FDn32

FDn32 – Northern Poor Dry-Mesic Mixed Woodland

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Poor Dry-Mesic Mixed Woodland (FDn32) is an occasional, pine-dominated community found mostly within the Northern Superior Uplands ecological Section of Minnesota (Figure 1). Scattered occurrences can be found on Beltrami Island and may occur elsewhere in the Northern Minnesota and Ontario Peatlands ecological section. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

Commercial Trees and Management Opportunities

As a commercial forest, FDn32 sites offer a selection of several crop trees and a few possible structural conditions. Jack pine, black spruce, red pine, quaking aspen, and white pine are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on FDn32 sites (see Suitability Tables). Paper birch and balsam fir 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.

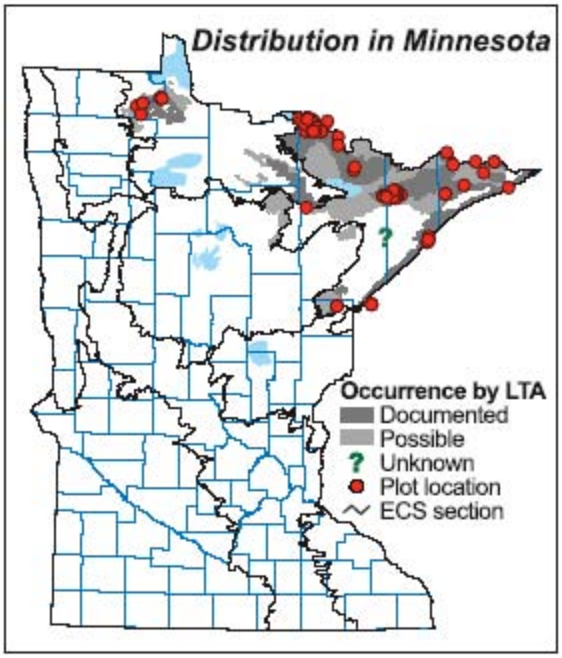


Figure 1. The range of FDn32 forests in Minnesota (shaded) and distribution of releve samples (red dots).

All of these highly suited species are native trees that have occupied FDn32 sites for a long time and have had the opportunity through successive generations to adapt to physical conditions typical of these sites. The consequence of fire suppression, commercial logging, and settlement in the past century has been to promote much more quaking aspen and balsam fir than was usual **(PLS/FIA-1)**. The increased abundance of these trees and the loss of pine seed-trees complicates our interpretations and the use of natural regeneration models as silvicultural strategies.

Natural Silvicultural Approaches

In the historic landscape, most FDn32 stands (57%) were young and under the age of 55 years **(PLS-1)**. Nearly all of these forests resulted from catastrophic fires that killed most canopy trees and created young forests with clear dates of origin. Clear-cutting and clear-cutting with reserves are the silvicultural systems that best match the canopy loss and regeneration opportunities typical of young FDn32 sites. Jack pine, quaking aspen, and paper birch are all considered open regeneration strategists on FDn32 sites and should respond positively to these management strategies. If old red pines are present, seed tree systems with significant soil disturbance best matches the natural pattern that favored a higher proportion of red pine in the initial cohort.

About 25% of the native landscape was occupied by transitioning FDn32 forests between 55 and 95 years old **(PLS-1)**. At this time, senescence or fire-injury of initial-cohort jack pine and aspen created regeneration and recruitment opportunities for trees in gaps. We believe that both surface fire and outbreaks of pests helped to accelerate natural transitions. Where aspen was an important component of the initial-cohort canopy, we envision patchy surface fires creating a variety of gap sizes that led to regeneration opportunities for aspen, red pine, and white pine.

Very large openings favored regeneration of aspen; large openings favored red pine; smaller opening favored white pine. Just looking at the pattern of supercanopy pines in mature and old FDn32 forests, the pattern of partial retention spanned the entire range of systems described as seed-tree, shelterwood, or group selection. Regardless of pattern, the fundamental idea of a system designed to mimic transitioning FDn32 forests affected by surface fire should be aimed at modest regeneration of aspen, establishment or release of red pine, and ingress of white pine. Presumably this kind of transition led to the FDn32a community type favoring red and white pine.

Alternatively, natural senescence or outbreaks of spruce budworm created gaps in transitioning FDn32 woodlands. Where jack pine was the initial-cohort dominant the ever-present pulse of balsam fir created sites that were at risk for either catastrophic fire or spruce budworm infestation. Fire simply regenerated jack pine and returned these sites to the pool of young FDn32 woodlands. The pattern of budworm disturbance is for stands to have outbreaks during the fir pulse and then experience chronic, but reduced mortality after that. Senescing aspen and larger fir were removed from the canopy, leaving residual pines and paper birch in a pattern that also probably spanned the range of silvicultural systems described as seed-tree, shelterwood, or group selection. Regardless of system, the general silvicultural strategy would be to remove aspen, fir, and poor jack pine in order to regenerate some red pine and release advance regeneration of white pine or black spruce. If advance regeneration of white pine and black spruce are not present, then creating the right shelter combined with planting would be and appropriate set-up treatment. Presumably, this kind of transition led to the formation of older forests classified as the FDn32c,d,e types.

About 18% of the FDn32 landscape was mature forest estimated to be older than 95 years **(PLS-1)**. Our vision of the FDn32a forests is that the supercanopy was dominated by red and white pines that were reasonably vigorous and able hold the site until fire returned. Spruce, fir, birch, and even some aspen filled the matrix among the emergent pines. We doubt that the matrix was maintained by canopy disturbances as fine-scale as single or few-tree gaps. All of these species are affected by diseases or pests that probably selected them from the lower canopy to leave a sparse forest or rather large gaps. Our best guess is that silvicultural strategies aimed at maintaining pine standards above shorter rotations of aspen, birch, fir, and spruce would be more appropriate in a commercial setting. The removal of the lower canopy would be aimed at regenerating some pines, with greater removal favoring jack and red pine and smaller gaps favoring white pine.

FDn32c,d,e types, which are essentially mixtures of jack pine and black spruce, present a conundrum. These species have opposing silvicultural characteristics and life-requirements. No uniform silvicultural system can match the light and seedbed requirements to perpetuate these species in even mixture. It seems that there was simply a long period of temporal overlap of initial-cohort jack pine and ingressing black spruce. Selective silvicultural systems will favor perpetuation of black spruce and balsam fir above advance regeneration. Patch cuttings would favor jack pine, paper birch, and some aspen. There is no particular reason that selective cuttings and patches can’t be combined in reaction to the current distribution of early successional trees and advance regeneration of spruce and fir in order to perpetuate all species at the stand scale and maintain some structural characteristics of mature FDn32 woodland.

Management Concerns

FDn32 communities are nutrient poor, and a substantial amount of their nutrient capital is tied up in organic material. The organics include the mor humus, woody debris, and the often a carpet of mosses. All of the plants in this community are adapted to the episodic loss of the organic resource in hot fires. In our experience, severe burning results in exposure of rather large areas of bare rock that are slow to stock with trees, and often results in dense, stagnant regeneration where soils are sandy (MOP) or just deeper (NSU). Neither of these outcomes are particularly attractive in a commercial setting. Abundant deciduous trees and brush are usually a sign that the site has been enriched due to fire-suppression and total removal (e.g. biofuels) might be a valid tactic for improving the chances of conifer establishment. Alternatively, the purely coniferous and mossy sites have no species likely to compete with regenerating conifers. In these cases, conservation of the legacy groundlayer would probably allow for greater stocking and earlier differentiation of young conifers.

FDn32 communities occur either on shallow, loamy soils over bedrock or on well-sorted sand. These parent materials have different compaction and rutting risks to be mitigated by season of operation. FDn32a,c,e woodlands occur on stony till overlying glacially scoured bedrock. Soil texture ranges from coarse sandy loam to quite silty. Field verification of the texture is required to determine if compaction is a concern or not (see Acceptable Operating Season to Minimize Compaction tables). The bouldery parent material often gains enough skeletal strength from stones to support heavy equipment. In such cases, rutting is not likely. FDn32b,d communities occur on very well-sorted sand. These sands are not likely to compact. However, these woodlands occur often enough above a shallow water table to have some concerns about rutting. In general, by mid-summer the trees have lowered the water table to the point where rutting is unlikely. Field checking the depth to water table is the only way to make this determination, and a rough rule is to allow harvesting when the water table has fallen to about 20” below the soil surface.

