WFn53

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WFn53 – Northern Wet Cedar Forest

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Wet Cedar Forests (WFn53) are a common, but rarely extensive community found throughout the Laurentian Mixed Forest Province of Minnesota (Figure 1). Outliers to the southwest of this Province occur but never far from the core area. Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

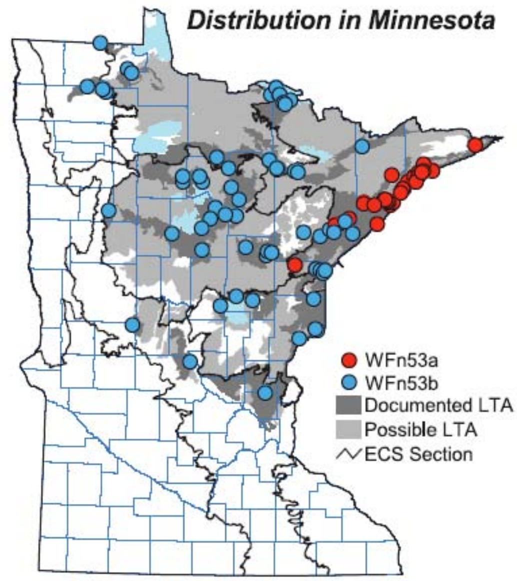

Figure 1. The range of WFn53 forests in Minnesota (shaded) and distribution of releve samples (red and blue dots).

Commercial Trees and Management Opportunities

As a commercial forest, WFn53 sites offer a wide selection of crop trees and possible structural conditions. White cedar, black ash, paper birch, balsam fir, and black spruce are all ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover when present on WFn53 sites (see Suitability Tables). White spruce and balsam poplar 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. Yellow birch is ranked as a fair choice of crop tree, but stands can be managed to maintain its presence for purposes other than timber production.

Among these species, balsam fir, white cedar, white spruce, black spruce, and tamarack were the dominant native trees that have occupied WFn53 sites for a long time and have had the opportunity through successive generations to adapt to physical conditions typical of these sites **(PLS/FIA-1)**. Black ash and paper birch are likewise native to WFn53 sites but occurred naturally at lower abundance. Between early logging and altered hydrology, the effects of settlement have been to promote much more black ash than was usual. Tamarack, has been effectively eliminated from these sites, and there is considerably less spruce in today's older forests. The increased abundance of black ash complicates our interpretations and the use of natural regeneration models as silvicultural strategies for the conifers.

Natural Silvicultural Approaches

In the historic landscape 32% of native WFn53 stands were young forest <55 years old **(PLS-1)**. Given that less just 5% of WFn53 forests were described as having been burned or windthrown **(PLS-3)**, it is clear that destructive agents other than these obvious catastrophes were involved to create so much young, WFn53 forest. Spruce budworm is the most obvious candidate for removing both the fir and spruce canopy component at a scale where we would have modeled young forest. For white cedar, windthrow is still the leading candidate for creating large holes in the canopy. Regardless, our interpretation is that young WFn53 forests were essentially the advance regeneration typical of older forests. Thus an agent like wind that is catastrophic to tall trees but not short ones would seem to fit best. Practices such as "careful logging" would obviously mimic the process. The distribution of desirable advance regeneration would essentially dictate the level and pattern of canopy removal. Pre-harvest attention to advance regeneration – inventory, cleaning, underplanting, etc. – is prerequisite. The natural shelterwood system, because of its emphasis on advance regeneration best fits this situation. Patch cutting would favor the early successional trees like balsam poplar and paper birch where we assume some level of soil disturbance and new establishment in the patches. Large gaps should favor balsam fir, black ash, and white cedar. Note that clearcutting, especially if advance regeneration is damaged in the process, comes with high risk of swamping (see Management Concerns).

Just 10% of the historic landscape was transitioning WFn53 forest between 55 and 75 years old **(PLS-1)**. The hallmark of this episode is the collapse of initial-cohort balsam fir and the release of longer-lived conifers, especially white cedar. Selective thinning of balsam fir throughout the period to release other conifers would match this process. Alternative, removing all balsam fir at its commercial peak within the period would be a good stand-improvement strategy. However, both of these strategies are based upon the assumption of adequate presence of longer-lived trees like white cedar and spruce – meaning that there is no need of a silvicultural system that incorporates a regeneration strategy. In our experience, there is a fair amount of transition-age WFn53 forest with inadequate advance regeneration of white cedar and spruce to transition these stands by removal alone. In such cases the fir crop could be mostly sacrificed to achieve the desired future composition of long-lived conifers. Fir would be used as a silvicultural tool to achieve two goals. First, dense fir is nature's herbicide and it provides a natural opportunity for planting trees where shrub and even herb density is low. Second, it is an excellent shelter that provides considerably more thermal and wind protection than do hardwoods. Thus, the shelterwood system where fir removal is accompanied by planting of cedar or spruce in the openings could be a successful strategy for transitioning WFn53 forests where the desired future condition is an old conifer stand.

In the historic landscape most (34%) WFn53 forest were mature and between 75 and 105 years old **(PLS-1)**. This was an extended period of white cedar dominance that is silviculturally significant for two reasons. First, this was a period where the volume and value of cedar sawtimber steadily increases. Second, this was cedar's best chance at establishment and recruitment of advance regeneration. Silvicultural treatments like pruning, removing culls, crown release, or improving cone production would precede harvest near the close of the episode at about 105 years. Because of cedar's high regenerant index (4.7, **R-2**) there should be no site preparation required for a catch of regeneration during the intermediate treatments. Also important is the initial ingress of both black and white spruce into mature WFn53 forests. Somehow assuring spruce establishment during this stage is required if the goal it to take a stand forward to its old, mixed-conifer condition. This is something that just doesn't seem to be naturally happening in modern forests as the regeneration indices of both black and white spruce are just fair and old forests with ~20% abundance of spruce are nearly gone from the landscape **(PLS/FIA-1)**. Just looking at the regeneration indices for either spruce, their problems of getting established in mature WFn53 forests could be related to seedbed or light. If planting were to overcome seedbed problems, then it is clear that they need rather large openings to compete with other trees trying to recruit in the openings. The group selection system would approximate the right level of canopy removal. Presumably, groups of select cedar would be removed for a while with the goal of spruce establishment and allowing more vigorous pockets of cedar to continue to grow. Planting spruce could precede or follow the removal depending upon experience.

About 15% of the historic landscape was WFn53 forest in its second transition, and at about 105-155 years of age **(PLS-1)**. This episode in the life a WFn53 forest is marked by the decline of white cedar and its replacement by spruce. Salvage cutting to remove old, canopy white cedars is a close silvicultural approximation. Naturally, this event most-likely was the result of overtopping by spruce, and certainly it released large spruce trees and poles, as otherwise we would have modeled the survey corner at a younger age. The release probably involved also the young cedars established during the mature growth-stage. If the natural regeneration is available, this kind of removal is a transitioning strategy with the goal of creating an old WFn53 forest. If not, it would resemble the windthrow event that created young WFn53 forests.

Just about 9% of the WFn53 landscape was forest older than 155 years **(PLS-1)**. The hallmark of these forests was the fine-scale mixture of trees and microhabitats of the groundlayer. This variety of seedbeds and seedling safe-sites seems to have contributed to the mixed conditions of old forests more so than variety of gap sizes. During this stage advance regeneration of spruce, white cedar, and fir filled small-to-large gaps in the canopy and could indefinitely maintain themselves. Single-tree or group-selection systems would mimic this process that maintained old WFn53 forests. Just looking at the modern data, this would strongly favor balsam fir, white cedar, and black ash as they have the largest banks of seedlings in older forests **(R-2)**. If the goal was to maintain an old forest structure with a fairly high component of spruce, then retention harvesting systems would best fit. The strategy would be to retain a matrix of spruce forest, but provide 1-2 tree-length gaps or strips to help spruce recruit given likely competition with species more tolerant of shade.

Management Concerns

WFn53 communities indicate poorly drained and structurally weak soils. Frozen soil conditions are required for operation of heavy equipment in order to avoid compaction or rutting. Because groundwater is moving in these communities, there will be many years where they never freeze to the point to where they can support heavy equipment. In addition, tip-up mounds and cradles, nurse-logs, and moss colonies create a diversity of seedbed conditions that seem important to WFn53 trees. Conserving this legacy as much as possible by operating on frozen ground and minimizing the impact of skidding by traffic control is important.

There is serious risk of swamping on WFn53 sites. The removal of too many trees, especially if followed by herbicide applications can seriously reduce the ability of the remaining vegetation to transpire and de-water the soils. The early-successional hardwoods **(PLS-2)**, because of their ability to regenerate vegetatively, played the critical role of helping to de-water WFn53 sites after the loss of forest canopy. Often, WFn53 sites are “lost” to black ash, speckled alder, willow, and wetland herbs when sites are denuded, chemically or mechanically.

The landscape balance of growth-stages and stand ages for the WFn53 community is similar to its historic condition **(PLS/FIA-1)**. This was a naturally fragmented community that occurred mostly as transitional borders between more expansive communities. Thus, we believe that wildlife populations are probably reacting to WFn53 habitat as they always have across the landscape.

Compositional changes would not seem to be much of a management concern. WFn53 sites were historically dominated by northern white cedar and they still are. To anyone familiar with the great consternation over cedar’s future in Minnesota, this is a surprising result. Cedar forests, both WFn53 and FPn63, are arguably the most diverse and botanically interesting in the state. For this reason we entertained the idea that our optimistic view was influenced by botanists over-sampling the nicest and most ecologically intact examples of the community; however, the unbiased FIA sampling also shows cedar doing well both as a tree **(PLS/FIA-1)** and in regenerative situations **(FIA-1)**. The great alarm, based also on FIA data, is mostly about the lack of young cedar cover-type. We too, show a depression of young cedar at the scale of an FIA plot where cedar is now just 11% of the trees compared to 18% historically. It is important to note that young WFn53 forests were not cedar cover-type, they were dominated by fir. In this community and several others, the cedar cover-type is something achieved late in the course of succession. Clearly, this is still true as cedar has very high abundance in mature (46%) and old (55%) FIA plots.

If we have overstated the security of cedar on WFn53 sites, our error is in not considering the security of WFn53 sites in general. These groundwater flux systems are incredibly sensitive to logging or any activity of settlement that alters the seasonal movement groundwater on these sites. Such alteration seems indelible to us as it tends to convert the site to another community composed of plants better adapted to the new hydrologic regime. Some WFn64 ash swamps and FPn73 alder swamps have scattered cedar snags that make us wonder about the site’s history. Also, the incredible five-fold increase of black ash on sites that we still recognize as WFn53 forest **(PLS/FIA-1)** makes us suspect conversion due to impeded drainage because ash is far more tolerant of ponding than cedar. Regardless, we still see WFn53 sites as prime habitat for white cedar that can be managed when silvicultural strategies for establishment and effective procedures for mitigating impact on the hydrologic regime can be demonstrated.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 1,505 corners within the primary range of the WFn53 community. At these corners, there were 3,932 bearing trees comprising the species that one commonly finds in WFn53 forests.

