APn81

APn81 – Northern Poor Conifer Swamp

Natural Disturbance Regime, Stand Dynamics, and Tree Behavior

Summary and Management Highlights

Northern Poor Conifer Swamp (APn81) is a common coniferous community found throughout the Laurentian Mixed Forest Province (Figure 1). Detailed descriptions of this community are presented in the DNR Field Guides to Native Plant Communities of Minnesota.

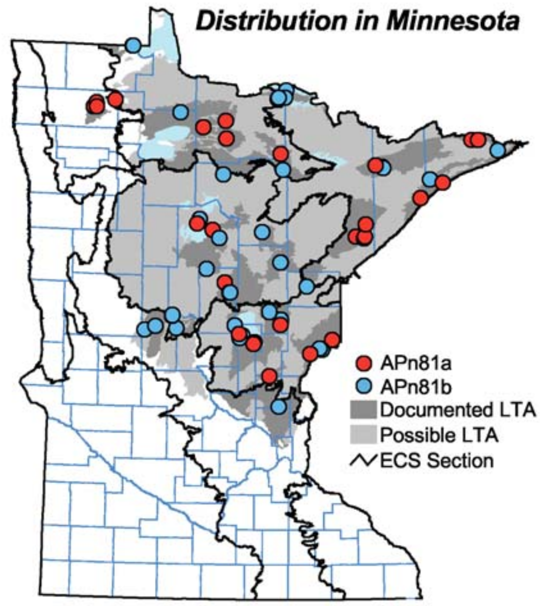


Figure 1. The range of APn81 forests in Minnesota (shaded) and distribution of releve samples (red and blue dots).

Commercial Trees and Management Opportunities
As a commercial forest, APn81 sites offer a very limited selection of crop trees and few structural conditions. Black spruce and tamarack are ranked as excellent choices as crop trees by virtue of their frequent occurrence and high cover-when-present on APn81 sites (see Suitability Tables). All other trees do not occur in commercial abundance on APn81 sites, and few are successful beyond germination.

Black spruce and tamarack have occupied APn81 sites for a long time and have had the opportunity through successive generations to adapt to harsh physical conditions typical of these sites. Fire suppression, commercial logging, and settlement in the past century have had little impact on the ability of these species to out-compete all other trees in acid peatlands. Only northern white cedar and balsam fir show a slight tendency to occupy these sites more so now than in the past **(PLS/FIA-1)**. Cedar and fir do not occur in sufficient quantity to confound our interpretations of historic data or alter silvicultural strategies aimed as black spruce and tamarack.

It is debatable as to whether APn81 sites can consistently produce merchantable wood by today's utilization standards. Radial growth comparable to richer sites occurs during the post-disturbance years. At some point radial growth essentially stops, and it is not uncommon for trees 4-8" in diameter to be 150 years old and have the last 100 years of growth confined to the outer inch of rings. Thus, the duration of the post-disturbance growth determines whether trees will reach merchantable diameter. We do not know why this period can be as short as 20 years or as long as 50. Stagnant radial growth is accompanied by a severe shortening of nodes in the crown, producing the characteristic "mop tops" of black spruce on these sites. Episodically in Minnesota, these tops have been marketed as ornamental trees during the Christmas holidays.

Natural Silvicultural Approaches
In the historic landscape, most APn81 stands (65%) were in the mature growth-stage **(PLS-1, PLS/FIA-1)**. At this time, we believe that the death of canopy trees and their replacement by advance regeneration was mostly the result of species-specific mortality from insects and disease such as larch sawfly, larch beetles, spruce budworm, and dwarf mistletoe. The pattern of this disturbance was probably similar to that of epidemics in other populations, whereby centers of infection spread across the landscape. Thus, silvicultural systems aimed at selective removal from above and expanding in size between frequent entries are good matches with the natural process. Strip shelterwoods perpendicular to the prevailing winds and progressing towards the prevailing winds are generally successful in naturally regenerating tamarack and black spruce in peatlands. The general idea is to have mature, seed-bearing trees upwind and adjacent to

recently cut strips. When the harvest strips are stocked, the adjacent strip of mature trees is ready for another entry. Group shelterwood approaches, especially where second and third entries are aimed at expanding the initial gaps (femelschlag) closely match the natural pattern and should result in adequate natural regeneration. We do not recommend selective harvesting because it is difficult to predict the ability of advance regeneration to respond to release. Small trees may well be young and able to respond to release, or they may be old, stunted individuals. Also, the canopy cover in APn81 forests is generally sparse, and the removal of individual trees or even groups of trees probably doesn't change the light environment enough to stimulate release. Regardless of the system, it is important to remember that slash and debris above the preserving environment of the saturated peat is the primary source of nutrients for the next generation of trees.