Other than balsam fir, all of the conifers that historically dominated FDn32 sites are in some peril and need restorative efforts. Jack, red, and white pine have essentially been eliminated from these sites, presumably because these sites are most commonly coppiced for aspen and seed trees were not often reserved. Black spruce populations are low, but extirpation doesn’t seem imminent. Reserving black spruce seed trees and allowing some stands to reach maturity where it is most competitive would help conserve the upland black spruce resource. It is important to note that a large proportion of FDn32 habitat occurs within the Boundary Waters Canoe Area (BWCA) wilderness, which was not sampled by FIA plots until 1999. Thus our use of 1990 FIA data eliminates the possibility of the BWCA contributing to our modern assessment of the FDn32 community. We are confident that the extensive windthrow in 1995 and several large fires since 1990 have regenerated some of the pine in FDn32 woodlands and that there are some older stands with black spruce. It is discouraging though to realize that modern forest management has not resulted in any significant, natural regeneration of pine on FDn32 sites outside of the BWCA.

Natural Disturbance Regime

Natural Rotations of Disturbance in FDn32 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**170 years**
Catastrophic windthrow photograph	**1,810 years**
Partial Canopy Loss, photograph	**210 years**

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 6,156 corners within the primary range of the FDn32 community. At these corners, there were 15,839 bearing trees comprising the species that one commonly finds in FDn32 forests.

The PLS field notes described about 9% of the FDn32 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands with some references to post-fire thickets. From these data, a rotation of 170 years was calculated for stand-replacing fire.

Elsewhere in the FDn32 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 1,810 years for windthrow.

FDn32 sites were also affected by 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 thickets, rocky barrens, 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 2% of the survey corners were described as such, resulting in a calculated rotation of 210 years for disturbances that maintained early and mid-successional trees on FDn32 sites. That more corners were described as burned (482) compared to windthrown (51) suggests that surface fires were the more prevalent cause of partial canopy loss.

The FDn32 community is similar to other communities occurring on the rocky, Canadian shield of northeastern Minnesota in that catastrophic fire was slightly more likely than surface fire. This is quite different from FDc, FDs, and FDw communities where surface fires prevailed. The overall rotation of any fire in this region is longer than anywhere else in the state. We believe that long winters and persistent snowpack diminished the probability of spring fires, which are more common to the southwest. However, the region is susceptible to summer and fall drought because of the shallow soils have very little ability to store water. Droughty soils and the general continuity of coniferous forest cover across the landscape allowed for extremely hot, damaging, and extensive fires when they eventually occurred. The near absence of mesic trees like sugar maple and basswood throughout the range of FDn32 is testimony to the effectiveness of fire in this community.

Natural Stand Dynamics & Growth-stages

Following stand-regenerating fire or very rarely windstorms, the overall pattern of compositional change in FDn32 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 FDn32, jack pine and quaking aspen are the species that benefit greatly from fire because they compete poorly with later-successional species ... first losing ground to paper birch and white pine and ultimately to fire-sensitive species like spruce and balsam fir. After losing the initial-cohort jack pine and aspen, the FDn32 community is extremely stable in its mature composition.

The FDn32 community is floristically woodland in that some light-loving plants occur in the groundlayer, often on outcrops of bedrock that lack enough soil for trees to grow. However, with regard to tree density, FDn32 behaves like forest. Early in its development it achieves high tree densities that vary little throughout the course of stand maturation. From their inception through the mature growth-stage, the mean distances to bearing trees are between 20 and 24 feet. The tree distances increase throughout stand maturation, which suggests enough initial stocking to exhibit self-thinning. The variances of these means are small, meaning that the FDn32 community was not as patchy as the understory flora would suggest.

Young Growth-stage: approximately 0-55 years

Over half (57%) of the FDn32 landscape in pre-settlement times was covered by forests estimated to be under 55 years old **(PLS-1)**. Mixed or monotypic conditions were equally likely for stands in this stage. Monotypic conditions were represented mostly by survey corners where all bearing trees were all jack pine, but corners attended by all quaking aspen were common as well. At survey corners with mixed composition, jack pine was still the most cited species, but quaking aspen and paper birch were also common. In describing young, burned stands the surveyors indicated that in addition to quaking aspen, jack pine, and paper birch, the initial-cohort included white and red pine as well **(PLS-3)**.

Fire was by far the most likely disturbance to regenerate FDn32 forests **(PLS-3)**. More often than not, these fires were hot, consuming, and stand-regenerating (see Natural Disturbance Regime). Undoubtedly, the shallow, droughty soils and the tendency for FDn32 woodlands to have understory spruce and fir contributed to the tendency for these sites to experience severe fire. The shallow, stony soils also limit the amount of mineral nutrients available to plants, meaning that much of the site's nutrient capital is held in organic matter that was at risk in a hot fire. Severe, nutrient-depleting fire strongly favored the regeneration of jack pine on these sites. It is probably significant that on FDn32 sites, that the jack pine trees are the closed-cone ecotype favored by catastrophic fire. Others have suggested that the presence of upland black spruce in the FDn32 community is due to spruce's ecological similarity to jack pine. Cited most often are the semi-serotinous cones of black spruce and its positive reaction to fire in peatlands. We saw no evidence of spruce being important in regenerating FDn32 woodlands **(PLS-1)**, and it was not especially important at survey corners described as having been burned **(PLS-3)**. We believe that black spruce is a component of the FDn32 community because it is nutrient-poor, more so than any fire-adaptations of black spruce.

Paper birch and quaking aspen also did well after fire. In richer environments we usually attribute post-fire regeneration of aspen and birch to vegetative means. In these situations we commonly see 4-times as much aspen as birch and suspect that it represents the difference between aspen suckers filling in among burned birch snags at their spacing in the older forest. In our limited experience of inspecting FDn32 sites after a fire, seed-origin birch and aspen can account for as much as half the young seedlings. Presumably this might explain the more equal balance of these species in young FDn32 woodlands **(PLS-1)**.

Young stands recovering from windthrow were not at all common **(PLS-3)**. Wind did, however, have a differential effect on composition in comparison to fire. Wind favored the regeneration of paper birch over regeneration of jack pine.

The ability of jack pine, quaking aspen, and paper birch to quickly dominate young FDn32 forests is a consequence of their persistence in the mature growth-stage **(PLS-1)**. For a pioneer species, aspen and birch show 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 aspen and birch were successful enough at maintaining clone rootstocks and scattered seed trees so that they could rapidly repopulate burned areas, even if the burned stand had reached the older growth-stages. Other initial-cohort trees like jack pine, red pine, and white pine also maintained a significant presence in older stands and were prepared to re-colonize following fires. White pine is similar to aspen and birch in that regeneration and recruitment in the older growth-stages seems possible. Red pine and especially jack pine show little natural establishment in mature stands **(R-2)**. Their persistence in older FDn32 forests must be attributed to modest recruitment after surface fires or perhaps their longevity.

Transitional Stage: approximately 55-95 years

About 25% of the historic FDn32 landscape was forest undergoing considerable compositional change as stands approached maturity **(PLS-1)**. Stands in this stage were more often mixed (74%) than monotypic. Monotypic conditions were represented by a surprising variety of trees. Jack pine and paper birch were most likely to occur in pure patches, but red pine, white pine, and quaking aspen were also common. At survey corners with mixed composition initial-cohort trees were still most common, but small-diameter spruce, balsam fir, and white pine were contributing to greater mixing of species about a survey corner.

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 40% relative abundance in the 20-year age class to just about 10% by the middle of the transition. The decline of jack pine follows that of aspen and is more coincident with the transition. The relative abundance of jack pine falls gradually from a peak of about 45% in the 50-year age class to about 10% in the 90-year age class.

Balsam fir also contributed significantly to the compositional movement that initiated 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 20% **(PLS-2)**. Curiously, just as it seems that 50-year old FDn32 stands were well on their way to the “spruce-fir climax,” the relative abundance of fir collapses to lower levels (~10% relative abundance) that we often see maintained into old-growth. It is highly unusual for trees to peak strongly and decline within compositional transitions, creating significant movement within the ordination **(PLS-4)** but not across growth-stages **(PLS-1)**. The notion that balsam fir in any way “prepares” sites for 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 FDn32 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 closely mirrors the combined loss of jack pine, aspen, and fir.

Mature Growth-stage: approximately >95 years

About 18% of the historic FDn32 landscape was mature forest where the rate of successional change slowed significantly and appears to have been very stable after 110 years **(PLS-4)**. About 95% of the stands in this stage were mixed. Paper birch, white pine, spruce, and fir were the species most mentioned, and there was a scattering of samples where these were the only species at a survey corner. The surveyors mentioned 18 different species of trees at survey corners that we modeled to be FDn32 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 hardwoods is rather good evidence that mature FDn32 forests probably were patches of habitat that had escaped fire for a long time. Apart from jack and red pine, the native trees show remarkably high survival and recruitment as seedlings and saplings **(R-2)**. That their regenerant indices are lower than their seedling and sapling indices is also suggestive of thickening duff and diminished establishment for all species other than balsam fir in mature stands. Apparently, once FDn32 woodlands reached maturity, nearly all of the component species could maintain their local populations through advance regeneration and fine-scale disturbance that killed canopy trees here and there. The fact that these woodlands were predominantly coniferous in their old age, might explain the better-than-average recruitment of conifers in the mid-story. These species do not have similar success when beneath a canopy of hardwoods, especially a canopy of sugar maple.

