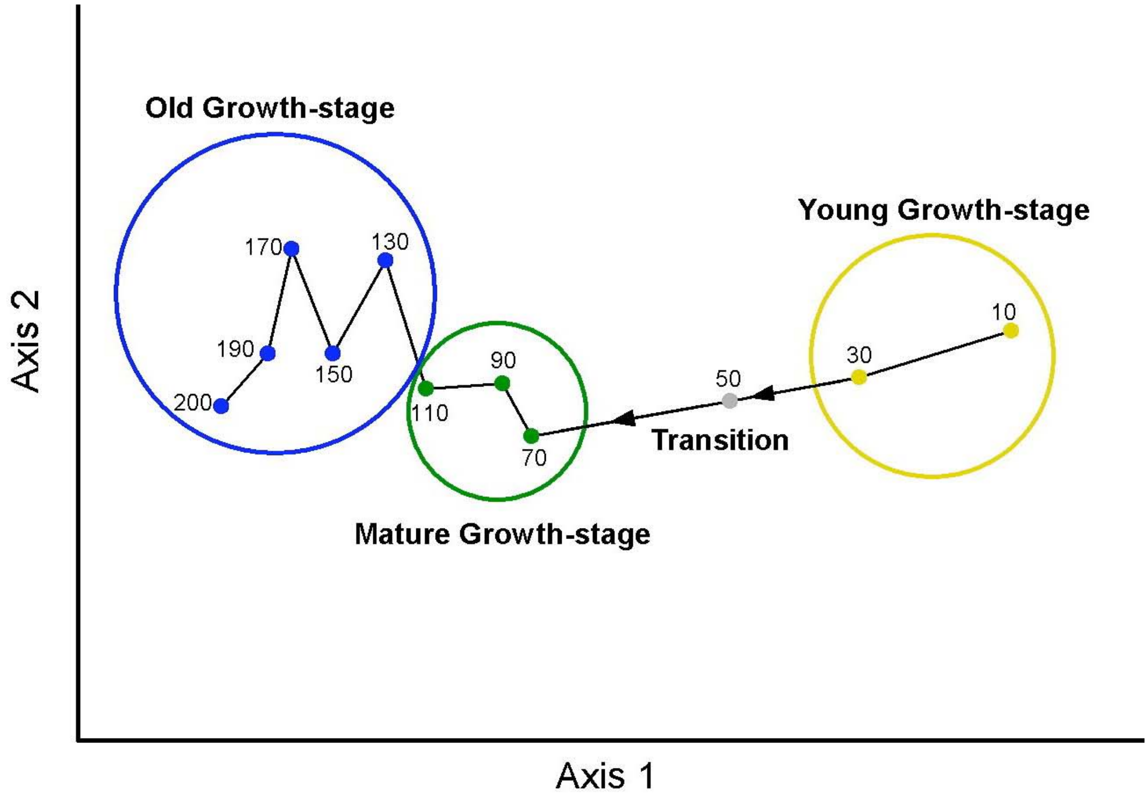
Tree	Burned		Windthrown		Maintenance		Mature	
Quaking (Bigtooth) aspen[1]	119	13%	45	26%	113	10%	1929	13%
White pine	225	24%	35	20%	259	24%	3170	22%
Red pine	404	44%	48	28%	501	46%	3486	24%
Jack pine	91	10%	9	5%	154	14%	936	6%
Paper birch	59	6%	24	14%	46	4%	2960	21%
Balsam fir	13	1%	4	2%	4	0%	855	6%
Black (White) spruce[1]	10	1%	6	3%	15	1%	890	6%
Red maple	1	0%	1	1%	1	0%	201	1%
Total (% of grand total, 16614)	922	5%	172	1%	1093	7%	14427	87%

1. The PLS surveyors did not consistently distinguish the more prevalent quaking aspen from big-toothed aspen; nor did they distinguish the more prevalent black spruce from white spruce on FDn33 sites.

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

(PLS-4) Ordination of Historic FDn33 Age-classes

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



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

(PLS-5) Historic Windows of Recruitment for FDn33 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 70-110 years	G-2 >110 years
Yes	Jack pine	0-30	Excellent	Fair to 60	--	--
Yes	Quaking aspen[1]	0-30	Excellent	Poor to 60	--	--
Yes	Red pine	0-30	Good	Fair	--	--
Minor	Big-toothed aspen	0-30	Fair	Poor	--	--
Yes	Paper birch	0-40	Good	Good	Fair to 100	--
No	Red maple	30-50	Poor	Poor to 80	--	--
No	White pine	40-50	Fair	Good to 60	--	--
No	Balsam fir	40-50	Fair	Good	--	--
No	Black spruce[1]	>80	--	Fair from 70	Fair	Good

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 with jack pine, red pine, and paper birch, 30-70 years
- **I-1:** ingress of seedlings under canopy of red pine, paper birch, white pine, with some decadent aspen and jack pine, 70-110 years
- **G-2:** gap filling during decline of mostly red pine , >190 years

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

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

1. Quaking aspen bearing trees couldn't be segregated from big-toothed aspen in the PLS notes for this community. The quaking aspen data probably include some big-toothed aspen, which we consider ecologically similar to quaking aspen. Similarly, **black spruce** bearing trees couldn't be segregated from white spruce. We consider black spruce to be ecologically similar to white spruce in this community.