A large proportion (35%) of native APn81 stands were young forest <55 years old **(PLS-1, PLS/FIA-1)**. Given that less than 3% of APn81 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, small diameter APn81 forest. We suspect chronic disease and perhaps following surface fires. What seems clear from the historic records is that young, re-initiated APn81 stands presented an environment where tamarack was highly successful by seeding into the open areas. Black spruce was less successful, but always present in substantial abundance. Clear-cutting with reserves, patch cutting, and variants of seed-tree cutting could all approximate the natural pattern of disturbances that created young APn81 forests. In all cases the reserved trees are favored in re-colonizing the harvested areas. Broadcast burning as site preparation is often employed when natural or augmented seeding of black spruce is part of the prescription. Most likely, burning releases mineral nutrients that are normally in short supply on APn81 sites. The ash and slash are the nutrient capital for the next generation of trees. Burning come with some risk, and it is debatable as to whether it is a sustainable practice because the natural rotation of fire is far longer (appx. 570 years) than a commercial rotation of tamarack and black spruce (appx. 80 years). Risk increases under dry conditions where burning can flatten the peat surface and diminish the drainage required for good tree growth. We suspect that at least some of the very wet, open, acid peatland communities (APn90, APn91) originated after severe fire in the forested APn communities like APn81.

Management Concerns

All APn81 communities occur on *Sphagnum* peat. Because of the weak organic substrate and poor drainage, the use of heavy equipment is restricted entirely to solidly frozen site conditions. There have been several attempts to use lighter, high-flotation equipment in order to extend the season of operation in Minnesota. In comparison to richer FPn swamps, APn81 sites have a fairly solid root mat near the surface. This mat can absorb some traffic, but multiple passes of even light equipment tend to eventually break through the living mat into the non-living peat. If ruts or trails fill with water that is open to sunlight and wind, the tendency is to promote decomposition of the side walls and bottom of the rut. This means that such trails will tend to continue to incise into the peat, making them useless for further traffic. On air photographs it is easy to spot past trails that haven't been used in 50 years and researchers believe that the trails of migratory caribou are still evident even though caribou were extirpated from Minnesota in the 1940s. APn81 sites are just rich enough to have inclusions of richer peatland communities that are probably centered over areas of upwelling groundwater. Also, input of surface runoff from adjacent uplands create a border of rich, soupy peat called a moat. In either case, these richer peatland communities have far less structural integrity than the APn81 mat and must be avoided. In the field, such areas can be identified by the presence of broad-leaved sedges and rough alder.

The landscape balance of growth-stages and stand ages for the APn81 community is not much different than it was historically **(PLS/FIA-1)**. Today, there is slightly more young forest (<55 years) and slightly less mature forest (>55 years) than in pre-settlement times. We believe that wildlife populations are probably reacting to APn81 habitat as they always have at a fine scale.

Commercial logging has imposed a pattern of hard, structural edges at a scale substantially finer than our natural vision of very large patches of continuous-canopy swamp.

Compositional changes are more of a concern. Most obvious is the reversal of abundance of tamarack and black spruce **(PLS/FIA-1)**. Statewide in all habitats, tamarack populations have plummeted relative to other trees. While the trend is evident in APn81 forests, tamarack is still and important and abundant tree. The loss of tamarack in wet-mineral soil habitats is nearly complete and more serious. Logging without regeneration is probably the proximal cause of tamarack's demise in the wet-mineral soil environments; however, the decline in peatlands is most likely the result of devastating outbreaks of larch sawfly and possibly larch beetles. In either case, silvicultural attempts to maintain local populations of tamarack are important in all native plant communities. On APn81 sites, this could be accomplished by leaving some tamarack seed-trees rather than always clear-cutting and seeding just black spruce.

Natural Disturbance Regime

Natural rotation of catastrophic and maintenance disturbances were calculated from Public Land Survey (PLS) records at 3,818 corners within the primary range of the APn81 community. At these corners, there were 9,566 bearing trees comprising the species that one commonly finds in APn81 forests.