This interpretation leaves us with two puzzles: the role of surface fire as a maintenance event and the persistence of intolerant jack and red pine into the mature growth-stage. Fire-scarred red and white pines are occasional and are certainly testimony that fires didn’t kill every tree. Also, the surveyors described a considerable amount of scattered pine timber at survey corners that contributed to our calculation of a 210-year rotation of events like surface fires that result in partial canopy loss. On the other hand, it is hard to stand in a mature conifer-dominated FDn32 forest with and understory choked with spruce and fir regeneration and a 5” duff layer of pine-straw and not envision a conflagration. Also obvious in the field is that it seems unlikely that a crown fire would carry through young and transitioning FDn32 forests where aspen is a dominant canopy tree. Our best guess is that mature FDn32 forests were not maintained by surface fire. Mature forests burned catastrophically. Younger forests, with aspen in the canopy and pulsing fir in the understory could have hot surface fires. Perhaps such fires allowed for modest regeneration of jack pine and red pine, and scarred fire-resistant red and white pines.

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?

Jack Pine

- ***excellent habitat suitability rating***
- ***early successional***
- ***open regeneration strategist***
- ***regeneration window at 0-20 years***

Suitability

FDn32 sites provide ***excellent habitat*** for jack pine trees. The perfect ***suitability rating*** of 5.0 for jack pine is influenced mostly by its very high presence (55%) as trees on these sites in modern forests **(R-1)**. When present, jack pine is an important dominant tree, contributing 35% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on FDn32 sites as sampled by releves. Northern fire-dependent forests in general offer fair-to-excellent habitat for jack pine trees (see Suitability Tables). Jack pine is favored on the poorer and drier communities, and FDn32, FDn12, and FDn22 provide the best options for growing jack pine.

Young Growth-stage: 0-55 years

Historically, jack pine was the dominant tree in young FDn32 stands recovering from any disturbance, but especially after fire **(PLS-1, PLS-2)**. Young jack pines represented 42% of the trees at survey corners described as burned, which is by far more than any other tree. Jack pine was also the leading species following windthrow, representing 28% of the trees at such survey corners. However, windthrow was a far less significant than fire in regenerating FDn32 forests. Jack pine's importance in the young growth-stage and its leading abundance following fire and windthrow is why we consider it to be an ***early successional*** species on FDn32 sites. In the young growth-stage, it was about equally likely for survey corners with jack pine bearing trees to be mixed or monotypic. Small-diameter jack pine regeneration coming in among larger trees was abundant for the first 20 years **(PLS-5)**. After that, jack pine regeneration was infrequent until the close of the young growth-stage. Overwhelmingly, small-diameter jack pine preferred to come in among other jack pines. We interpret this as jack pine showing early dominance and the ability to suppress other trees in a poor habitat. On FDn32 sites, jack pines produce cones that are strongly serotinous and we doubt that there was significant influx of jack pine seed much beyond the post-fire years.

Transition: 55-95 years

Natural succession, or transitioning of young FDn32 forests was driven in-part by the steady loss of initial-cohort jack pine leaving longer-lived paper birch and red pine **(PLS-1)**. We estimate that significant decline started at about age 50 and continued to about age 90 when jack pine abundance stabilized at about 10% relative abundance **(PLS-2)**. The jack pine establishment window lasted only until about age 60 **(PLS-5)**, meaning that we did not detect significant establishment or recruitment in transitioning FDn32 forests and suspect that second cohorts of jack pine could not develop without further disturbance. During the transition period, jack pine was present at most survey corners (~30%); however, only a third of these were still pure jack pine. It is possible that there was limited jack pine establishment and recruitment to bearing-tree size (~4" dbh) during the transition if the site was affected by surface fire. Otherwise, we do not envision recruitment. When present as smaller diameter trees, jack pines were among larger jack pine or red pine. We believe these trees were suppressed, but long-lived initial-cohort jack pine.

Mature Growth-stages >95 years

In mature FDn32 stands the relative abundance of jack pine stabilizes at about 10% and it persists into the older age-classes **(PLS-1, PLS-2)**. Although much diminished from earlier growth-stages, jack pine was still an important tree. 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 limited ability to establish and recruit seedlings in modern FDn32 forests diminishes the possibility of it responding to fine-scale disturbance. Most likely, the primary limitation to establishing seedlings is the tendency of jack pine to have mostly closed, serotinous cones in on FDn32 sites. It is important to note that while establishment is infrequent, the index values for regenerants and seedlings are not zero **(R-2)**. Unusually warm weather can open some cones, especially on older, senescent branches. We don't know if stimuli other than fire opened enough cones to maintain by recruitment, 10% relative abundance of jack pine in mature FDn32 woodlands. The high presence of jack pine at survey corners described as windthrown or suffering from partial canopy loss **(PLS-3)**, argues for some jack pine recruitment if given enough light on the forest floor. Jack pine's presence in subordinate canopy situations (situations 13 and 23, **FIA-1**) is also consistent with the idea of limited establishment and recruitment in older forests. Alternatively, it is possible that jack pines in the mature growth-stage were just long-lived individuals. Some of the oldest jack pine in the state occur on FDn32 sites, and many individuals live well beyond 100 years. However, it is problematic to claim senescence of jack pine as a partial driver of succession during the transition and then claim that about a quarter of the local population was actually much longer-lived. In habitat as poor as that of FDn32 sites, it is possible that contrast between choice microhabitats and some very poor ones caused great variation in jack pine longevity, but we doubt it. We favor the hypothesis of limited establishment and recruitment during the mature growth-stage. Whatever the mechanism, jack pine maintained enough presence in these older forests to dominate the reproduction when a severe fire finally occurred.

Regeneration Strategy

Jack pine's primary regenerative strategy on FDn32 sites is to dominate ***open habitat*** after stand-regenerating fire. In the historic PLS data this interpretation is supported by: (1) the fact that 40% of the bearing trees in young stands were jack pine **(PLS-1)**, (2) jack pine represented by far, the largest proportion of bearing trees at burned survey 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, PLS-2)**. The limited ability of jack pine to regenerate under a canopy in modern forests supports strongly the idea that rather open conditions are required for significant natural regeneration **(R-2)**.

Historic Change in Abundance

Today, jack pine seems to be extirpated from FDn32 sites. Most noticeable is the decline in young forests where jack pine historically was 40% of the bearing trees and now jack pines account for just 1% of the FIA trees **(PLS-FIA-1)**. The FIA plots recorded no jack pine in mature FDn32 woodlands. It is important to note that a large proportion of FDn32 habitat occurs within the Boundary Waters Canoe Area (BWCA) wilderness, which was not sampled by FIA plots until 1999. Thus our use of 1990 FIA data eliminates the possibility of the BWCA contributing to our modern assessment of the FDn32 community. We are confident that the extensive windthrow in 1995 and several large fires since 1990 have regenerated some jack-pine dominated FDn32 woodlands. It is discouraging though to realize that modern forest management has not resulted in any natural regeneration of jack pine outside of the BWCA. Silvicultural strategies aimed at restoring jack pine to young FDn32 woodlands is warranted.

Black spruce

- ***excellent habitat suitability rating***
- ***late-successional***
- ***small-gap regeneration strategist***
- ***regeneration window at >70 years***

Identification Problems

The PLS surveyors did not distinguish between black and white spruce. Thus, interpretations of PLS data for the more common black spruce should always be done knowing that some of these trees were likely white spruce. FDn32 releve samples show that for plots with spruce present: 6% have both species present; 11% are white spruce without black spruce; 83% are black spruce without white spruce. Silvics manuals point out substantial differences in habitat and life history between the species. However in our releve data and in the FIA data, we saw no difference in their tendency to be late-successional and perform well as advance regeneration in mature FDn32 woodlands. On poor uplands, these species seem to be rough ecological equivalents and there is no particular reason to discount interpretations of generic references to spruce in the PLS data.

Suitability

FDn32 sites provide ***excellent habitat*** for **black spruce** trees. The ***suitability ranking*** of 5.0 for black spruce is influenced mostly by its very high presence (53%) as trees on these sites in modern forests. When present, black spruce is an important co-dominant and sometimes dominant tree, contributing 25% mean cover in mature stands. This ranking is second highest among trees common on FDn32 sites, just a few points behind jack pine. FDn32 is the only FDn community that offers excellent habitat for black spruce.

The ***very poor suitability ranking*** of 0.3 for **white spruce** is based upon its 10% presence and very low mean abundance of just 2% when present. In general, we don’t consider FDn32 sites as suitable for white spruce.