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

(R-1) Suitability Ratings of Trees on FDn33 Sites

This table presents an index of suitability for trees in FDn33 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 FDn33

Tree	Percent Presence as Tree	Mean Percent Cover When Present	Suitability Index*
Red pine (Pinus resinosa)	49	35	4.9
Paper birch (Betula papyrifera)	47	19	4.7
White pine (Pinus strobus)	31	27	4.7
Quaking aspen (Populus tremuloides)	35	20	4.5
Jack pine (Pinus banksiana)	18	18	4.0
Balsam fir (Abies balsamea)	20	14	4.0
Big-toothed aspen (Populus grandidentata)	15	19	3.8
Red maple (Acer rubrum)	27	10	3.8
Black spruce (Picea mariana)	6	46	3.7

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

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

(R-2) Natural Regeneration and Recruitment of Trees in Mature FDn33 Stands

This table presents an index of regeneration for FDn33 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 FDn33 communities. Changes in the index values from one stratum to another can be used to estimate regenerative bottlenecks, whether establishment (R-index) or recruitment (SE-, SA-, or T-indices).

Natural regeneration indices for regenerants, seedlings, saplings, and trees common in the canopy of Northern Dry-Mesic Mixed Woodland – FDn33

Trees in understory	% presence R, SE, SA	R-index	SE-index	SA-index	T-index
Red maple (Acer rubrum)	77	4.7	4.7	4.3	3.5
Paper birch (Betula papyrifera)	73	2.5	2.5	4.2	4.3
Balsam fir (Abies balsamea)	65	4.2	4.3	4.0	3.3
Quaking aspen (Populus tremuloides)	52	4.2	4.3	4.3	4.5
White pine (Pinus strobus)	43	4.0	4.0	3.5	4.3
White spruce (Picea glauca)	31	2.0	2.2	2.7	2.5
Red pine (Pinus resinosa)	29	1.3	1.2	3.3	4.8
Big-toothed aspen (Populus grandidentata)	19	2.0	1.8	3.3	3.8
Black spruce (Picea mariana)	8	1.3	1.3	3.0	3.5
Jack pine (Pinus banksiana)	8	0.3	0.3	2.2	4.0

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

% presence: the percent of 124 FDn33 sample plots with that species present under 10m tall (R, SE, SA layers)
R-index: index of representation as true seedling or under 10cm tall
SE-index: index of representation as seedlings under 2m tall
SA-index: index of representation as saplings 2- 10m tall
T-index: index of representation as a tree >10m tall
All indexes: equally weight (1) presence, (2) mean cover when present, and (3) mean number of reported strata, the frequency distributions of which are segmented equally by area into 5 classes.

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

(FIA-1) Structural Situations of Trees in Mature FDn33 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples FDn33 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.

Species	Tree Count	Structural Situations					
		11	22	12	23	13	33
Jack pine	**32**	**0%**	**22%**	**0%**	**19%**	**0%**	**59%**
White pine	**30**	**0%**	**3%**	**0%**	**3%**	**0%**	**93%**
Black spruce	**6**	**17%**	**17%**	**17%**	**50%**	**0%**	**0%**
Red pine	**22**	**5%**	**50%**	**18%**	**9%**	**0%**	**18%**
White spruce	**32**	**0%**	**9%**	**6%**	**15%**	**12%**	**59%**
Big-toothed aspen	**23**	**48%**	**0%**	**17%**	**9%**	**4%**	**22%**
Paper birch	**738**	**5%**	**35%**	**13%**	**23%**	**10%**	**14%**
Quaking aspen	**2445**	**44%**	**12%**	**19%**	**5%**	**9%**	**10%**
Red maple	**341**	**6%**	**20%**	**19%**	**26%**	**24%**	**6%**
Balsam fir	**424**	**8%**	**16%**	**35%**	**13%**	**24%**	**5%**