The PLS field notes described about 2% of the WFn53 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands. From these data, a rotation of 800 years was calculated for stand-replacing fire.

Elsewhere in the WFn53 landscape, the surveyors described lands as windthrown and lacking suitable-sized trees for scribing. Such corners were encountered at about 4% of the time, yielding an estimated rotation of 360 years for windthrow.

Also at WFn53 sites were references to what we have interpreted as some kind of partial canopy loss, without any explicit mention of fire or windthrow. Most references were to sparse forest or thickets with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked cedar forests. About 1% of the survey corners were described as such, resulting in a calculated rotation of 340 years for disturbances that maintained cedar trees on WFn53 sites. That more corners were described as windthrown (59) compared to fire (28) suggests that windthrow the more prevalent cause of partial canopy loss.

Natural Rotations of Disturbance in WFn63 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**800 years**
Catastrophic windthrow photograph	**360 years**
Partial Canopy Loss, photograph	**340 years**

All northern wet forests (WFn) have similar disturbance regimes and share in common very long rotations of catastrophic fire. It is unlikely that fire played an important role in regenerating these forests. The rotation of 360 years for catastrophic windthrow is also typical of WFn communities. This seems remarkably long, given the tendency of trees to root shallowly on saturated soils and the mechanical weakness of wet soil. Rotations of 300-400 years are a third to a tenth that observed for the surrounding terrestrial forests of the northern floristic region. The rotation of 340 years for maintenance disturbances is the longest calculated for WFn forests. We believe that of the WFn communities WFn53 is the most stable hydrologically, meaning that root loss and stress due to fluctuation of the water table did not contribute as much to patchy canopy loss as it did in ash-dominated wet-forest.

Natural Stand Dynamics & Growth-stages

WFn53 forests are among several wetland communities where a particular hydrologic regime translates into dominance of a single species. Here, the flux of groundwater in shallow aquifers strongly favors northern white cedar. There is little “succession” because white cedar is abundant in all growth-stages. Proximal disturbances like fire and windthrow, while noteworthy in the PLS records, were not the main means of re-setting stands to a youthful structure and composition to be followed by predictable compositional changes that we attribute to gap maturation processes. For wetland dominants like white cedar, we favor the approach of considering their vulnerability in light of the hydrologic regimes that allow for their dominance. Storm events that erode drains and lower base water tables, cycles of drought, the ebb and flow of beaver populations, unusual and extended spring ponding, and outbreaks of diseases and pests targeting stressed trees probably had as much to do with the mortality of trees on WFn53 sites as did events as obvious as fire or windthrow.

A second critical difference between terrestrial and wetland communities regarding succession and stand dynamics is that the wetland communities are linked by a single process. For the past 6,000 years the climate of Minnesota has favored the expansion and development of wetland forests. The swamping, or paludification, of terrestrial sites has been a rather unidirectional process of peat accumulation, rising water tables, greater predictability of depth to the water table, and increased acidification by *Sphagnum* mosses. Along the way, different species of trees are favored and tend to dominate wetland forests that are at a particular stage of this process. That is, there is an ontogeny of wetland forest types that is evident both spatially and in the temporal reconstructions of vegetation change preserved in the peat strata. WFn53 forests are associated with the “mixed-mire pathway” of wetland development. Some WFn53 forest are on fairly deep peat and are part of the pathway as cedar swamp that includes also the FPn63 community. Some WFn53 forests are on wet mineral soil with a veneer of mucky peat, and these sites will ultimately become peatier if Minnesota’s climate continues to favor landscape paludification. These cedar-dominated peatlands commonly succeed black ash forest, and they will in turn be succeeded by rich, tamarack or spruce peatland forests. ***This is significant because the sort-term stand dynamics tend to reflect the long-term ontogeny.*** In this case young, small-diameter WFn53 cedar stands tend to have compositional and structural similarities with WFn64 black ash swamps. Old, large-diameter WFn53 stands start to resemble FPn tamarack/black spruce swamps. Disturbances that re-initiate WFn53 forests can set back this process, but eventually the gains towards tamarack/spruce swamp will outweigh the regressions to ash swamp.

The general compositional dynamics of WFn53 forests is for rather steady change, with modest acceleration from about the 50-year age-class to the 80- or 90-year age classes **(PLS-4)**. Younger stands are dominated by fir with cedar and some hardwoods like black ash and paper birch; middle-aged stands are strongly dominated by cedar; old stands are a balance of fir, cedar, and spruce. It is important to note that while compositional trends are evident, it is hardly succession in that initial-cohort trees persist throughout the cycle – no species is totally replaced by another. The actual movement in ordination space is small in comparison to terrestrial communities subject to catastrophic, site-altering disturbance. When such events, e.g. beaver flooding, stream incision, etc., happen on WFn53 sites they become another NPC Class because there is no inherent recovery mechanism.

The general structural dynamics of WFn53 forests is uninteresting as tree density changes very little throughout the course of stand maturation. Young and transitioning forests had mean distances of 22 feet from survey corners to their bearing trees. This density is typical of fully stocked wet forest. Mature and second transition forests had mean distances of 20 feet for bearing trees. Old forests were a bit sparser with 24 feet from a bearing tree to its corner on average. This steady density is probably the consequence of the canopy dominants being conifers, which tend to not expand crowns as much as hardwoods.

Young Growth-stage: 0-55 years
About 32% of the WFn53 landscape in pre-settlement times was covered by forests estimated to be under 55 years old **(PLS-1)**. Most often these stands were of mixed composition (60%). Mixed corners mostly involved white cedar or balsam fir in combination with each other, but there was a long list of species that could co-occur with the three dominants. Many species clearly came from adjacent, upland habitats (e.g. jack pine), and were not likely to succeed beyond the earliest post-disturbance years. About 40% of the survey corners were monotypic, and this is the only growth-stage where that was at all common. All cases of bearing trees being the same species involved either balsam fir or white cedar.

Upon occasion (2%) the surveyors mentioned fire in association with a WFn53 survey corner **(PLS-3)**. At these corners white cedar, balsam fir, and spruce were mentioned most often as the bearing trees. These species are among the most fire-sensitive in the state and we doubt that they were really post-fire regeneration. More likely these were small-diameter trees skipped in a fire because of the wet WFn53 habitat, as it is fairly common for this community to be included in uplands that burned regularly. Because of the high water table and weak, peaty substrate we believe that windthrow did contribute to the regeneration of WFn53 stands. The surveyors described about 3% of the landscape as wind-affected or blown down. White cedar, balsam fir, and black ash were the prevalent species to occupy a WFn53 site after blowdown. The natural rotations of fire (800 years) and windthrow (360 years) were way too long to create the observed balance of growth-stages across the WFn53 landscape **(PLS-1)**. Clearly, small-diameter fir and cedar stands were initiated by means other than just fire and wind. Balsam fir and spruce were affected by widespread outbreaks of spruce budworm, that might well have worked in concert with windthrow to create a disturbance that the surveyors considered notable. By comparison, white cedar and black ash had few pests or diseases able to cause stand-scale mortality. Perhaps, this is why these species generally dominated northern wet-forests (WFn).

More than anything, young WFn53 forests resemble the understory of old ones. The presence and abundance of understory balsam fir, white cedar, and black ash are very high in modern WFn53 forests **(R-2)**. Any agent that removed canopy trees and left advance regeneration intact, would have created a stand compositionally similar to what we observed at young survey corners. Windthrow is the most likely candidate to remove the canopy but not shorter trees. The most interesting consequence of this model of stand regeneration is the dominance of balsam fir in the initial-cohort. Fir occurs in almost all northern forests, and commonly it achieves high understory density at some point during stand maturation. Normally, fir is absent from the initial cohort and its abundance comes in the form of a pulse during self-thinning, followed by a collapse of local populations that we believe is the result of density-dependent mortality mediated by spruce budworm. Balsam fir is an abundant initial-cohort tree only in cedar-dominated wetland forest – WFn53 and FPn63. Fir still shows a pulse of abundance in these communities, but in this case it starts with a high proportion of fir in the initial age-class. The incredibly high abundance of fir in young WFn53 forests would seem to preclude fire or flooding as stand-initiating events as fir is incredibly sensitive to both disturbances. This is interesting in that vernal ponding is characteristic of ash-dominated wet forest. Meaning that the tendency to pond or not might explain why some northern wet forests end up being dominated by either ash, or by cedar/fir respectively.

Transitional Stage: 55-75 years
About 10% of the historic WFn53 landscape was forest undergoing compositional change as stands approached maturity **(PLS-1, PLS-4)**. About 94% of transitioning survey corners were of mixed composition. Nearly all corners had fir bearing trees in combination with other trees. Black ash and paper birch were the most common trees to occur in combination with fir, but white cedar was often present as well.

The transition stage is driven almost entirely by a sharp decline in the abundance of balsam fir **(PLS-1)**. Fir's plummet of about 40% relative abundance between the 50- and 80-year age-classes **(PLS-2)** is responsible for much of the community's compositional "movement" in the transition stage **(PLS-4)**. Balsam fir is naturally senescent and susceptible to budworm attacks at these ages.

The collapse of fir populations had the effect of releasing initial-cohort white cedar, and provided an environment where cedar was able to establish new trees or recruit suppressed seedlings. The rapid response of cedar to the fir vacuum would favor the idea that advance regeneration was released. This seems quite possible in that cedar has excellent ability to establish and recruit seedlings under a mature canopy in modern forests **(R-2)**. The pattern of fir pulses being followed by ingress or increase of other conifers (including cedar) is repeated in the PLS data for a wide range of communities in their northern floristic regions. Fir seems to prepare sites for conifers and direct succession towards a coniferous conclusion involving cedar, white spruce, or white pine rather than mesic hardwoods. The fact that this happens in communities with such different ecological function – fire-dependent, mesic hardwoods, wet forests, and rich peatland forests – would seem to preclude a single, mechanistic link between fir and conifer regeneration. In WFn53 forests, downed wood or woody debris is the primary substrate for tree seedlings. In this situation, it seems easier to guess that decayed fir itself is a prime substrate for conifers. Possibly, the increase in cedar in transitioning WFn53 forests was a reaction to a general increase in available woody substrate relative to pools, which do not seem to be good places for cedar seeds to germinate. Successful recruitment of the cedar seedlings though, seems to be limited to the WFn53 and FPn63 communities in the modern landscape.