Natural Rotations of Disturbance in APn81 Forests Graphic	
	Banner text over photo
Catastrophic fire photograph	**570 years**
Catastrophic windthrow photograph	**520 years**
Partial Canopy Loss, photograph	**85 years**

The PLS field notes described about 1% of the APn81 landscape as recovering from stand-regenerating fire. Nearly all such records were of burned-over lands with some references to post-fire thickets. From these data, a rotation of 570 years was calculated for stand-replacing fire using a 5-year recognition window.

Elsewhere in the APn81 landscape, the surveyors described lands as windthrown and lacking suitable-sized trees for scribing. Such corners were encountered at about 3% of the time, yielding an estimated rotation of 520 years for windthrow, using a 15-year recognition window.

More common at APn81 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 thickets or to swamp with distances to bearing trees that were intermediate between the distances for burned/windthrown lands and what is typical for fully stocked tamarack and black spruce forests on peat. To the surveyors, “swamp” included a broad range of structural conditions from open, wet meadow to forest. About 6% of the survey corners were described as such, resulting in a calculated rotation of 85 years for disturbances that maintained early-successional tamarack on APn81 sites. That more corners were described as windthrown (65) compared to burned (29) suggests that wind was the more prevalent cause of partial canopy loss. Because peat is a weak substrate it is not surprising that windthrow was prevalent; however, bole-weakening disease (e.g. red-rot, various butt and root rots) probably contributed to the toppling of mature trees in a scattered pattern as well.

There are but two forested AP communities, APn81 and APn80. The rotation of 570 years for fire and 520 years for windthrow in APn81 is substantially shorter than that experienced by APn80 forests. It seems most likely that this is the case because APn81 sites are enough richer than APn80 sites to have a continuous canopy capable of carrying crown fire and taller trees more likely to topple in heavy winds. The trend of decreasing nutrients and wetter conditions in AP communities results in shorter and more widely spaced trees, to the point where catastrophic disturbance is not evident by looking at the “trees,” and to the point to where we no longer recognize them as forest (APn90, APn91) in spite of fairly high density of “bonsai” tamarack and black spruce.

Unlike terrestrial forest sites, there is some succession and ontogeny among wetland communities, which happens over centuries of development. The accumulation of *Sphagnum* peat into raised domes isolated from mineral-rich groundwater and the ultimate flattening of the high domes is the ontogeny of AP communities: starting with APn81 and succeeding to APn80, APn91, and finally APn90. Because severe fires can burn both the trees and peat down to a drought-flattened water table, they can significantly interrupt this ontogeny and confound our interpretation of the role of fire. Open APn91 communities may well have been APn81 sites set back by fire. Had we chosen to recognize APn91 communities as burned APn81 sites, we would have concluded that fire was far more common and influential in controlling the dynamics of APn81 forests. We chose to not do this because APn91 communities also form naturally by processes that don’t involve fire. The historic influence of fire on APn81 sites is recorded in the peat stratigraphy itself as ash layers or just missing strata as burned *Sphagnum* leaves very little ash. The missing strata or ash layers are called “recurrence” horizons and it is common to see several of these, about one per millennium, in a 5,000-year stratigraphic record. Because recurrence horizons are hard to detect, we believe that fire influenced these sites at a minimum of every thousand years, making our estimate of about 500 years seem reasonable. In either case, using prescribed fire to regenerate black spruce on APn81 sites at commercial rotation (<100 years) seems far more frequent than was natural.

Natural Stand Dynamics

APn81 forests are among several peatland communities where a particular hydrologic regime translates into dominance of black spruce or tamarack. Here, the growth of *Sphagnum* mosses has elevated the growing surface above any groundwater enriched with dissolved mineral salts. Dilute rainwater and dust (dryfall) are the primary input of water and nutrients for plants. Extremely acid surface waters (pH <5.5) and the waterlogged conditions favor the preservation of organic matter rather than recycling. Under these stark conditions, only tamarack and black spruce prevail and succession is perceived only as change in the relative abundance of these two species.

A critical difference between terrestrial and peatland communities regarding succession and stand dynamics is that the peatland 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. APn81 forests belong to the “mixed-mire pathway” of wetland development, meaning that APn81 sites tend to succeeded rich FPn tamarack swamps and will eventually develop into sparsely forested or open bog. ***This is significant because the sort-term stand dynamics tend to reflect the long-term ontogeny.*** In this case young APn81 stands tend to have compositional and structural similarities with FPn72 or FPn82 tamarack swamps. Old APn81 stands start to resemble APn80 bog. Disturbances that re-initiate APn81 forests can set back this process, but eventually the gains towards bog outweigh the regressions to tamarack swamp.