Young Growth-stage: 0-55 years

Historically, black spruce was present in just trace amounts in young FDn32 stands **(PLS-1, PLS-2)**. Young spruce represented just 3% of the trees at survey corners described as burned, well behind fire-tolerant species like the pines, quaking aspen, and paper birch **(PLS-3)**. In spite of semi-serotinous cones and positive response to fire in peatlands, black spruce’s affinity was clearly for undisturbed mature forest (9%) in this upland setting. Small-diameter black spruce was detected as early as the 30-year age-class **(PLS-5)**, but it never reached 1% relative abundance of recruiting bearing trees throughout the growth-stage. All occurrences of black spruce in the young growth-stage were as the smallest tree at the corner, and it was always in mixture with other species. Most occurrences were of small-diameter spruce trees in the presence of larger-diameter jack pine, and a few were beneath larger paper birch. Our interpretation is that black spruce played no important role in regenerating FDn32 woodlands.

Transition: 55-95 years

As stands transitioned to mature conditions black spruce increased dramatically in abundance **(PLS-1)**. This increase was continuous and steady throughout the period until black spruce became a dominant tree **(PLS-2)**. Small-diameter, black spruce regeneration coming in among larger trees was first detected in the 30-year age-class but it became a significant component of the woodland at about age 70 **(PLS-5)**. In fact, all of the black spruce detected during the transition were the smaller-diameter trees at survey corners, which is typical of new colonization. Ingress of black spruce during the transition could be related to the development of feathermoss seedbeds which typify older FDn32 woodlands. A switch from litter enriched with aspen leaves to conifer needles might also have improved black spruce’s chances of establishment and recruitment. The lower regenerant index for black spruce **(R-2)** would suggest that these seedbeds were not optimal for black spruce but all trees, save balsam fir, exhibit depressed establishment in older FDn32 woodlands. Compared to other trees, establishment of black spruce under a canopy follows only to fir and white pine, and its recruitment of seedlings and saplings is superior to all other trees. Our interpretation is that black spruce populations increased during the transition because of its excellent ability to establish and recruit seedlings as the soils and seedbeds got increasingly poor.

Mature Growth-stage: >95 years

In the mature growth-stage, black spruce abundance continued to increase, averaging a third of the trees in all samples older than 95 years **(PLS-1, PLS-2)**. Throughout this episode, black spruce occurred only at survey corners of mixed composition. It was about equally likely for black spruce to be the largest tree or smallest tree at survey corners. This is typical of an ingressing species developing a bank of understory seedlings and saplings over a long time. Small-diameter black spruce regeneration was coming in among larger trees abundantly in age-classes spanning the mature growth-stage, suggesting excellent establishment and recruitment in the ingress window **(PLS-5)**. At this time, spruce regeneration was coming in beneath almost any species of tree including itself. Our interpretation is that black spruce is a climax species on FDn32 sites and could maintain its populations indefinitely until catastrophic fire would regenerate the woodland.

Regeneration Strategy

Black spruce's primary regenerative strategy on FDn32 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 jack pine and paper birch on FDn32 sites. In the historic PLS data this interpretation is supported by: (1) the fact that black 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) its best recruitment window is an ingress window **(PLS-5)**. In modern forests, black spruce shows good ability to establish seedlings under a canopy **(R-2)**. Established seedlings have an excellent chance of recruiting to sapling and tree sizes. Spruce's 55% presence as poles in tree stands (situation 23) high for small-gap species and more aligned with trees that do well in larger gaps **(FIA-1)**. Our interpretation is that black spruce functioned well in any sized gaps due to abundant advance regeneration.

Historic Change in Abundance

Today black spruce is less abundant than it was historically **(PLS/FIA-1)**. This is evident only in the mature growth-stage where it once accounted for 31% of all trees and now it represents 10% of the trees in FIA subplots. We believe that the management trend on FDn32 sites has been to coppice aspen and that the black spruce seed source has been substantially diminished on uplands. When the seed source is present, black spruce continues to perform well as a late-successional tree on FDn32 sites.

Red Pine

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***open (large-gap) regeneration strategist***
- ***regeneration window at 0-50 years***

Suitability

FDn32 sites provide ***excellent habitat*** for red pine trees. The ***suitability rating*** of 4.6 for red pine is a due mostly to its high mean cover-when-present (37%) on these sites in modern forests **(R-1)**. Red pine is also commonly found (28% presence) on FDn32 sites. For long-lived conifers with greater cover-when-present than presence, we often suspect the loss of seed source, and believe that they would increase significantly if they were planted more often or if seed trees were more numerous. The ranking is third, behind jack pine and black spruce. All of the northern fire-dependent forest communities offer excellent habitat for red pine (see Suitability Tables).

Young Growth-stage: 0-55 years

Historically, red pine was an occasional tree in young FDn32 stands recovering mostly from fire **(PLS-1, PLS-2)**. Young red pines represented just 5% of the trees at survey corners described as burned, well behind jack pine, quaking aspen, paper birch and white pine **(PLS-3)**. Although windthrow was infrequent, red pines represented 4% of the trees at corners affected by stand-regenerating wind. This percentage is slightly less than that after fire, and it seems that windthrow offered similar opportunities for red pine regeneration in an open environment. The relative abundance of red pine increases slowly throughout the period, but there is little evidence that this was accomplished by establishment and recruitment well after a fire. Small-diameter red pine regeneration was detectable only in the young growth-stage, and it was never abundant **(PLS-5)**. Our interpretation is that red pines were part of the initial-cohort of trees, but their stem-counts were low in comparison to the density of quaking aspen suckers and what is often “dog-hair” thick jack pine seedlings after very hot fires. The surveyors described regenerating FDn32 woodlands most often and thickets in comparison to any other physiognomic class.

Transition: 55-95 years

As stands transitioned to mature conditions red pine increased in relative abundance, presumably because of its ability to outlive initial cohort aspen and jack pine **(PLS-1)**. We estimate that this increase started at low abundance following disturbance until it peaked at about 15% relative abundance in the 90-year age-class **(PLS-2)**. Small-diameter red pine regeneration was not detected during the transition **(PLS-5)**. At this time it was ten-times more likely for red pines to be the largest tree at a survey corner than the smallest tree. All of this suggests that red pine’s rise to importance during the transition was related more to survival than any regenerative effort. It is as if substantial amounts of red pine regeneration persisted in suppression beneath aspen and jack pine and were quite efficient in replacing these trees as they senesced and died. Because red pine achieved peak abundance and dominance at the close of the transition, we consider it to be a ***mid-successional*** species on FDn32 sites.

Mature Growth-stage: >95 years

The mature growth-stages is marked by the slow and steady decline of red pine **(PLS-2)**. The peak in relative abundance at the seam between the transition and mature growth-stage is mostly the result of good initial establishment and possibly some recruitment during the young growth-stage **(PLS-5)**. More so than any other FDn32 tree, regeneration of red pine was over early (~50 years) in the successional cycle. There is just fair evidence of establishment and recruitment of seedlings in modern mature stands **(R-2)**. Our interpretation is that longevity alone is what carried red pine into stands estimated to be older than 95 years.

Regeneration Strategies

Red pine’s primary regenerative strategy on FDn32 sites is to establish seedlings in ***open habitat*** after stand-regenerating fire. In the historic PLS data this interpretation is supported by: (1) the fact that red pine was present as an initial-cohort tree **(PLS-1)**, (2) red pine was among the trees at burned and windthrown corners **(PLS-3)**, and (3) red pine's peak regeneration was in the post-disturbance window **(PLS-5)** with it's absolute peak being the initial age-class. Red pine's fair regenerant and seedling indices beneath the canopy of modern forests is most in line with species that need substantial light for establishment **(R-2)**.

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

Historic Change in Abundance

Today, red pine seems to be extirpated from FDn32 sites. Historically, red pine was and ever-present tree on FDn32 sites at about 3-15% relative abundance **(PLS-2)**. The FIA plots did not record even 1% of red pine in mature FDn32 woodlands in any growth-stage **(PLS/FIA-1)**. It is important to note that a large proportion of FDn32 habitat occurs within the Boundary Waters Canoe Area (BWCA) wilderness, which was not sampled by FIA plots until 1999. Thus our use of 1990 FIA data eliminates the possibility of the BWCA contributing to our modern assessment of the FDn32 community. We are confident that the extensive windthrow in 1995 and several large fires since 1990 have regenerated some red pine in FDn32 woodlands. It is discouraging though to realize that modern forest management has not resulted in any natural regeneration of red pine outside of the BWCA. Silvicultural strategies aimed at restoring red pine to FDn32 woodlands is warranted.