It is highly unusual for a tree to have a “U-shaped” abundance curve, as is the case for balsam fir on these sites. Normally, trees simply increase or decrease across the age-classes as stands recover from disturbance, presumably due to unidirectional changes in light, seedbed, and soil conditions associated with stand maturation. Also, common are species that have peak abundance associated with the breakup of the initial-cohort canopy. Mid-successional minima can’t be associated with site-disturbance cycles, which are our usual mental picture of succession. For balsam fir on WFn53 sites, our best guess is that the mid-successional event that is deleterious to balsam fir is for there to be too much fir itself to the point of encouraging outbreaks of spruce budworm or in populations of fungi that attack and degrade the root systems of balsam fir. Balsam firs in the mature growth-stage then, represent the survivors of budworm outbreaks or root-rot attacks during the transition, and those trees are the legacy of fir in the older forest. It is possible that the density-dependent cycling of fir on WFn53 sites is the main initiator of compositional change.

Mature Growth-stage: 75-105 years

About 34% of the historic WFn53 landscape was mature cedar forest **(PLS-1)**. Stands in this stage were more often mixed (84%) than monotypic (16%). Monotypic conditions were represented entirely by survey corners where all bearing trees were white cedar. At survey corners with mixed composition, most were combinations of cedar and balsam fir. However, there was a long list of incidental species including several species of hardwoods led by paper birch. By the mature growth-stage it is also clear that spruce, probably both black and white spruce, will be an important component of the older forest.

The mature growth-stage is characterized most by the dominance of WFn53 sites by white cedar **(PLS-1)**. Cedar abundance peaks at this time at about 70% relative abundance in the 90-year age-class **(PLS-2)**. This growth-stage is also characterized by a minimum of fir abundance, at about 5% abundance in the 90-year age-class. Hardwoods like black ash and paper birch decline to low abundance during the mature growth-stage; swamp conifers like black spruce and tamarack ingress at this time. Significant succession was going on in mature forests, but the movement in ordination space is muted by the dominance of cedar **(PLS-4)**. Just looking at the hardwoods and swamp conifers, the successional trend is unidirectional and what one expects if succession follows the developmental, “mixed mire” pathway were ash is succeeded by, cedar, which is in turn succeeded by spruce and tamarack. This change is accompanied by increasingly stable and mossy understory conditions.

The inverse relationship between white cedar and balsam fir on WFn53 sites is a puzzle because no unidirectional change in site character during stand maturation can explain it **(PLS-1)**. We can think of no direct interaction that might explain the alternation of cedar and fir. For example, if a fir canopy promoted white cedar regeneration more so than it own seedlings – and vice-versa – then alteration of the canopy would be expected. "Kind" treatment of the seedlings of a competing species has no place in ecological theory as it violates what we know of natural selection. This leaves only the possibility that one species is passively reacting to cyclic fluctuations in the populations of the other. Balsam fir is a good candidate for the independent species because it has pulses of abundance that have been observed in both space and time that are linked to outbreaks of spruce budworm that depend to some extent upon fir abundance. White cedar is a poor candidate in that it has few diseases and pests and has the potential to live across several successional cycles. Our best guess is that cedar has the ability to maintain advance regeneration on WFn53 sites **(R-2)** that is periodically released when the fir overstory collapses. This is most likely to occur when initial-cohort of fir dies because that fir population is all about the same age and at its greatest abundance. In older growth-stages the loss of canopy fir is probably due to chronic but lower impact of budworm, meaning that it can compete with cedar for canopy space.

Second Transition Stage: 105-155 years
About 10% of the historic WFn53 landscape was forest undergoing compositional change as stands approached old-growth **(PLS-1, PLS-4)**. About 82% of transitioning survey corners were of mixed composition. Most survey corners were some combination of white cedar, balsam fir, and spruce. Monotypic conditions were represented entirely by cases where all bearing trees were white cedar.

The second transition is best described as a period where white cedar declines in abundance and other conifers replace it rather equally. White cedar, balsam fir, white spruce, black spruce, and tamarack all had the ability to maintain a presence in older WFn53 forests. Cedar's fall is to us a mystery. Northern white cedar is arguably the longest-lived species in Minnesota and is among the record-setters on the continent, with some individuals over 1,000 years old. It has virtually no serious pests or diseases in comparison to other trees in the state. Fire is the only serious threat to old cedars and there is little evidence of fire in the WFn53 community. Nonetheless, there are enough old age-classes for WFn53 to convince us that there was certainly less cedar in old forests than in mature ones, and that the decline starts in the second transition. The same decline is seen in other communities and in all cases, cedar loses to white spruce. Our best guess is that the decline of white cedar is influenced by overtopping by white and possibly black spruce in old forests. By far, white spruce has greater representation in the tall canopy classes of releves in comparison to white cedar. White spruce has some small-diameter regeneration in the mature growth-stage **(PLS-5)**, which must have been adequate to support its increase during the second transition and dominance of old forests.

Old Growth-stage: approximately >155 years
About 9% of the historic WFn53 landscape was estimated to have been stands older than 155 years **(PLS-1)**. Nearly all (93%) of the corners with these large old trees were mixed in composition. White cedar, spruce, balsam fir, and tamarack are nearly equal in abundance at mixed survey corners. All instances of monotypic survey corners were where white cedar represented all of the bearing trees.

Old WFn53 stands are inherently mixed at a fine scale, which allows for a diverse mixture of other trees with varying regenerative strategies to occur about the core population of white cedar. In the field, it seems obvious that variety of substrate conditions control the distribution of both canopy tree species and groundlayer plants. Pools of water often in windthrow cradles, nurse logs, moss hummocks, alternating patches of minerotrophic and acidic mosses, raised tree bases, alder stools, etc. create micro-topography with as much as 2 feet of relief with highs and lows that interact differently with the water table. Only a few other forest communities carry the fine-scale biological diversity that is expressed in old WFn53 forests. The significance of both the biological and topographic diversity is that it seemingly helps to carry forward the legacy of most species in old WFn53 forests. All of the trees common in the old growth-stage are present at some level in young, re-initiated stands **(PLS-1)**. Also, this diversity tends to yield a young forest that resembles strongly the advance regeneration (R-2) and does not change much (PLS-4) after disturbance removes the canopy trees.

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?

Northern White Cedar

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap regeneration strategist***
- ***regeneration window at 70-90 years***

Suitability

WFn53 sites provide ***excellent habitat*** for white cedar trees. The perfect ***suitability rating*** of 5.0 for white cedar is influenced mostly by its very high presence (83%) as trees on these sites in modern forests **(R-1)**. When present, white cedar is the dominant tree, contributing 39% mean cover in mature stands. The ranking is perfect, because no other tree or plant has a higher presence and cover on WFn53 sites as sampled by releves. Northern wet forests (WFn) in general offer good-to-excellent habitat for northern white cedar (see Suitability Tables). Among the WFn communities, WFn53 is the best habitat for cedar trees.

Young Growth-stage: 0-55 years

Historically, at 18% relative abundance white cedar was an important tree in young WFn53 forests **(PLS-1, PLS-2)**. Young cedars represented 54% of the trees at survey corners described as burned **(PLS-3)**. We do not believe though that WFn53 forests burned in the same sense that upland forests did. More likely, the survey corner was burned but not nearby ash/cedar swales and the surveyors used some small-diameter (<8") cedar in the unburned wetlands as bearing trees. White cedar was substantially more important after windthrow, representing 67% of the trees at such survey corners. Small-diameter white cedar regeneration coming in among larger trees was not detected during the young growth-stage **(PLS-5)**. All cedar records in the young growth-stage were as the largest tree at a corner. Apparently, the effect of wind was to leave the better-established, larger-diameter cedars that we modeled to be under 55 years old.

Transition: 55-75 years

The transition is the period of greatest compositional change in WFn53 forests **(PLS-4)**. The changes were driven by the senescence and decline of balsam fir and its replacement by other species. More than any other species, white cedar was positioned to replace the initial-cohort fir **(PLS-2)**. At this time it was about equally likely for cedars to be the largest tree at a corner as it was for it to be the smallest tree. For this reason, we believe that the increase in relative abundance of cedar during the transition involved both recruitment of suppressed initial-cohort trees and new establishment. There is a clear pulse of small-diameter regeneration during the transition **(PLS-5)**, and cedar had more success than any other species in this environment. Consistent with this idea is cedar's leading presence at survey corners showing partial canopy loss **(PLS-3)**, and its perfect SA-index **(R-2)** which is typical of trees able to recruit to the subcanopy and then replace canopy trees directly. For cedar to dominate mature forests so strongly, we believe that it must have achieved subcanopy dominance during the transition.

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Mature Growth-stage: 75-105 years

The mature growth-stage is the period where white cedar strongly dominates WFn53 forests **(PLS-1)**. Obscured by data smoothing in Figure **PLS-2** is a strong peak of cedar abundance with a maximum of 75% relative abundance in the 90-year age-class. Because of cedar's peak abundance in the mature growth-stage, we consider it to be a ***mid-successional*** species. During the mature growth-stage there was a balance of cases where cedar was the largest tree at a survey corner, where is was the smallest tree, and where all bearing trees were cedar. This is typical of a tree with an extended window of recruitment. Cedars alive during the mature growth stage involved at least two cohorts: the initial-cohort and a cohort recruited between the 50-90 year age-classes. Peak recruitment occurred in the 70-90 year age-classes **(PLS-5)**. When cedars were the smallest tree at survey corners, it was by far most common for the younger cedars to be below older, parent cedars. This explains in part the tendency of cedar to form pure groves or just dominate mature WFn53 sites. There was also a high proportion of cases where smaller-diameter cedars were among larger paper birch.

Second Transition: 105-155 years
White cedar's rise to dominance in mature forests was a consequence of its ability to compete with, recruit with, and outlive balsam fir. Its fall, starting at the 90-year age class and characterizing the second transition seems to be a consequence of cedar's inability to accomplish the same things in the presence of spruce **(PLS-1, PLS-2)**. Cedar's fall is to us a mystery. Northern white cedar is arguably the longest-lived species in Minnesota and is among the record-setters on the continent, with some individuals over 1,000 years old. It has virtually no serious pests or diseases in comparison to other trees in the state. Fire is the only serious threat to old cedars and there is little evidence of fire in the WFn53 community. Nonetheless, there are enough old age-classes for WFn53 to convince us that there was certainly less cedar in old forests than in mature ones, and that the decline starts in the second transition. The same decline is seen in other communities and in all cases, cedar loses to white spruce. Our best guess is that the decline of white cedar is influenced by overtopping by white and possibly black spruce in old forests. By far, white spruce has greater representation in the tall canopy classes of releves in comparison to white cedar.