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

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

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

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

(PLS/FIA-1) Abundance of FDn33 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 FDn33 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 - 125		~ 125	> 125	
	Young		T1		Mature		T2	Old	
Quaking (Big-toothed) Aspen	40%	79%	||		9%	48%	|	7%	37%
Jack Pine	15%	–	|		7%	–	|	2%	–
Red Pine	17%	1%	⌉		27%	1%	||	16%	1%
Paper Birch	16%	5%	⌉		19%	26%	|	14%	18%
Balsam Fir	1%	7%	⌉		4%	11%	⌉	5%	15%
White (Black) Spruce	–	1%	⌉		5%	1%	⌉	13%	1%
White Pine	–	0%	⌉⌉		19%	1%	⌉⌉	30%	19%
Red Maple	–	4%			1%	9%		2%	0%
White Cedar	–	0%			2%	1%		2%	8%
Miscellaneous	11%	3%			7%	2%		9%	1%
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	14%	30%	27%	30%	44%	39%		15%	1%

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 6,807 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 2,615 FIA subplots that were modeled to be FDn33 sites.

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

Forest Health Considerations

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.

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.

Jack Pine

Agent	Growth stage	Concern/ Effect
Jack pine budworm	All stages	Mortality
Armillaria root disease	"	"
Diplodia blight & canker	Regeneration	Mortality
Gall rust	"	"
Root collar weevil	"	"
White pine weevil	"	Topkill, forking
Bark beetles	Pole-sized and larger	Mortality
Stem decay = red rot	"	Volume loss
Stem rusts	"	Volume loss/ growth reduction

WATCHOUTS!

• In the northwest and west-central counties, jack pine budworm is a cyclic problem that causes significant topkill and mortality. Stands older than 50 years are at high risk for mortality due to budworm outbreaks. Use a 45 to 50 year rotation age in these areas to prevent adverse stand impacts from jack pine budworm.

• Elsewhere, jack pine budworm outbreaks are infrequent, so rotation ages can be much higher but should be based on pathological rotation age.

• Open-grown stands, characterized by wolfy jack pines, create conditions suitable for jack pine budworm build-up. Harvesting and regenerating these types of stands should be a priority. Maintain optimally stocked stands, between 70 and 100 sq ft of basal area.

• Susceptibility of mature and over-mature stands to bark beetles is high when droughty weather and/or jack pine budworm defoliation occur.

• Avoid creating pine slash and fresh cut products in or adjacent to red and jack pine stands from February 1 to September 1 in order to prevent the buildup of bark beetles and mortality losses due to their subsequent attack of standing, live pines.

• When planning intermediate 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, rust cankers, dead branches, and dead or broken tops.

• Regeneration growing below red pine overstory trees may not survive due to the accumulation of *Diplodia* infections

Balsam Fir

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

WATCHOUTS!

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

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

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

Red Maple

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

WATCHOUTS!

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

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

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.

Black Spruce

Agent	Growth stage	Concern/ Effect
Armillaria root disease	All stages	Mortality
Dwarf mistletoe	“	“
Spruce budworm	“	Topkill, mortality
Butt rot and stem decay	Pole sized and larger	Volume loss

WATCHOUTS!

• Dwarf mistletoe can be controlled by broadcast burning or by using the “5 foot cutting rule” during harvest. All living black spruce needs to killed in order to eradicate dwarf mistletoe on a site. If it is not feasible to use the 5 foot rule, some type of site preparation (hand cutting, winter shearing, herbicides, combination treatments) is needed to eliminate all living black spruces prior to regenerating black spruce on the site.

• If dwarf mistletoe pockets are present on or near a timber sale, adjust sale boundaries to include them and use the pockets as landings.

• If the stand has an unmerchantable edge due to dwarf mistletoe, Site Level Guidelines allow harvest or shearing of that edge. Treat a minimum width of 2 chains into the adjacent stand in order to prevent the spread of dwarf mistletoe onto the harvested site.

• Resurvey harvested sites after 1 to 2 years in order to find any black spruce that survived. All living spruces should be killed or cut down. Repeat 10 years after the initial harvest.

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

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

FDn33 - Acceptable Operating Season to Minimize Compaction and Rutting

Primary Soils	Secondary Soils	Not Applicable

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

Plants below indicate wetter inclusions in FDn33 that are more susceptible to compaction and rutting. They are listed in descending order of presence.

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

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

Foot Notes

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

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

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

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

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

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

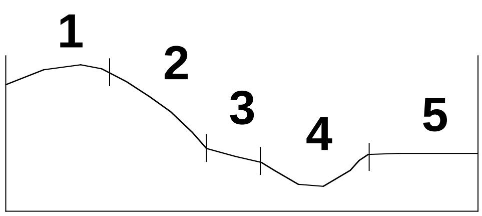
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

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

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

4. Landscape Position

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



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

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

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

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

   W Winter – the ground is snow covered or partially frozen

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

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

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

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

Public Land Survey

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

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

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

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

Modern Forest

Releve Samples

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

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

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

For more information on the releve method and NPC Classification:

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

FIA Samples

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

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

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

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

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

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

Link to the USFS website, north central