Quaking Aspen

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

Suitability

FDn32 sites provide ***excellent habitat*** for quaking aspen trees. The ***suitability rating*** of 4.2 for quaking aspen is influenced mostly by its high presence (35%) as trees on these sites in modern forests **(R-1)**. When present, quaking aspen is an important co-dominant tree, contributing 15% mean cover-when-present in mature stands. The ranking is fourth, following jack pine, black spruce, and red pine on FDn32 sites as sampled by releves. As long as the soils are fairly deep (not FDn22), northern fire-dependent forests provide good-to-excellent habitat for quaking aspen (see Suitability Tables). Among these, FDn32 is about as good as any with exception of the more mesic FDn43 community.

Young Growth-stage: 0-55 years

Historically, quaking aspen was an important component of young FDn32 stands recovering mostly from stand-regenerating fire **(PLS-1, PLS-2)**. Young aspen represented 24% of the trees at survey corners described as burned, which is second only to jack pine **(PLS-3)**. Aspen was the leading species following windthrow, representing 28% of the trees at such survey corners. Young FDn32 corners with quaking aspen trees present were mostly mixed in composition (72%), but often (28%) all of the bearing trees were quaking aspen. Its dominance in the young growth-stage and its peak abundance following fire and windthrow is why we consider quaking aspen to be an ***early successional*** species on FDn32 sites. Small-diameter, quaking aspen regeneration was most often observed coming in among larger trees in the 0-30 year post-disturbance window **(PLS-5)**. This is typical of early successional species, and we interpret this as quaking aspen showing excellent ability to recruit into under-stocked areas of burned stands. The presence of smaller diameter aspen could be due natural variation among suckers that are more-or-less connected to parent rootstocks, but it is more likely that seed-origin trees were the smaller ones filling in among the suckers.

Transition: 55-95 years

Transitioning of young FDn32 forests was driven in-part by fairly rapid loss of initial-cohort quaking 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 40% relative abundance to about 10% by the middle of the transition. Small-diameter aspen regeneration was detectable in just the 60-year age-class **(PLS-5)**. These smaller trees were beneath just about any other initial-cohort tree, including itself. We interpret this as mostly as modest replacement of itself in large-gaps as some of the initial-cohort aspen started to senesce.

Mature Growth-stage: >95 years

In mature FDn32 stands the relative abundance of aspen held steady between 5-10% of the bearing trees **(PLS-1, PLS-2)**. Small-diameter quaking aspen regeneration coming in among larger trees was not detected during this growth-stage **(PLS-5)**. When present as the smaller tree at a survey corner, quaking aspen mostly among larger black spruce, jack pine, white pine, or itself. The ability of aspen to recruit seedlings or suckers through all height strata in modern FDn32 forests is surprising, suggesting that it can persist under a regime of fine-scale disturbance on FDn32 sites **(R-2)**. Its regeneration indices (3.3-4.5) are quite in line with species able to regenerate in ***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 FDn32 sites is to dominate ***open habitat*** after stand-regenerating fires. In the historic PLS data this interpretation is supported by: (1) the fact that 24% of the bearing trees in young stands were quaking aspen **(PLS-1)**, (2) aspen represented a large 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 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.

The releve sampling of mature FDn32 forests suggests, however, that quaking aspen is able to function also as a ***large-gap strategist*** with good establishment and excellent recruitment in the understory strata **(R-2)**. Its regeneration indices (3.3-4.5) are most in line with large-gap strategists. 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, quaking aspen is an important and often dominant tree on FDn32 sites **(PLS/FIA-1)**. Most (74%) young FDn32 stands are dominated by aspen, which is a significant increase over the historic condition where aspen accounted for 24% of the trees in young stands. Aspen also shows considerable gains in the mature growth-stage where it now has 43% relative abundance compared to just 7% in the pre-settlement forest. Our interpretation is that quaking aspen has benefited greatly from logging on rotations that are much shorter than the natural fire cycle and also benefiting from the general loss of conifers on the FDn32 landscape.

White Pine

- ***excellent habitat suitability rating***
- ***late-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 0-40 years***

Suitability

FDn32 sites provide ***excellent habitat*** for white pine trees. The ***suitability rating*** of 4.1 for white pine is influenced mostly by its presence (26%) as trees on these sites in modern forests **(R-1)**. When present, white pine is an important co-dominant tree, contributing 17% mean cover in mature stands. The ranking is fifth, following jack pine, black spruce, red pine, and quaking aspen on FDn32 sites as sampled by releves. Except for FDn12, all FDn communities offer excellent habitat for white pine trees.

Young Growth-stage: 0-55 years

Historically, white pine was a rare tree in young FDn32 stands recovering mostly from fire **(PLS-1, PLS-2)**. Young white pines represented 10% of the trees at survey corners described as burned, well behind jack pine, and quaking aspen **(PLS-3)**. Although windthrow was infrequent, white pines represented 7% of the trees at corners affected by stand-regenerating wind. This percentage is slightly less than that after fire, and it seems that windthrow offered similar opportunities for white pine regeneration in an open environment. The relative abundance of white pine increases slowly throughout the period, but there is little evidence that this was accomplished by establishment and recruitment well after a fire. Small-diameter white pine regeneration was most detectable only in the young growth-stage, and it was never abundant **(PLS-5)**. Our interpretation is that white pines were part of the initial-cohort of trees, but their stem-counts were low in comparison to the density of quaking aspen suckers and what is often “dog-hair” thick jack pine seedlings after very hot fires. The surveyors described regenerating FDn32 woodlands most often and thickets in comparison to any other physiognomic class.

Transition: 55-95 years

As stands transitioned to mature conditions white pine increased in relative abundance, presumably because of its ability to outlive initial cohort aspen and jack pine **(PLS-1)**. We estimate that this increase started at low abundance following disturbance until it reached a plateau of 10-15% relative abundance in the 80-year age-class **(PLS-2)**. Small-diameter white pine regeneration was present only in the first age-classes of the transition **(PLS-5)**. At this time, white pine was about twice as likely to be the largest tree at a survey corner as it was for it to be the smallest tree. Most likely the large trees were in the initial-cohort, and the smaller trees are those that were established later in the young growth stage. This suggests that white pine’s rise to importance during the transition involved both superior survival in comparison to jack pine and aspen, and modest regeneration and recruitment. When white pine was the smaller tree at a corner, it was mostly coming in among larger red pines or larger white pines. Our interpretation is that white pine was able to fill-in among initial cohort red and white pine after shorter-lived, initial-cohort species died early in the transition.

Mature Growth-stage: >95 years

The mature growth-stages is marked constant presence of white pine at about 10% relative abundance **(PLS-1)**. Small-diameter white pine regeneration was not detected during this period **(PLS-5)**. It was also not common for white pines to be the smaller tree at survey corners in the mature growth-stage, but when that was the case it was mostly beneath larger white pines. Our interpretation is that most of the large white pine in the mature growth-stage were individuals of the initial-cohort or they were trees established during the young growth-stage where we detected some recruitment. Thus, good survival and great longevity are the main reasons that white pine was important in older woodlands. White pine’s success recruiting beneath itself suggests that where white pine was better stocked initially, rather pure groves of white pine could form over time. Because white pine has peak abundance in mature woodlands, we consider it to be a ***late-successional*** tree.

Regeneration Strategies

White pine's primary regenerative strategy on FDn32 sites is to fill ***large-gaps***. It is most successful at this beneath itself or red pines, but also did well when gaps formed within the declining canopy of initial-cohort quaking aspen and jack pine. In the historic PLS data this interpretation is supported by: (1) the fact that white pine abundance rises steadily in response to the decline of the initial-cohort species **(PLS-1, PLS-2)**, (2) it was most abundant at survey corners showing partial canopy loss **(PLS-3)**, and (3) it peak of recruitment was in the 40-year age class which corresponds with the decline of initial-cohort aspen. The recruitment indices (3.8-4.3, **R-2**) are most in-line with species that tend to do well in large-gaps. Our general interpretation is that white pine enjoyed a fairly long window of establishment after fires (0-40 years, **PLS-5**), but initial-cohort white pines were overtopped by faster growing aspen and jack pine. These seedlings survived in suppression; there was supplemental establishment of white pine throughout the young growth-stage; and recruitment was accomplished in partial shade afforded by large gaps in the initial-cohort canopy.

Historic Change in Abundance

Today, white pine seems nearly extirpated from FDn32 sites. Historically, white pine was and ever-present tree on FDn32 sites at about 5-10% relative abundance **(PLS-1)**. The FIA plots show just 2% white pine in mature FDn32 woodlands compared to 10% historically **(PLS/FIA-1)**. No young white pines were sampled by FIA subplots, and it didn't appear in any regenerative situation **(FIA-1)**. It is important to note that a large proportion of FDn32 habitat occurs within the Boundary Waters Canoe Area (BWCA) wilderness, which was not sampled by FIA plots until 1999. Thus our use of 1990 FIA data eliminates the possibility of the BWCA contributing to our modern assessment of the FDn32 community. We are confident that the extensive windthrow in 1995 and several large fires since 1990 have regenerated some white pine in FDn32 woodlands. It is discouraging though to realize that modern forest management has not resulted in any natural regeneration of white pine outside of the BWCA. Silvicultural strategies aimed at restoring white pine to FDn32 woodlands is warranted.