Old Growth-stage: >155 years
In the old growth-stage white cedar abundance was considerably diminished from its peak in the mature growth-stage, but still it was the most abundant tree **(PLS-1)**. During this time cedar had a healthy balance of diameters relative to other trees. It was still about equally likely for cedars to be the smallest tree as it was for it to be the largest tree at a survey corner. Although we detected no small-diameter regeneration based upon our stringent rules **(PLS-5)**, it would seem that trees established while it was at peak abundance (~80-110 year age-classes) were surviving well into the old growth-stage. Also, there still was a fair amount of survey corners where all trees were cedar (7%). Possibly, cedar's persistence in old forests was at least subsidized by replacing itself in pure groves free of the overtopping influence of spruce. When cedar was the smallest tree at a survey corner it was most often among larger-diameter cedars. In our releve data, cedar has excellent regeneration indices **(R-2)**, meaning that it is quite capable of establishing and recruiting seedlings under a cedar-dominated canopy. Most impressive is its perfect SA-index, meaning that it is successful recruiting seedlings to sapling and pole size. Our interpretation is that cedar could indefinitely maintain a population in old forests through establishment and recruitment.

Regeneration Strategies
White cedar's primary regenerative strategy on WFn53 sites is to establish advance regeneration and then recruit in canopy gaps. It was most successful at this when ***large-gaps*** formed within a declining canopy of initial-cohort balsam fir. In the historic PLS data the large-gap interpretation is supported by: (1) the fact that white cedar abundance responds to the decline of initial-cohort balsam fir during the transition where we presume large-gaps **(PLS-2)**, (2) it has high presence at survey corners where we interpret partial canopy loss, and (3) it has peak regeneration in a gap window rather than an ingress or post-disturbance window **(PLS-5)**. The high percent of white cedar poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that tend to regenerate well in large gaps.

The releve sampling of mature WFn53 forests would suggest that white cedar can also recruit well in ***small-gaps***. Its excellent indices of regeneration are most in line with small-gap strategists. In the FIA data, cedar's high presence as subordinate seedlings (situations 12 and 13) is also consistent with a species that can do well in small-gaps **(FIA-1)**. The persistence of cedar in old forests is the most compelling reason to believe that cedar could maintain itself in small-gaps historically.

Historic Change in Abundance
Today, white cedar is about as abundant as it ever was on WFn53 sites. There is some pattern of change among the growth-stages as there is now less cedar in younger forests and more in older ones **(PLS/FIA-1)**. In young forests, cedar historically had 18% relative abundance and now has just 11%. In mature forests where cedar strongly dominated historic stands at 67% abundance, today

just 46% of the trees are cedars. Because of statewide concerns driven mostly by our limited ability to regenerate cedar stands, much less cedar has been harvested and now many of passed-over stands have entered the old growth-stage. Today there is more old WFn53 forest (14%) and more cedar in old forests (55%) than there was historically. Foresters familiar with past assessments of cedar's plight in Minnesota, will most likely be surprised that there is a community where cedar seems to be doing well and functioning much as it once did. There is no questioning the loss of cedar in terrestrial communities, where past exploitation has eliminated seed trees and abnormally high deer populations frustrate foresters attempts to improve local populations of cedar through planting. On wetter sites like WFn53, cedar seems to be doing just fine as long as seed trees are present and as long as stands are allowed to mature beyond the loss of the initial-cohort at about age 50. Our vision of WFn53 sites and also FPn63 sites is that they have always been refugia for white cedar trees. Historically, fires skirted around these sites eliminating cedar from terrestrial forests like FDn43 that in time were capable of supporting cedar as long as a seed source was nearby. Our interpretation is that leaving WFn53 forests alone will assure a future for cedar, but we should not overlook the silvicultural importance of these sites as a seed source for restoring cedar on adjacent uplands.

Black Ash

- ***excellent habitat suitability rating***
- ***mid-successional***
- ***large-gap (small-gap) regeneration strategist***
- ***regeneration window at 40-70 years***

Suitability

WFn53 sites provide ***excellent habitat*** for black ash trees. The high ***suitability rating*** of 4.8 for black ash is influenced mostly by its high presence (42%) as trees on these sites in modern forests **(R-1)**. When present, black ash is an important co-dominant tree, contributing 24% mean cover in mature stands. The ranking is second, following white cedar on WFn53 sites as sampled by releves. All northern wet forest (WFn) communities offer excellent habitat for black ash (see Suitability Tables).

Young Growth-stage: 0-55 years

Historically, at 7% relative abundance black ash was an occasional tree in young WFn53 stands recovering from stand-regenerating disturbances **(PLS-1, PLS-2)**. Young black ash represented 7% of the trees at survey corners described as burned **(PLS-3)**. We do not believe though that WFn53 forests burned in the same sense that upland forests did. More likely, the survey corner was burned but not nearby ash swales and the surveyors used small diameter (<8") ash in the unburned wetlands as bearing trees. Black ash was less important following windthrow, representing just 4% of the trees at such survey corners. Because of the high water table and weak, peaty soils in WFn53 communities we believe that windthrow was quite common but it seemed to favor the advance regeneration of conifers more so than ash. Young WFn53 corners with black ash trees present were entirely mixed, but there weren't enough examples to conclude that black ash had a preference to co-occur with any particular species. Small-diameter ash regeneration doesn't appear until the 40-year age-class near the conclusion of the young growth-stage **(PLS-5)**. At this time it was more common for ash bearing trees to be the smaller tree at a corner. Our interpretation is that there is usually advance regeneration of black ash in WFn53 forests of any age **(R-2)**, and that canopy removal results in the release of at least some ash seedlings and saplings but not to the extent of balsam fir. Late in the growth-stage, it seems likely that the loss of some initial-cohort fir provided further opportunities for the establishment and recruitment of black ash.

Transition: 55-75 years

The transition is the period of greatest compositional change in WFn53 forests **(PLS-4)**. The changes were driven by the senescence and decline of balsam fir and its replacement by other species. At least for the initial transition years, black ash benefited reaching peak abundance of about 10% in the 60-year age-class **(PLS-2)**. Because of this abundance peak in the transition, we consider black ash a ***mid-successional*** tree on WFn53 sites. Small-diameter ash regeneration occurred in fair abundance during the transition **(PLS-5)**. At this time, it was about three-times as likely for ash to be the smallest tree at a survey corner. At such corners, it was most common for smaller-diameter ash to be among larger balsam fir or paper birch. Our interpretation is that there is usually some black ash advance regeneration present in WFn53 forests, and the disintegration of the fir canopy provided its best opportunity for release in the course of succession.

Mature Growth-stage: 75-105 years

The mature growth-stage is the period where white cedar strongly dominates WFn53 forests **(PLS-1)**. Although black ash made some gains in abundance during the transition, it didn't nearly equal the success of white cedar. Throughout this period the abundance of ash drops slowly, stabilizing at about 3% relative abundance in the 110-year age-class **(PLS-2)**. Small-diameter ash regeneration was not detected in the mature and older age-classes **(PLS-5)**. At this time it was more common for black ash to be the largest tree at a survey corner, which would seem to us to be trees recruited early in the transition. There were cases of black ash being the smallest tree at a corner and when it was, it was far more common for the smaller trees to be among larger-diameter ash. Otherwise, smaller black ash were occasionally below white cedar or paper birch. Our interpretation is that within the cedar-dominated matrix of WFn53 forests, there were inclusions where ash was successful in establishing mature groves. Possibly, these inclusions were places that resisted the formation of a mossy ground cover, which seems to diminish substantially the establishment of ash seedlings in favor of conifers.

Second Transition and Old Growth-stage: 105-155 years and older
From the second transition on, the relative abundance of black ash is stable at about 3% and it plays no further role in succession **(PLS-1, PLS-2)**. In WFn53 forests and wet-mesic hardwood forests, it is not unusual for black ash to be older than 155 years, and very large ash are often older than 200 years. Thus, it is possible for initial-cohort black ash to survive into old growth-stages, but we believe that black ash don't live that long in very wet habitats like WFn53. It seems more likely that the persistence of black ash in old WFn53 forests was the result of continued establishment and recruitment. Small-diameter black ash regeneration was not detected during the old growth-stage using our restrictive half-diameter rule **(PLS-5)**; however, smaller diameter trees were abundant. It was about four-times as likely for an ash to be the smallest tree at a survey corner than it was for it to be the largest. The most compelling argument for sustained presence of black ash in old WFn53 forests is its regenerative performance in modern forests. Black ash has excellent indices of establishment and recruitment in mature and old forests sampled by releves **(R-2)**. Our interpretation is that historically, black ash had adequate establishment and regeneration under a canopy to sustain 3% relative abundance.

Regeneration Strategies
Black ash's primary regenerative strategy on WFn53 sites is to establish advance regeneration and then recruit in canopy gaps. Historically, it was most successful at this when ***large-gaps*** formed within a declining canopy of initial-cohort balsam fir. In the PLS data the large-gap interpretation is supported by: (1) the fact that black ash abundance responds to the decline of initial-cohort balsam fir during the transition where we presume large-gaps **(PLS-2)**, and (2) it has peak regeneration in a gap window rather than an ingress or post-disturbance window **(PLS-5)**. The fairly high percent of black ash poles under trees (situation 23) in the FIA data **(FIA-1)** is also a characteristic of species that can regenerate well in large gaps.

The modern data favor the notion that black ash is a ***small-gap*** species. Black ash's excellent indices of regeneration are most in line with small-gap strategists **(R-2)**. In the FIA data, ash's high presence as subordinate seedlings (situations 12 and 13) is especially indicative of a species that can succeeds in small-gaps **(FIA-1)**. Thus, it would seem that black ash doesn't much care about gap size and can respond to about any level of partial canopy removal.

Historic Change in Abundance
Today, black ash has dramatically replaced balsam fir and cedar on WFn53 sites **(PLS/FIA-1)**. In all growth-stages, modern black ash abundance is about 5-times what it was historically. This is especially important in the young growth-stage – where black ash is now 45% of the trees compared to just 7% historically – because regenerating WFn53 stands to not start out as a coniferous community, perhaps diminishing the chances of the site being cedar-dominated. We doubt that this is a consequence of modern logging as little cedar or ash is sold in comparison to other trees. Our best guess is that an impact of this magnitude is related to altered hydrology. Black ash has greater tolerance to fluctuations of the water table and vernal ponding than the conifers. Also the mossy seedbeds that usually favor conifer regeneration over that of black ash also seem to disappear when the seasonal water-regime becomes more variable. In such cases, the tendency of WFn53 sites is to regress towards the ash-dominated WFn64 community.

Paper Birch

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

Identification Problems

Often, the PLS surveyors distinguished yellow from paper birch, but not always. WFn53releve samples show that for plots with birch present: 9% have both species present; 23% are yellow birch without paper birch; 68% are paper birch without yellow birch. For this analysis, tree records were biased towards paper birch because we assigned generic references to "birch" to the more common paper birch. Thus our interpretation of paper birch's historic behavior, should be done knowing that some "birch" bearing trees were yellow birch. We believe that for most silvicultural decisions, these species similar enough to treat together.

Suitability

WFn53 sites provide ***excellent habitat*** for paper birch trees. The ***suitability rating*** of 4.5 for paper birch is influenced mostly by its presence (40%) as trees on these sites in modern forests **(R-1)**. When present, paper birch is a minor co-dominant tree, contributing 10% mean cover in mature stands. The ranking is third, following white cedar and black ash on WFn53 sites as sampled by releves. Northern wet forests in general offer fair-to-excellent habitat for paper birch (see Suitability Tables). The WFn53 community is by far, the best for paper birch.

Young Growth-stage: 0-55 years

Historically, paper birch was an occasional tree in young WFn53 stands **(PLS-1, PLS-2)**. During this stage its abundance peaked at 8% of all trees and for this reason we consider paper birch an ***early successional*** species on WFn53 sites. Young paper birch represented 8% of the trees at survey corners described as burned **(PLS-3)**, but we doubt that WFn53 sites really burned because of the immediate success of fire-sensitive trees like white cedar and balsam fir. The sample size of paper birch at windthrown corners is too low for any judgment about its reaction to that disturbance. Small-diameter paper birch regeneration was abundant post-disturbance **(PLS-5)**, and was especially high in the initial age-class. We believe that paper birch's ability to maintain a modest bank of advance regeneration in older forests **(R-2)**, is largely responsible for the small diameter trees released after disturbance more so than any new establishment. We do believe though that paper birch reacted very favorably to the open conditions and was able to effectively compete with fir and cedar in achieving a place in the canopy.

Transition: 55-75 years

As stands transitioned to mature conditions paper birch changed little in abundance **(PLS-1)**. While fir was dying and cedar was succeeding, paper birch abundance held steady at 8%. At this time it was about twice as likely for paper birch to be the largest tree at a survey corner as it was for it to be the smallest one. This is typical of an initial-cohort tree that is able to outlive others. Small-diameter paper birch regeneration was still fairly common throughout the period **(PLS-5)**, and it seems that some was effective in recruiting to tree size as gaps formed in the fir canopy. Our interpretation is that most initial-cohort paper birch just lived through the transition. If there were modest losses, there was enough gain by establishment and recruitment in large gaps to keep paper birch at its young forest abundance.

Mature Growth-stage: 75-105 years

The behavior of paper birch in the mature growth-stage is similar to that of the transition. Basically there was very little change in relative abundance **(PLS-1, PLS-2)**. The difference from the transition is that small-diameter paper birch regeneration was scant during the period **(PLS-5)**, and there was an increasing tendency for paper birch to be the largest tree at a survey corner. We believe that most of this birch was established in the young growth-stage, recruited during the transition, and lived through the mature growth-stage with little mortality. When paper birch was the smallest tree at a corner most trees were now below white cedar, and there were several cases where smaller birch were among larger balsam fir or parent birch.

Second Transition and Old Growth-stage: 105-155 years and older

In stands older than about 100 years, the relative abundance of paper birch is stable at about 5% **(PLS-1, PLS-2)**. Birch plays no further role in successional dynamics. We did not detect any small-diameter paper birch regeneration at this time, but this is true of all species other than spruce **(PLS-5)**. We believe that birch's steady persistence was the result of limited establishment and recruitment in old, undisturbed wet forest. At this time it was about 3-times as likely for paper birch bearing trees to be the largest tree at a survey corner as it was for it to be the smallest one. This means, that if paper birch was persisting by relying on its advance regeneration and canopy gaps, it did so with a fairly small bank of seedlings and saplings. In modern WFn53 forests, paper birch has good, and steady indices of recruitment (3.2-3.3, **R-2**), which we believe is adequate to maintain 5% relative abundance.

Regeneration Strategies

On WFn53 sites paper birch's primary regeneration strategy is to recruit advance regeneration and possibly establish some new seedlings in the ***open*** after a disturbance has removed large patches of canopy trees. It seems unlikely that much of this regeneration was from stump sprouts as we believe fire was not important in this community **(PLS-3)**. In the historic PLS data the open regeneration-strategy interpretation is supported by: (1) the fact that paper birch abundance peaks in the young growth-stage **(PLS-1, PLS-2)**, and (2) birch's peak abundance as small-diameter regeneration was in the initial age-classes **(PLS-5)**. In the FIA data, paper birch has peak abundance as seedlings or saplings among similar-sized trees (situations 11 and 22), which is typical of an initial-cohort tree **(FIA-1)**. In the releves, paper birch has good indices of regeneration (3.2-3.3) which is more in-line with species able to recruit in ***large-gaps*** **(R-2)**. Undoubtedly this trait allowed for the persistence of paper birch during periods with little canopy mortality. We doubt that WFn53 forests ever suffered from extensive stand-regenerating catastrophes, and we believe that paper birch was favored over the lowland conifers under a regime of higher light levels ranging from large- to very large gaps.

Historic Change in Abundance

Today, paper birch is about as abundant on WFn53 sites as it was historically **(PLS/FIA-1)**. In the mature growth-stage there is a bit less today (5%) as compared to historic times (8%). Otherwise the growth-stage comparisons are within a percent.

Balsam Fir

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

Suitability
WFn53 sites provide ***excellent habitat*** for balsam fir trees. The ***suitability rating*** of 4.3 for balsam fir is influenced mostly by its high presence (46%) as trees on these sites in modern forests **(R-1)**. When present, balsam fir is a minor co-dominant tree, contributing just 6% mean cover in mature stands. The ranking is fourth, following white cedar, black ash, and paper birch on WFn53 sites as sampled by releves. Northern wet forests in general offer poor-to-excellent habitat for balsam fir. By far, fir is most favored on WFn53 sites (see Suitability Tables).

Young Growth-stage: 0-55 years
Historically, at 52% abundance balsam fir was the dominant initial-cohort tree in young WFn53 regeneration patches **(PLS-1, PLS-2)**. Its high initial abundance is evidence that few canopy gaps were created by fire, to which balsam fir is very sensitive. In the young-growth stage, small-diameter balsam fir regeneration was abundant **(PLS-5)**. At this time balsam fir was about equally likely to be the largest tree at a survey corner as it was to be the smallest tree. Our interpretation is that fir had good advance regeneration in most forests and that large regeneration gaps allowed for immediate recruitment of fir from any stratum. Supporting this argument is the excellent performance of balsam fir under a canopy in modern stands, with high indices of regeneration **(R-2)**. Balsam fir's ability to react immediately by increasing in abundance when regeneration gaps formed is an argument for its ability to function as an ***early-successional*** tree on WFn53 sites. Obscured by data-smoothing in Figure **PLS-2** is the fact that fir abundance builds from about 30% immediately after disturbance to a unbelievable peak near 80% in the 40-year age-class after which it precipitously declines. We doubt that fir achieved 80% abundance, but we do believe that fir achieved high density to the point of stagnation late in the young growth-stage. Because of this clear peak in abundance well after the stand-regenerating disturbance, we consider balsam fir to be primarily a ***mid-successional*** species.

Transition: 55-75 years
The transition to mature conditions is defined by the collapse of initial-cohort balsam fir **(PLS-1)**. Fir's plummet of about 50% relative abundance between the 50- and 80-year age-classes **(PLS-2)** is responsible for much of the community's compositional "movement" in the transition stage **(PLS-4)**. Our vision of young WFn53 forests is that of a thicket-like release advance regeneration of everything from seedlings to poles as fir is unequalled on these sites in maintaining high abundance in all strata **(R-2)**. By the transition, we believe that local fir populations had undergone severe self-thinning and was at peak volume – which in northern Minnesota rarely escapes an outbreak of spruce budworm. Along with the trees, small-diameter fir regeneration declines during the transition as well **(PLS-5)**. It would seem that whatever was killing canopy firs was influencing the understory firs as well but not as much. It was still common for fir to be the smallest tree at a survey corner (48% of all corners) in comparison to cases where fir was the largest tree (32%). For balsam fir though, this is actually a fairly high proportion of trees, as fir is normally very dominant in the understory. Our interpretation is that WFn53 sites are such good balsam fir habitat that it is always abundant, but not always as a tree. The transition seems to be a consequence of fir reaching such high abundance in the young growth-stage that density-dependent mortality in the form of budworm outbreaks or possibly root diseases was working to kill fir trees and some advance regeneration.

Mature Growth-stage: 75-105 years
The mature growth-stage is a period of cedar dominance where balsam fir abundance as a tree is minimal compared to younger or older growth-stages **(PLS-1)**. During this time, we detected only

trace amounts of small-diameter balsam fir regeneration (PLS-5), but this is the usual result in age-glasses this old. The tendency of fir to often be the largest tree at a survey corner is gone, as by this time it is now 4-times as likely for a fir to be the smallest tree at a corner. The mature growth-stage represents a period where fir abundance changes from that of a common canopy tree, to being best represented in the understory. This is evident by fir's poorer tree index (3.8) in comparison to its excellent regeneration indices (4.8-5.0) in modern mature WFn53 forests (R-2).

It is highly unusual for a tree to have a "U-shaped" abundance curve (PLS-1). Normally, trees simply increase or decrease across the age-classes as stands recover from disturbance, presumably due to unidirectional changes in light, seedbed, and soil conditions associated with stand maturation. Also, common are species that have peak abundance associated with the breakup of the initial-cohort canopy. Mid-successional minima can't be associated with site-disturbance cycles, which are our usual mental picture of succession. For balsam fir on WFn53 sites, our best guess is that the mid-successional event that is deleterious to balsam fir is for there to be too much fir itself to the point of outbreaks of spruce budworm or in populations of fungi that attack and degrade the root systems of balsam fir. Balsam firs in the mature growth-stage then, represent the survivors of budworm outbreaks or root-rot attacks and are the legacy of fir in the older forest. It is possible that the density-dependent cycling of fir on WFn53 sites is the main initiator of compositional change.