Paper Birch

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

Suitability

FDn32 sites provide ***good habitat*** for paper birch trees. The ***suitability rating*** of 3.7 for paper birch is influenced mostly by its high presence (34%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is an minor co-dominant tree, contributing just 9% mean cover in mature stands. The ranking is sixth among trees common on FDn32 sites as sampled by releves. In general, only the richer FDn communities (FDn33, FDn43) offer excellent habitat for paper birch (see Suitability Tables).

Young Growth-stage: 0-55 years

Historically, paper birch was an important tree in young FDn32 stands recovering from catastrophic disturbance **(PLS-1)**. Young paper birch represented 15% of the trees at survey corners described as burned, following only jack pine and quaking aspen **(PLS-3)**. Our interpretation is that this percentage is too high if birch was relying solely on stump sprouts for regeneration. It seems likely that sprouting and seeding were both viable regeneration strategies for paper birch in the post-fire environment. Young birch trees responded even better to windthrow, representing 26% of the trees at windthrown survey corners. Most likely this is a consequence of paper birch's ability to maintain greater advance regeneration in older woodlands in comparison to red and jack pine **(R-2)**. Windthrow, however, was infrequent and not very important as a means of regenerating trees on FDn32 sites. Because paper birch increases during the young growth-stage **(PLS-2)** we believe that it had some ability to recruit into under-stocked areas of burned stands. Small-diameter paper birch regeneration was abundant following disturbance until the 40-year age-class **(PLS-5)**. At this time, it was coming in among initial-cohort aspen, jack pine, and larger birch. These may well have been seed-origin paper birch trying to keep pace with aspen suckers, stump-sprout birch, and fast-growing jack pine. Because paper birch was clearly an important initial-cohort tree and because its primary window of establishment was immediate after disturbance, we believe that it was able to function somewhat as an ***early-successional*** tree on FDn32 sites.

Transition: 55-95 years

As stands transitioned to mature conditions paper birch increased in abundance, due in part to its ability to outlive initial cohort aspen, but also due to successful establishment throughout the young growth stage **(PLS-5)**. Because paper birch reaches a clear peak of abundance in the transition, we consider it to be primarily a ***mid-successional*** tree on FDn32 sites **(PLS-2)**. Throughout northern Minnesota, paper birch was historically associated with conifers more so than with other hardwoods. In contrast, aspen was positively associated with other hardwoods, especially oak. Some have suggested that the tendency of communities like FDn32 to become increasingly coniferous explains the longer window of recruitment for paper birch in comparison to quaking aspen. Almost always in the northern floristic region, birch regeneration is coincident with the pulse of fir abundance. Our data would seem to corroborate this idea in that paper birch is the only initial-cohort hardwood to have even fair recruitment in the G-1 gap window that spans the transition where aspen declines and stands become conifer-dominated **(PLS-5)**. During this period, birch regeneration could be beneath any initial-cohort species, but it was especially successful beneath itself, aspen, and pine. Almost no small-diameter birch occurred among larger fir trees. If there was a connection between birch and balsam fir it was not a direct one.

Mature Growth-stage: >95 years

During the mature growth-stage, the relative abundance of paper birch declines from its peak abundance in the 90-year age-class **(PLS-2)**. Small-diameter birch regeneration was not detected during the mature growth-stage **(PLS-5)**. We doubt that this represents the true absence of advance regeneration of birch because it has good-to-excellent regenerative abilities beneath a canopy in modern forests **(R-2)**. At this time it was about equally probable for birch to be the largest tree at a survey corner as it was for it to be the smallest tree. This is probably a consequence of its long window of recruitment. When birch was the smaller tree at a corner, it was mostly (31%) among larger diameter birch, but it was common also below black spruce, white pine, or jack pine. We interpret this as birch having enough regenerative success, especially in birch-dominated patches, to persist at about 10% relative abundance regardless of how old the stands became.

Regeneration Strategies

FDn32 sites provide enough opportunities for paper birch for it to be an important or dominant tree throughout the course of a long succession. Thus, it is clear that birch has multiple strategies for regeneration and survival, and that those strategies were successful in all growth-stages. Birch achieved dominance by using it's primary regenerative strategy of filling ***large-gaps***. It was most successful at this when the gaps were forming within a declining canopy of quaking aspen and to some extent jack pine and other paper birch. In the historic PLS data this interpretation is supported by: (1) the fact that paper birch abundance peaks in response to the decline of the initial cohort species **(PLS-2)**, (2) it is abundant at survey corners showing partial canopy loss **(PLS-3)**, and it has fair establishment in a gap window **(PLS-5)**. The high percent of paper birch poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate best in large gaps. In the releve data paper birch has high presence in the understory and shows good ability to establish regenerants and excellent ability in recruiting them to taller strata **(R-2)**. The index values of 3.0-4.2 in the regenerating layer are most in line with species that do well in large-gaps. As long as there were large-gaps in older FDn32 forests, there was some paper birch. Surface fires and outbreaks of spruce budworm are the most likely agents to create large gaps.

Paper birch was also able regenerate and sometimes dominate ***open habitat*** after stand-regenerating fires. We believe that the initial cohort of young birch was composed of both stump sprouts and seed-origin trees. Birch's regenerative ability after fire is evident in the PLS data by: (1) its high relative abundance in young stands **(PLS-1)**, (2) its respectable presence at burned survey corners **(PLS-3)**, and (3) its peak regeneration in the post-disturbance window even though it continued to do well long after stand initiation **(PLS-5)**. Paper birch also has considerable presence in the canopy of young, post-logging stands (situations 11 and 22), which is typical of trees that do well in the open **(FIA-1)**.

Historic Change in Abundance

Today, paper birch remains an important and often dominant tree on FDn32 sites **(PLS/FIA-1)**. Young stands have significantly less paper birch (8%) than they did historically (19%), but birch is still an important tree. Most likely, this is the consequence of logging not providing as many seeding opportunities for birch as did fire. Mature forests today have just about as much birch as they ever did. This is probably testimony of birch's regenerative ability in large-gaps, which are still created by spruce budworm and perhaps other diseases and pests in older FDn32 woodlands.

Balsam Fir

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

Suitability

FDn32 sites provide ***good habitat*** for balsam fir trees. The ***suitability rating*** of 3.4 for balsam fir is influenced mostly by its presence (26%) as trees on these sites in modern forests **(R-1)**. When present, balsam fir is an occasional co-dominant tree, contributing 9% mean cover in mature stands. The ranking is seventh among trees common on FDn32 sites as sampled by releves. As long as the soils are fairly deep (not FDn22), northern fire-dependent forests offer good-to-excellent habitat for balsam fir (see Suitability Tables). Among these, FDn32 offers limited commercial opportunities for balsam fir.

Young Growth-stage: 0-35 years

Historically, balsam fir was a minor tree in young FDn32 stands **(PLS-1, PLS-2)**. Balsam firs represented just 3% of the trees at survey corners described as burned, well behind fire-tolerant species like jack pine, aspen, paper birch, red pine, and white pine **(PLS-3)**. Nonetheless, the presence of any balsam fir on burned lands is surprising given its well-known sensitivity to fire. One would also guess that fire-sensitive trees like balsam fir would be substantially more abundant at windthrown corners, but this wasn't the case as fir represented just 1% of the trees at windthrown survey corners. Because of balsam fir's affinity for wetter habitats included in the FDn32 landscape, we believe that the few, small-diameter firs showing up in post-burn situations were coming from unburned wetlands near burned survey corners. Small-diameter balsam fir regeneration coming in among larger trees was absent immediately after fire. Balsam fir regeneration fir first appears in the 30-year age-class **(PLS-5)**. It was far more common for fir to be the smallest tree at a survey corner, which is typical of an ingressing species. It was most adept at coming in among larger-diameter aspen and paper birch, but there were some references to small-diameter fir occurring among larger jack pine. Our interpretation is that young firs were absent from the actual burned patches of FDn32, but its widespread presence in habitats less likely to burn, assured local seed sources. Post-fire thickets of quaking aspen, paper birch, and jack pine 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 under a canopy in modern stands, with high indices of regeneration **(R-2)**.