Second Transition and Old Forest: 105-155 years and older

In WFn53 forests older than about 105 years, the abundance of balsam fir steadily recovers from its minimum in the mature growth-stage (PLS-1). Balsam fir's high relative abundance in these older growth-stages is certainly the result of its ability to maintain a healthy bank of advance regeneration beneath a canopy (R-2). Apparently, these seedlings and saplings find small canopy gaps and recruit often enough to maintain 10-20% relative abundance of trees in old WFn53 forests. Both fir and spruce were benefiting from gaps that were forming in the cedar canopy at this time. The persistence of fir in old growth-stages is an important feature of WFn53 sites in that it enables balsam fir to dominate the young growth-stage when an event like a windstorm extensively removes the canopy.

Regeneration Strategies

Balsam fir's primary regenerative strategy on WFn53 sites is to maintain a bank of regenerants and seedlings in older forests that recruit well in newly-formed canopy gaps. We believe that seedling and sapling fir can recruit in gaps of any size, but the pulse of fir abundance at the close of the young growth-stage was almost certainly a ***large-gap*** phenomenon. Other than that, most evidence points towards a ***small-gap*** strategy. 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), 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).

Historic Change in Abundance

Across Minnesota the trend of balsam fir populations is for there to be substantially more than there was historically. This is most evident in communities where fire was at least an occasional visitor. The WFn53 community is one of the exceptions to this broad rule, probably because fire never played an important role in regenerating these forests. The departure from historic times is most evident in the young growth-stage where fir once accounted for 52% of the trees and now has 24% relative abundance (PLS/FIA-1). In the mature growth-stage, the trend is reversed with fir being more abundant (17%) than it once was (10%). In old forests, balsam fir is about as abundant as it ever was. Black ash is the obvious benefactor of fir's demise in young forests. Whatever creates young WFn53 forests today is different from the past. Our favored hypothesis is that the effect of settlement has been to alter site hydrology by making it more variable, which favors ash over fir. Anything that affects the flux of groundwater, the hallmark feature of wet forests, might account for the loss of fir. Given fir's obvious affinity for drier habitats that once burned but now don't, and given its sensitivity to ponding – we would guess that impeded drainage has most often caused fir's demise on these sites. Activities like building roadbeds or not maintaining culverts in the face of all-time high beaver populations are likely culprits. The alternative hypothesis is that because of fire suppression on the landscape, fir populations have grown to the point to where spruce budworm attack is chronic and not subject to alternating periods of severe mortality or rest. We entertained this idea locally for older WFn53 forests and it is interesting that balsam fir is present at about old-forest levels (~20%) today in all growth-stages possibly because the cycles of budworm outbreak are no longer as strong as they once were. Regardless, balsam fir is no danger in Minnesota. It is important though to explore its silvics on WFn53 sites as it seems linked to the success of white cedar – a species that is in some peril.

Black & White Spruce

- ***excellent habitat suitability rating for black spruce***
- ***good habitat suitability rating for white spruce***
- ***late successional***
- ***large-gap (small-gap) regeneration strategists***
- ***regeneration windows at >40 years***

Identification Problems

The PLS surveyors did not distinguish between black and white spruce. In WFn53 forests these species have nearly equal presence. WFn53 releve samples show that for plots with spruce present: 3% have both species present; 42% are white spruce without black spruce; 55% are black spruce without white spruce. It is frustrating to deal with these species together as there is very little co-occurrence in the releves. Mercifully, the modern data that we have from releves and FIA sampling – where the species are distinguished – is not so different that we couldn't consider them equivalent enough for most management situations.

Suitability

WFn53 sites provide ***excellent habitat*** for **black spruce** trees. The ***suitability ranking*** of 4.0 for black spruce is influenced mostly by its presence (24%) as trees on these sites in modern forests **(R-1)**. When present, black spruce is a minor co-dominant tree, contributing just 9% mean cover in mature stands. The ranking is fifth, following white cedar, black ash, paper birch, and balsam fir on WFn53 sites as sampled by releves. The WFn53 community is the only northern wet forest to provide even good habitat for black spruce (see Suitability Tables).

WFn53 sites provide ***good habitat*** for **white spruce** trees. The ***suitability ranking*** of 3.6 for white spruce is influenced mostly by its presence (18%) as trees on these sites in modern forests **(R-1)**. When present, white spruce is a minor co-dominant tree, contributing just 8% mean cover in mature stands. The ranking is sixth among trees common on WFn53 sites as sampled by releves. The WFn53 community is the only northern wet forest to provide even good habitat for white spruce (see Suitability Tables).

Young Growth-stage: 0-55 years

Historically at just 3% relative abundance, spruce was not an important tree in young WFn53 stands **(PLS-1)**. Young spruce represented 14% of the trees at survey corners described as burned **(PLS-3)**, but we doubt that WFn53 corners burned often. Upon rare occasion, it is possible that black spruce by virtue of its semi-serotinous cones seeded in on burned wet forest if there was enough of a moss layer to carry a light fire. Spruce was less important following windthrow, representing just 3% of the trees at such survey corners. Small-diameter spruce regeneration was not detected until the 50-year age-class **(PLS-5)**, and there were not enough spruce bearing trees under the age of 55 to draw any conclusions about recruitment preferences.

The lack of spruce in young, small-diameter regeneration patches of WFn53 forest is puzzling because whatever killed the canopy trees left plenty of advance regeneration of balsam fir, which is ecologically similar to spruce. Admittedly, white or black spruce do not have the ability of fir to develop advance regeneration on these sites, but it must have been enough for spruce to ultimately co-dominate WFn53 sites by establishment and recruitment under a canopy **(R-2, PLS-1)**. It would seem that whatever opened large canopy gaps in these forests effectively killed canopy spruce and fir, the advance regeneration of spruce, but not small firs. We know of no agent that does this.

Transition: 55-75 years

During the transition, balsam fir populations are crashing and cedar is succeeding. Even with all of this "action" of mortality and replacement, spruce really didn't react to these opportunities. There was a modest increase in abundance to about 5% **(PLS-2)**. Still, there was little evidence of spruce ingress as we detected very little small-diameter spruce regeneration during the G-1 transition window (PLS-5). Just looking at FIA data, it would appear that the modest increase in transitional spruce and our detection of at least some spruce regeneration would most likely be that of white spruce rather than black. There were not enough spruce bearing trees at transitional diameters to even guess if there was any recruiting preference. Thus, the continued delay of any improvement in spruce abundance just adds to the notion that regenerative events killed both spruce trees and their regeneration – and that some aspect of stand maturation was yet to appear and improve spruce's chances of establishment.

Mature Growth-stage: 75-105 years
In the mature growth-stage (>55 years), spruce abundance slowly increases but it does not yet become an abundant tree (PLS-1, PLS-2). Small-diameter spruce regeneration is now consistently present and increasingly abundant (PLS-5), but still was ranked as poor based upon our standard rules. Contrary to the usual pattern, spruce bearing trees at this time tended to more often be the largest tree at a corner. Most likely, these trees were white spruce established during the transition. There was no clear preference for coming in among certain species of larger trees, but the leading cases were of smaller-diameter spruce occurring among larger-diameter cedar or other spruce. Something seems to have been going on beneath the canopy of white cedar that was starting to provide safe-sites for spruce seedlings.

Second Transition: 105-155 years
The second transition is marked by the decline of white cedar and its replacement by other conifers, including black and white spruce (PLS-1, PLS-2). Small-diameter spruce regeneration is increasingly common (PLS-5). At this time it was about equally likely for spruce to be the largest tree at a corner as it was for it to be the smallest one. This is usual for species that have had some extended success at establishing and recruiting seedlings, which for spruce had been going on since about the 50-year age class but at low levels. If we had to guess, we believe that the larger trees were white spruce and that the later cohort was black spruce. When spruce was the smaller tree at a survey corner, it occurred most often among larger spruce, which suggests that some patches of WFn53 habitat were moving towards pure spruce.

We really don't know if spruce was reacting passively to the decline of white cedar or if it caused the demise of cedar. Neither black or white spruce has great success establishing seedlings beneath and uninterrupted canopy, with just fair regeneration rankings (R-2). Species with such regeneration indices almost always will respond to greater amounts of available light. So it makes perfect sense that spruce might benefit from the loss of canopy cedars. The puzzle is that we saw a very muted response of spruce to the loss of the balsam fir canopy in the first transition. The response was so slight that we were forced to hypothesize that regeneration events wiped out extensive areas of spruce trees and regeneration, i.e. spruce was just gone from the local landscape and it took quite some time for it to recover. Alternatively, spruce played an active role in the demise of white cedar. The most obvious possibility is to imagine spruce overtopping and suppressing old, but short cedars. Spruce, white spruce in particular, can achieve great height on sites as rich as WFn53 forest, and our releves support the idea that if stands are old and mixed, the spruce are consistently taller than cedar.

Old Growth-stage: >155 years
The tendency of spruce to increase relative to all other trees as stands age is the reason we consider it to be ***late-successional*** in WFn53 forests. By the time stands were this old, only spruce showed small-diameter regeneration using our half-diameter rule (PLS-5). At this time it was more likely for spruce to be the smallest tree at a survey corner, which indicates to us that it was building advance regeneration at pole diameters as stands got very old. When the smaller tree at a corner, it was most commonly among larger cedar and spruce, but there was a rather long list of cases with other species. Our interpretation is that spruce could sustain itself by establishment and recruitment in old WFn53 forests.

We don't believe that there was a spruce climax forest on WFn53 sites because spruce has such low indices of regeneration (R-2). Normally, climax species are unequalled in their ability to out-compete all other trees in the understory. In this case it would seem that cedar and balsam fir are the inheritors of WFn53 sites. Perhaps we are stumbling because of our insistence that diminishing light is a characteristic of old WFn53 forests. Perhaps substrate for seedlings has something to do with succession and substrates favorable for spruce aren't common in young regeneration patches. A clue that this might be the case is the arrival of tamarack among old, large-diameter WFn53 trees **(PLS-1, PLS-2)**. Tamarack is always intolerant and spruce seems so on these sites. It is unusual for mature and old WFn53 forest to form a continuous canopy (25-75% cover), which would seem to allow for these trees. If this community follows the paradigm of succession following ontogeny (see Natural Stand Dynamics), then old WFn53 forests should develop groundlayers similar to those of cedar or tamarack peatlands. These communities differ from WFn53 forests in that they have less fluctuation of the water table, they are considerably mossier, and nitrogen is increasingly available as ammonia. Perhaps these are the conditions that favored spruce regeneration in old WFn53 forests.

Regeneration Strategies

On WFn53 sites, the primary regenerative strategy of spruce is to establish a seedling bank and then recruit individuals in canopy gaps. It seems to us that the opportunities for this were limited to late-successional forests where the groundlayer was more favorable for germination. The primary reason that we believe spruce to be a gap species is its low abundance in any small-diameter situation, whether a young PLS survey corner **(PLS-1)** or as saplings in sapling stands (situation 11) in the FIA data **(FIA-1)**. Also in the PLS data, spruce's presence as small-diameter regeneration in the gap and ingress windows points towards establishment and regeneration with a substantial amount of overtopping trees around **(PLS-5)**. The high presence of white and black spruce in all subordinate situations (situations 12, 23, and 13) at FIA subplots is typical of species that recruit in ***large-gaps*** or ***small-gaps*** **(FIA-1)**. White spruce has just fair indices of regeneration **(R-2)** and shows difficulty recruiting to heights over 2m, which is typical of species needing very large-gaps and typical of species that should benefit from release. Black spruce too has just fair indices of regeneration and shows difficulty at establishment, which is typical of a large-gap species but the poor R- and SE- indices could be a problem with seedbeds more than light.

Historic Change in Abundance

Today, spruce is no longer an important tree on WFn53 sites **(PLS/FIA-1)**. This is most evident in the old growth-stage where spruce had 23% relative abundance historically, but now it is at 2%. This is not due to a lack of old WFn53 forests as there is more today than ever. In younger growth-stages spruce is at about half its former abundance, but it was never very common at that time. It seems obvious that white cedar is the tree to benefit from less spruce in old WFn53 forests. We believe that the loss of spruce is related to poor establishment in modern times. That is, cedars remain dominant on these sites because spruce doesn't often invade and overtop cedar any more. The primary evidence for this are the fair regeneration indices for spruce **(R-2)**. These indices are very low for spruce in comparison to other communities. Even in the presence of a layered sugar maple canopy, spruce tend to have higher regeneration indices (e.g. MHn45). Also, the typical canopy of WFn53 forests is not that continuous (25-75%), which makes us believe that available light isn't the problem. There must be a problem with the seedbed. Possibly it is not as mossy as it once was; however, the abundance of spruce seedlings is not strongly correlated with overall moss cover in our releves. If moss seedbeds are important it would have to be a particular species. The big difference in germination between cedar and spruce is that cedar is favored on richer and much warmer substrates, whereas spruce is favored on poorer and colder substrates. A lack of the more acidic *Sphagnum* mosses could account for both shortcomings from spruce's perspective. We favor this idea because gone also from old WFn53 forests is tamarack, which we often associate with a *Sphagnum* seedbed.

Balsam Poplar

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

Identification Problems
The PLS surveyors normally distinguished between quaking aspen and balsam poplar. WFn64 releve samples show that for plots with these trees present: 7% had both species; 43% are quaking aspen without balsam poplar; 50% are balsam poplar without quaking aspen. The following account is restricted to the explicit surveyor references to balsam poplar or "balm-of-Gilead." Most likely we have slightly underestimated the amount of balsam poplar historically because we did not assign generic "aspen" to balsam poplar. We consider quaking aspen and balsam poplar to be ecologically equivalent for most silvicultural considerations on these sites.

Suitability
WFn53 sites provide ***good habitat*** for balsam poplar trees. The ***suitability rating*** of 3.3 for balsam poplar is mostly affected by high cover-when-present (16%) on our releves **(R-1)**. Balsam poplar's presence is just 8%. Balsam poplar can thrive on northern wet forest (WFn) sites as long as the peaty surface isn't too thick. Its best opportunity is on the WFn55 sites, but it is often good on WFn53 sites (see Suitability Tables).

Young Growth-stage: 0-55 years
Historically, at 3% relative abundance balsam poplar was a minor tree in young WFn53 stands recovering from stand-regenerating disturbance **(PLS -1)**. Young balsam poplars were not recorded at burned or windthrown survey corners **(PLS-3)**, but we believe that this is just sampling omission for an infrequent tree as balsam poplar is favored on recently disturbed sites elsewhere. Small-diameter balsam poplar regeneration was abundant in the post-disturbance window, peaking in the initial age-class **(PLS-5)**. Because balsam poplar trees and regeneration was most abundant immediately following disturbance, we consider it to be an ***early successional*** species.

Transition: 55-75 years
During the transition, the abundance of balsam poplar is halved, to barely measurable levels of 1-2% **(PLS-2)**. Small-diameter balsam poplar regeneration was not detected during this stage, nor in any of the following growth-stages **(PLS-5)**. At this time all records of balsam poplar (and quaking aspen for that matter) were as the largest tree at a survey corner. This is typical of an initial-cohort tree that is not often subsidized by establishment or recruitment much beyond the first post-disturbance years. Our interpretation is that most balsam poplar establishment was immediate and that they were starting to die during the transition.

Mature, Second Transition, and Old Growth-stages: 75-105 years, 105-155 years, and older
By the time WFn53 forests were older than 75 years, balsam poplar bearing trees were nearly absent and sporadically distributed among age-classes. There are insufficient data to make any interpretations concerning its historic behavior or regenerative success in forests this old. However, it does seem to keep appearing from time-to-time among bearing trees of fairly large diameter. Our best guess is that there were enough fine-scale disturbances that provided both light and mineral soil substrate (e.g. tip-ups) for the odd balsam poplar to succeed.

Regeneration Strategies
Balsam poplar's primary regenerative strategy on WFn53 sites is to dominate ***open habitat*** after stand-regenerating disturbance or the formation of very large regeneration gaps. There are no records available to describe its reaction to fire or windthrow, but in other communities fire is usually considered beneficial. In the historic PLS data the open strategy interpretation is supported only by the fact that balsam poplar bearing trees are more consistently present in young stands **(PLS-1)** and we detected balsam poplar regeneration only in the post-disturbance

window (PLS-5). In the FIA data, balsam poplar is reported to occur in a variety of situations some consistent with open regeneration strategists (situations 11 and 22) and others more typical of a ***large-gap*** species (situations 12 and 23, FIA-1). The releve sampling of mature WFn53 forests is also consistent with the idea that balsam poplar needs open habitat or very large gaps for establishment and recruitment. Its indices in the regeneration strata (2.5-2.8, R-2) are quite in line with open strategists, but it is possible that very large gaps might allow for some recruitment as well.

Historic Change in Abundance
Today, balsam poplar is 2-3 times more abundant on WFn53 sites than it was historically (PLS/FIA-1). This is particularly true of the young growth-stage where it is now 9% of the FIA trees compared to just 3% at survey corners of similar age. Although there is not a lot of industry pressure to cut WFn53 forests, some are harvested by clear-cutting, and balsam poplar is favored when that happens.

(PLS-1) Historic Abundance of WFn53 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the WFn53 community by growth-stage. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow, green, and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

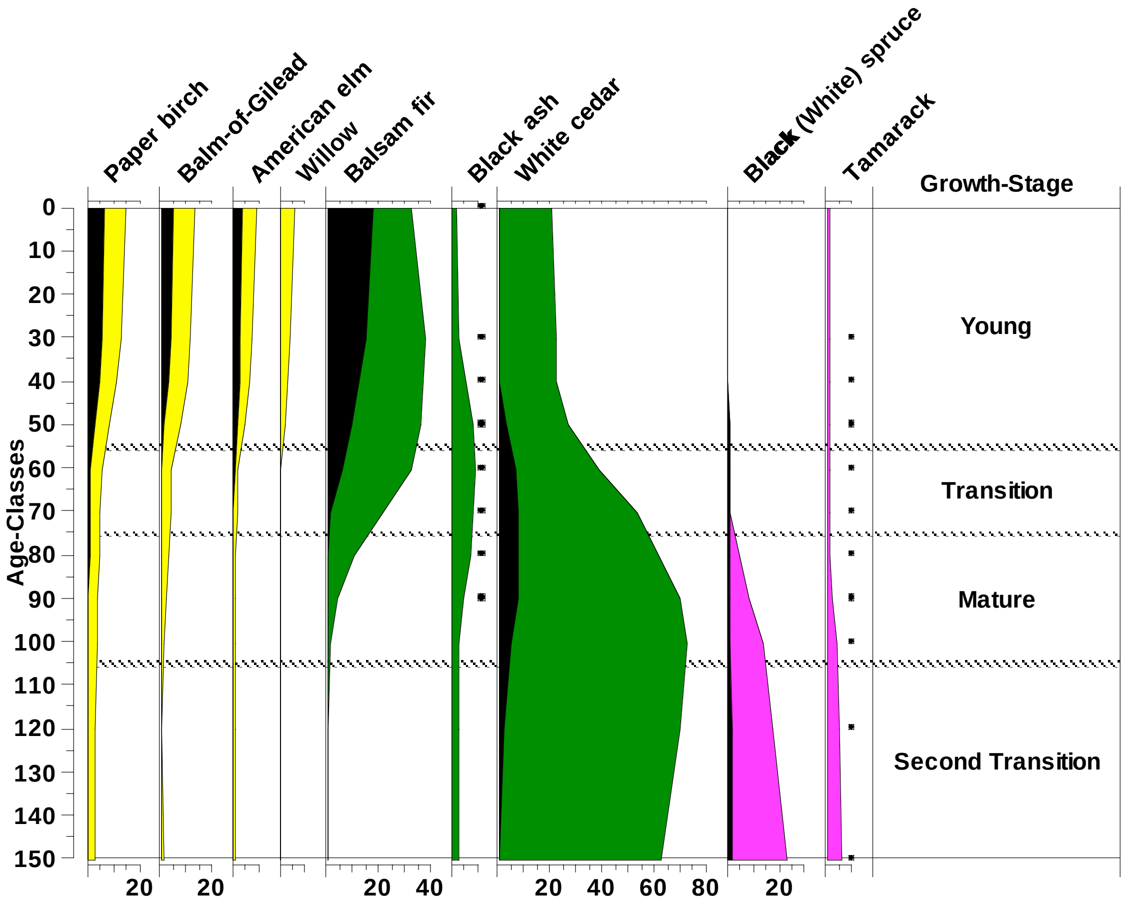
Dominant Trees	Forest Growth Stages in Years				
	0 - 55	55 - 75	75 - 105	105 - 155	> 155
	Young	T1	Mature	T2	Old
Balsam Fir	**52%**	ǀǀ	**7%**	⌉⌉	**21%**
Black Ash	**7%**	ǀ	**4%**	ǀ	**3%**
Balsam Poplar	**3%**	ǀ	**2%**	⟋	**2%**
Paper birch	**8%**	⟋	**8%**	ǀ	**5%**
White Cedar	**18%**	⌉⌉	**67%**	ǀǀ	**26%**
Tamarack	**2%**	ǀ	**1%**	⌉⌉	**11%**
Black (White) Spruce[1]	**3%**	⌉	**7%**	⌉⌉	**23%**
Miscellaneous	**10%**		**6%**		**11%**
Percent of Community in Growth Stage in Presettlement Landscape	**32%**	**10%**	**34%**	**15%**	**9%**

1. The PLS surveyors did not consistently distinguish white and black spruce, which are about equally present on WFn53 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 WFn53

Graphed for the individual species of WFn53 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 dots.