Transition: 55-95 years

The transition to mature conditions is initiated by a burst of balsam fir recruitment late in the young growth-stage, and the collapse of that population to start the transition **(PLS-2)**. This pulse of fir reaches about 20% relative abundance in the 40-50 year age-classes, and drops to about 10% by the 70-year age class. About 16% of all bearing trees in the early transition were recruiting fir, contributing to its fair ranking in the gap window **(PLS-5)**. Smaller diameter firs could be beneath about any initial cohort tree, but it favored replacing aspen and birch rather than surviving beneath red and white pine. It did not occur at all beneath late-successional trees like black spruce or itself. Young aspen and birch stands must have offered especially good habitat for establishing balsam fir, because this pulse of fir regeneration is a feature common to many northern forest communities where the initial stages are aspen-dominated and fir is important in later growth-stages. Equally impressive is the collapse of fir populations before the transition stage concludes. Between age classes 50 and 60 years, the relative abundance of fir drops ~15%. Balsam fir is short-lived, however, the rapid collapse of the transitional cohort must have involved mortality well short of fir's normal life span. The destructive agent, perhaps spruce budworm, must have been density-dependent as fir populations never again approach those of the transition stage or show such rapid decline.

Mature Growth-stage: >95 years

Early in the mature growth-stage balsam fir abundance stabilized at about 10-15% and it persisted at similar abundance throughout the older growth-stages **(PLS-1)**. Balsam fir's ability to decisively replace the initial-cohort trees and reach peak abundance during the transition stage is why we consider fir a ***mid-successional*** species, although its behavior in the older growth-stages is more typical of a ***late-successional*** species. Balsam fir's relative abundance in the mature growth-stage was in part, the result of ingress and recruitment in the G-1 gap window **(PLS-5)**. In modern FDn32 woodlands, fir is unequalled in developing advance regeneration **(R-2)**, which is the hallmark of a late-successional tree. During the mature growth-stage smaller fir trees tended to occur among larger black spruce, paper birch, and white pine. It was rare to see small firs among larger ones in woodlands this old. It seems as if pulses of fir regeneration occurred in these older FDn32 woodlands, but these episodes were short-lived and not sustained by continued reproduction. In the mature growth-stage we envision patches of pulsing fir moving about, in contrast to the widespread condition of fir abundance at the seam between young and transitioning woodlands. Density-dependent mortality, most likely due to spruce budworm, would explain this kind of behavior.

Regeneration Strategies

Balsam fir's primary regenerative strategy on FDn32 sites is to satiate the groundlayer with seedlings and to then recruit saplings in ***small-gaps***. It was successful at doing this under any other tree, other than itself. In the historic PLS data this interpretation is supported by: (1) the fact that balsam fir abundance is steady throughout the older growth-stages **(PLS-1, PLS-2)** and, (2) it is most abundant at survey corners in mature, undisturbed conditions **(PLS-3)**. The high percentage of balsam fir seedlings in the FIA data (situations 12 and 13) is also characteristic of species successful in small gaps **(FIA-1)**. Most significant though, is its incredible ability to establish and recruit seedlings under a canopy in modern stands **(R-2)**.

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

Historic Change in Abundance

Today populations of balsam fir are considerably higher in FDn32 forests than they were historically **(PLS/FIA-1)**. We believe that this is a consequence of fire suppression and fir's obvious abilities to function as a shade-tolerant, small-gap strategist. The increase in fir is evident in the young growth-stage where it now represents 15% of the young trees in FIA samples. We believe that historically, post-fire FDn32 stands started with almost no balsam fir, whereas now they have significant initial presence after logging. Fir abundance has also doubled since historic times in mature woodlands, but mature woodlands now represent just 5% of the FDn32 landscape. The ratio of fir regeneration to actual trees is very high **(R-1, R-2)**. Thus, the increase in tree abundance in modern stands brings with it substantial amounts of understory fir, perhaps because stands no longer start from "scratch" as they did after intense fires. Fir abundance in the understory now offers a competitive challenge for less tolerant crop trees, and invites outbreaks of spruce budworm.

(PLS-1) Historic Abundance of FDn32 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the FDn32 community by growth-stage. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

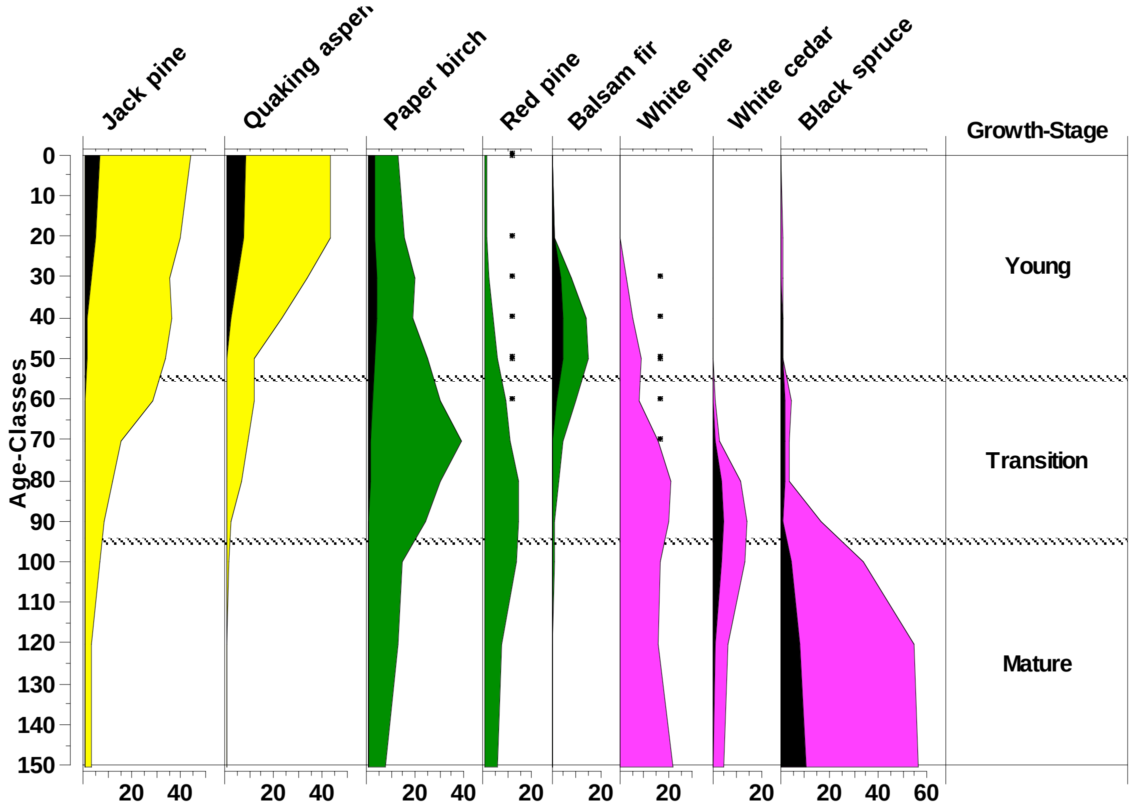
Dominant Trees	**Forest Growth Stages in Years**		
	0 - 55	**55 - 95**	**> 95**
	Young	**T1**	**Mature**
Jack Pine	**40%**	ǀǀ	**10%**
Quaking Aspen	**24%**	ǀǀ	**7%**
Paper Birch	**19%**	ǀ	**17%**
Red Pine	**3%**	⌉	**5%**
White Pine	**5%**	⌉	**10%**
Balsam Fir	**6%**	⌉	**13%**
Black (White) Spruce[1]	**1%**	⌉⌉	**31%**
Miscellaneous	**2%**		**7%**
Percent of Community in Growth Stage in Presettlement Landscape	**57%**	**25%**	**18%**

1. The PLS surveyors did not consistently distinguish the more prevalent black spruce from white spruce on FDn32 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 FDn32

Graphed for the individual species of FDn32 trees is their relative abundance (%) as PLS bearing trees by age class. Species with good-to-excellent suitability have graphs colored as follows: early successional (yellow); mid-successional (green); late-successional (magenta). The data were smoothed from adjacent classes (3-sample moving average). Black insets show the proportion of bearing trees that were small-diameter trees that were presumably recruiting to bearing tree size (~4" dbh, see **PLS-5**). For infrequent trees, the presence of small-diameter trees is indicated by black dots rather than insets.