WFn53, 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 WFn53 Trees Following Disturbance

Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent WFn53 forests. The columns represent our interpretation of disturbance at the survey corners. Shading associates trees that peak in the same disturbance category.

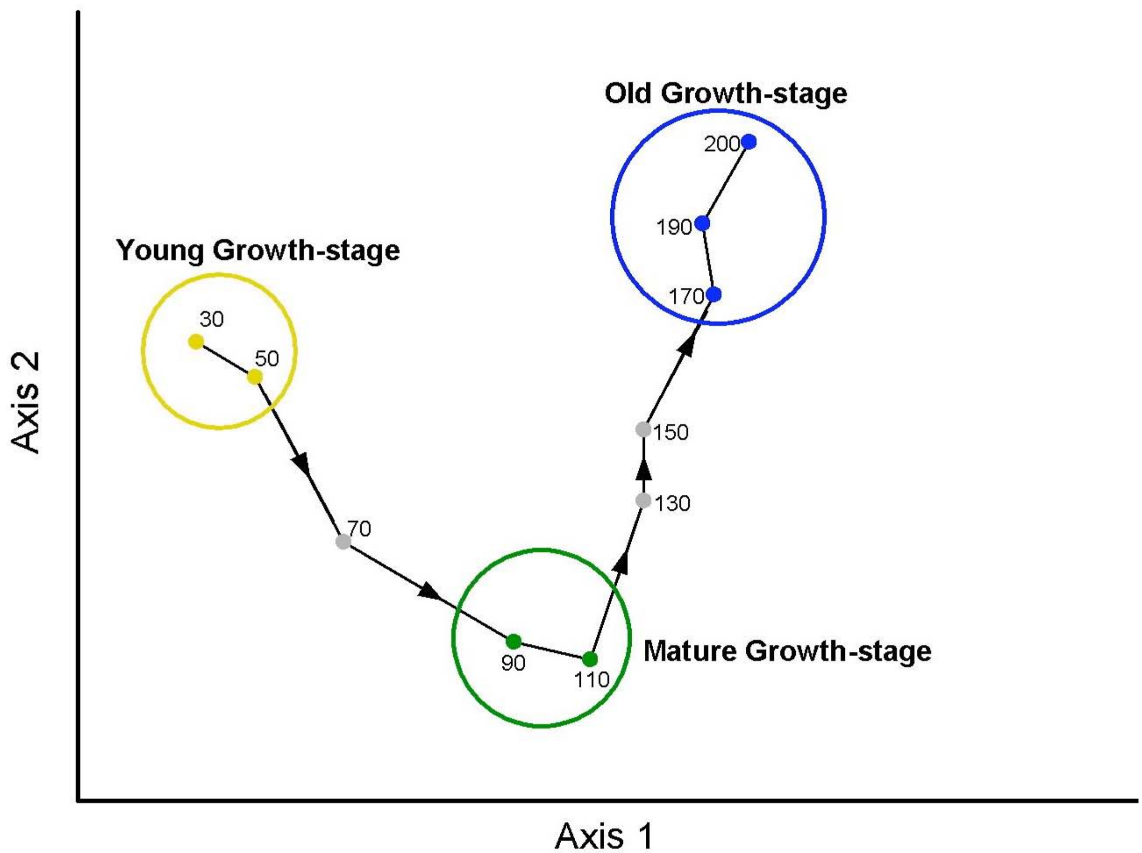
Tree	Burned		Windthrown		Maintenance		Mature	
White or Black spruce[1]	8	14%	4	3%	0	0%	346	10%
Black ash	4	7%	8	7%	1	2%	175	5%
White cedar	32	54%	78	67%	29	60%	1582	47%
Balsam fir	10	17%	22	19%	15	31%	896	27%
Paper birch	5	8%	4	3%	3	6%	290	9%
Balsam poplar	0	0%	0	0%	0	0%	32	1%
Yellow birch	0	0%	0	0%	0	0%	45	1%
Total (% of grand total, 3589)	59	2%	116	3%	48	1%	3366	94%

1. The PLS surveyors did not consistently between black and white spruce, which are about equally present on WFn53 sites.

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

(PLS-4) Ordination of Historic WFn53 Age-classes

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



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

(PLS-5) Historic Windows of Recruitment for WFn53 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 50-80 years	I-1 80-110 years	G-2 110-150 years	I-2 >150 years
Yes	Balsam poplar	0-30	Excellent	Poor to 40	--	--	--
Yes	Paper birch	0-30	Excellent	Fair to 70	--	--	--
Yes	Balsam fir	30-50	Excellent	Poor to 60	--	--	--
Yes	Black ash	40-70	Poor	Fair to 70	--	--	--
Minor	White spruce[1]	40-80	Poor	Poor	Poor	Poor	Poor
Yes	White cedar	70-90	--	Excellent	Good	Poor	--
No	Yellow birch	60	--	Poor	--	--	--
No	Black spruce[1]	>130	--	Fair from 50	Fair	Fair	Fair

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 balsam fir and white cedar with some balsam poplar, paper birch, and black ash, 50-80 years
- **I-1:** ingress of seedlings under canopy of cedar with some paper birch, balsam fir, and white or black spruce, 80-110 years
- **G-2:** gap filling during decline of white cedar, 110-150 years
- **I-2:** ingress of seedlings under a canopy of white cedar, balsam fir, and white or black spruce, >150 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; **light green** = trees with peak regeneration in gaps formed during the decline of the initial cohort; **purple** = trees with peak regeneration by ingress under a mature canopy or by filling small gaps in old forests

1. The PLS surveyors did not consistently distinguish black and white spruce on WFn53 sites, where they are nearly equal in presence. FIA data were reconciled with the PLS data to interpret differences in recruitment.

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

(R-1) Suitability Ratings of Trees on WFn53 Sites

This table presents an index of suitability for trees in WFn53 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 WFn53			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
White cedar (Thuja occidentalis)	**83**	**39**	**5.0**
Black ash (Fraxinus nigra)	**42**	**24**	**4.8**
Paper birch (Betula papyrifera)	**40**	**10**	**4.5**
Balsam fir (Abies balsamea)	**46**	**6**	**4.3**
Black spruce (Picea mariana)	**24**	**9**	**4.0**
White spruce (Picea glauca)	**18**	**8**	**3.6**
Balsam poplar (Populus balsamifera)	**8**	**16**	**3.5**
Yellow birch (Betula alleghaniensis)	**17**	**5**	**2.7**
*Suitability ratings: **excellent**, **good**, **fair**			

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

(R-2) Natural Regeneration and Recruitment of Trees in Mature WFn53 Stands

This table presents an index of regeneration for WFn53 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 WFn53 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 Wet Cedar Forest – WFn53					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Balsam fir (Abies balsamea)	**86**	**5.0**	**5.0**	**4.8**	**3.8**
White cedar (Thuja occidentalis)	**86**	**4.7**	**4.5**	**5.0**	**5.0**
Black ash (Fraxinus nigra)	**82**	**4.8**	**4.8**	**4.7**	**4.5**
Paper birch (Betula papyrifera)	**53**	**3.2**	**3.2**	**3.3**	**4.0**
White spruce (Picea glauca)	**35**	**2.7**	**2.7**	**2.2**	**3.3**
Yellow birch (Betula alleghaniensis)	**34**	**3.8**	**4.0**	**3.8**	**3.0**
Black spruce (Picea mariana)	**25**	**2.3**	**2.5**	**3.0**	**3.5**
Balsam poplar (Populus balsamifera)	**15**	**2.7**	**2.8**	**2.5**	**3.3**

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

% presence: the percent of 102 WFn53 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 WFn53 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples WFn53 forests. The purpose of the table is to provide a general impression of how often a species is seen certain regenerative situations: canopy of a regenerating forest (situations 11, 22), in the subcanopy (situations 12, 23), or in the seedling bank below a remote canopy (situation 13). The situation of trees in older stands at tree height (33) provide no insight about regeneration. Species are ordered by the sum of their percents in 12 and 13 situations, which generally ranks them as would shade-tolerance ratings. The total number of trees counted for each species is presented to provide a sense of reliability.

Species	Tree Count	Structural Situations					
		11	22	12	23	13	33
White cedar	2561	3%	24%	20%	19%	5%	28%
Balsam fir	1014	14%	12%	29%	17%	26%	2%
Black ash	1066	13%	18%	21%	14%	23%	10%
Yellow birch	31	13%	6%	0%	0%	13%	68%
Paper birch	237	28%	22%	8%	12%	12%	17%
Black spruce	112	8%	29%	20%	19%	4%	21%
Balsam poplar	123	11%	22%	15%	17%	7%	28%
White spruce	45	9%	11%	13%	7%	13%	47%

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 WFn53 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 WFn53 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 - 75		75 - 105		105 - 155		> 155	
	Young		T1		Mature		T2		Old	
Balsam Fir	**52%**	**24%**	ǀǀ		**7%**	**17%**	⌉⌉		**21%**	**18%**
Black Ash	**7%**	**45%**	ǀ		**4%**	**20%**	ǀ		**3%**	**12%**
Paper birch	**8%**	**7%**	)		**8%**	**5%**	ǀ		**5%**	**6%**
White Cedar	**18%**	**11%**	⌉⌉		**67%**	**46%**	ǀǀ		**26%**	**55%**
Tamarack	**2%**	**0%**	ǀ		**1%**	**2%**	⌉⌉		**11%**	**0%**
White Spruce (incl. Black)	**3%**	**2%**	⌉		**7%**	**4%**	⌉⌉		**23%**	**2%**
Balsam Poplar	**3%**	**9%**			**2%**	**4%**			**2%**	**3%**
Miscellaneous	**7%**	**2%**			**4%**	**0%**			**9%**	**4%**
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	**32%**	**22%**	**10%**	**15%**	**34%**	**23%**	**15%**	**26%**	**9%**	**14%**

Natural growth-stage analysis and landscape summary of historic conditions is based upon the analysis of 1,505 Public Land Survey records for section and quarter-section corners. Comparable modern conditions were summarized from 2,746 FIA subplots that were modeled to be WFn53 sites.

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

Forest Health

White Cedar

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

WATCHOUTS!

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

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

Balsam Fir

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

WATCHOUTS!

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

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

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

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.

White Spruce

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

WATCHOUTS!

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

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

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

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

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

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