FDn32, 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 FDn32 Trees Following Disturbance

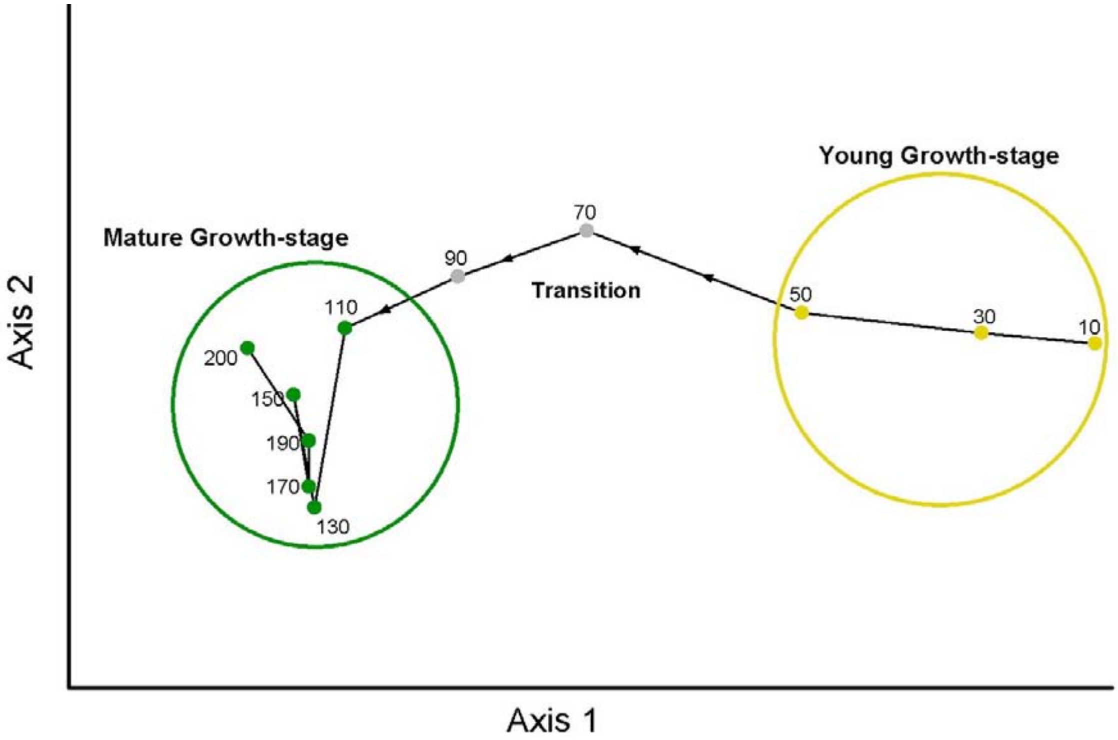
Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent FDn32 forests. The columns represent our interpretation of disturbance at the survey corners. Shading associates trees that peak in the same disturbance category.

Tree	Burned		Windthrown		Maintenance		Mature	
Jack pine	**463**	**42%**	**38**	**28%**	**84**	**25%**	**3723**	**27%**
Quaking aspen	**261**	**24%**	**25**	**23%**	**72**	**22%**	**2368**	**17%**
Paper birch	**161**	**15%**	**28**	**26%**	**65**	**20%**	**3013**	**22%**
Red pine	**59**	**5%**	**4**	**4%**	**25**	**8%**	**764**	**5%**
White pine	**106**	**10%**	**7**	**7%**	**49**	**15%**	**1175**	**8%**
Black spruce	**30**	**3%**	**4**	**4%**	**27**	**8%**	**1562**	**11%**
Balsam fir	**30**	**3%**	**1**	**1%**	**8**	**0%**	**1226**	**9%**
Total (% of grand total, 15378)	**1110**	**7%**	**107**	**1%**	**330**	**2%**	**13831**	**90%**

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

(PLS-4) Ordination of Historic FDn32 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-4, file *Figures_Tables_Documentation*

(PLS-5) Historic Windows of Recruitment for FDn32 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 0-50 years	G-1 50-90 years	I-1 >90 years
Yes	**Jack pine**	**0-20**	**Fair**	**Poor to 60**	**--**
Yes	**Quaking aspen**	**0-30**	**Good**	**Poor to 60**	**--**
Yes	**Paper birch**	**0-40**	**Good**	**Fair to 80**	**--**
Yes	**White pine**	**0-40**	**Fair**	**Poor to 60**	**--**
Minor	**Red pine**	**0-50**	**Fair**	**--**	**--**
No	**Balsam fir**	**40-50**	**Good from 30**	**Fair to 60**	**--**
No	**Black spruce**[1]	**>120**	**Poor at 30**	**Fair from 70**	**Excellent**

Recruitment windows from ordination **PLS-4**:

- **P-D:** post-disturbance filling of understocked areas, 10-50 years
- **G-1:** gap filling during decline of initial-cohort jack pine, quaking aspen, and paper birch, 50-90 years
- **I-1:** ingress of seedlings under canopy of black, spruce, white spruce, and paper birch, with some balsam fir, white pine, and decadent jack pine, >90 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; **gold =** trees with peak regeneration later in the P-D window; **purple** = trees with peak regeneration by ingress under a mature canopy or by filling small gaps in old forests

1. Black spruce bearing trees couldn’t be segregated from white spruce in the PLS notes for this community. The black spruce data probably include some white spruce, which we consider ecologically similar to black spruce.

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

(R-1) Suitability Ratings of Trees on FDn32 Sites

This table presents an index of suitability for trees in FDn32 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 FDn32

Tree	Percent Presence as Tree	Mean Percent Cover When Present	Suitability Index*
Jack pine (Pinus banksiana)	**55**	**35**	**5.0**
Black spruce (Picea mariana)	**53**	**25**	**5.0**
Red pine (Pinus resinosa)	**28**	**37**	**4.6**
Quaking aspen (Populus tremuloides)	**35**	**15**	**4.2**
White pine (Pinus strobus)	**26**	**17**	**4.1**
Paper birch (Betula papyrifera)	**34**	**9**	**3.7**
Balsam fir (Abies balsamea)	**26**	**9**	**3.4**

*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 FDn32 Stands

This table presents an index of regeneration for FDn32 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 FDn32 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 Poor Dry-Mesic Mixed Woodland, FDn32

Trees in understory	% presence R, SE, SA	R-index	SE-index	SA-index	T-index
Paper birch (Betula papyrifera)	**74**	**3.0**	**4.0**	**4.2**	**3.5**
Balsam fir (Abies balsamea)	**70**	**4.5**	**4.8**	**4.7**	**3.5**
Black spruce (Picea mariana)	**69**	**3.5**	**4.7**	**5.0**	**4.5**
Quaking aspen (Populus	**64**	**3.3**	**4.5**	**4.3**	**4.0**
White pine (Pinus strobus)	**45**	**3.8**	**4.3**	**3.8**	**4.0**
Jack pine (Pinus banksiana)	**28**	**1.2**	**1.8**	**3.5**	**4.8**
Red pine (Pinus resinosa)	**20**	**2.0**	**2.2**	**3.3**	**4.5**

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

% presence: the percent of 80 FDn32 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 FDn32 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples FDn32 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**
Black spruce	33	6%	55%	6%	55%	6%	0%
Balsam fir	410	16%	14%	16%	14%	26%	3%
Quaking aspen	1808	52%	10%	52%	10%	8%	8%
Paper birch	317	8%	37%	8%	37%	4%	23%
White pine	4	0%	0%	0%	0%	0%	100%
Jack pine	18	0%	11%	0%	11%	6%	50%
Red pine	20	10%	60%	10%	60%	0%	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 FDn32 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 FDn32 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 -55		**55 - 95**		**>95**	
	Young		**T1**		**Mature**	
Jack Pine	**40%**	**1%**	ǀǀ		**10%**	**0%**
Quaking Aspen	**24%**	**74%**	ǀǀ		**7%**	**43%**
Paper Birch	**19%**	**8%**	ǀ		**17%**	**16%**
Red Pine	**3%**	**--**	⌉		**5%**	**--**
White Pine	**5%**	**--**	⌉		**10%**	**2%**
Balsam Fir	**6%**	**15%**	⌉		**13%**	**27%**
Black or White Spruce	**1%**	**1%**	⌉⌉		**31%**	**10%**
Miscellaneous	**2%**	**1%**			**7%**	**2%**
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	**57%**	**56%**	**25%**	**39%**	**18%**	**5%**

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 6,156 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 1,708 FIA subplots that were modeled to be FDn32 sites.

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

Forest Health Considerations

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.

Black Spruce

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.

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.

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.

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.

Paper Birch

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.

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.

FDn32 - 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 FDn32 that are more susceptible to compaction and rutting. They are listed in descending order of presence.

Balsam fir (C) (*Abies balsamea*)
Mountain maple (*Acer spicatum*)
Woodland horsetail (*Equisetum sylvaticum*)
Lady fern (*Athyrium filix-femina*)

Palmate sweet coltsfoot (*Petasities frigidus*)
Drooping woodreed (*Cinna latifolia*)
Common oak fern (*Gymnocarpium dryopteris*)
Swamp red currant (*Ribes triste*)

(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

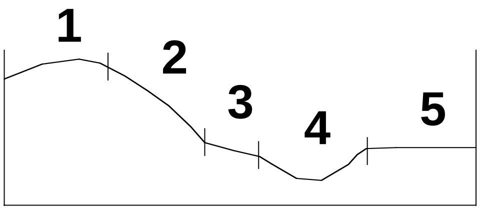
   Poor – water saturation occurs within 10 inches of the surface for most of the growing season

   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