Thus, the general compositional dynamics of APn81 forests is for younger stands to be dominated by tamarack. Throughout succession, the proportion of black spruce steadily increases relative to tamarack, but it does not totally replace it **(PLS-1)**. The fact that both species are important in the initial cohort and that both are present in very old APn81 forests means that there is no true succession. The range of movement in ordination space **(PLS-4)** in miniscule in comparison to forests where pioneer species are totally replaced by late-successional trees. There was not enough consistent movement in the ordination or enough data in very old growth-stages for us to confidently assign growth-stages. For any particular stand, the relative abundance of tamarack versus black spruce probably relates to a historic event. Nuance differences after disturbance that favored one species over the other could account for the relative abundance of black spruce and tamarack in the stand, as could species-specific diseases that preferentially leave either species. For the purpose of discussion, we have arbitrarily set the seam between young and mature APn81 forests at age 55.

The general structural dynamics of APn81 forests is more like woodland than that typical of Minnesota’s northern forests. Tree density tends to increase with stand age, suggesting that it takes some time for trees to occupy the available growing space following a disturbance. In young APn81 stands the average distance of bearing trees to their corners was 28 feet. In mature and old APn81 forests the distance of bearing trees to their corners decreases to just 19 feet. Stocking in the mature APn81 forest is rather tight compared to terrestrial coniferous forests and could be the result of stagnation, where stands tend to achieve the condition of having evenly-spaced, similar-diameter, equally competitive trees.

Young Growth-stage: 0-55 years

About 35% of the APn81 landscape in pre-settlement times was covered by forests estimated to be under 55 years old **(PLS-1)**. Most often these stands were monotypic (71%). For these survey corners, tamarack was sole species far more often (86%) in comparison to black spruce (14%). About 29% of all survey corners assigned to the young growth-stage were mixtures of black spruce and tamarack.

The surveyors described some young APn81 forests as having been burned. About 1% of the PLS corners were burned (PLS-3), and fire strongly favored tamarack (86%) over black spruce (14%). Both species effectively seed onto burned peat, often to the point of overpopulation. However tamarack consistently overtops black spruce in this situation, and biased selection of the larger trees as bearing trees might explain the apparent preponderance of tamarack in young APn81 forests (PLS-1). Unlike black spruce, tamarack is able to produce suckers from its extensive, shallow root system. Although consistently mentioned in the silvicultural literature, the importance of tamarack's ability to reproduce by vegetative means after a fire seems unexplored and probably unimportant silviculturally. The semi-serotinous cones of black spruce allow for significant release of seeds after forest fires, and broadcast burning is a traditional silvicultural method of site preparation for black spruce seeding. Based upon our silvicultural experience one would think that black spruce would be favored in the post-fire environment, but our results show the opposite. Apparently, tamarack is simply more aggressive and efficient at capturing growing space in the open.

Windthrow was more common than fire, affecting 2% of the PLS corners. Because of the high water table and weak organic substrate it seems likely that windthrow significantly contributed to the regeneration of APn81 stands. About 84% of the trees at windthrown corners were tamarack compared to 16% black spruce (PLS-3). Both black spruce and tamarack are well-equipped to regenerate by vegetative means following windthrow. Branch nodes are able to produce adventitious roots from which arise new upright stems or growth of existing branches. Because black spruce tends to hold lower branches longer than tamarack, it is not uncommon to see parent spruces surrounded by rings of seedlings where their drooping, lower branches have been "buried" by the growth of *Sphagnum* moss. Either tree can produce strings of layering seedlings along their windthrown boles.

However, the natural rotations of fire (570 years) and windthrow (520 years) are too long to create the observed balance of growth-stages across the APn81 landscape (PLS-1). Thus, it seems clear that small-diameter APn81 stands were initiated by means other than just fire and wind. As is often the fate of monocultures, or near-monocultures like APn81 forests, outbreaks of disease or pests can have catastrophic consequences over large areas. Outbreaks or larch sawfly since about 1900 have converted thousands of acres of mixed APn81 stands to spruce cover-type. At this writing, larch beetles are having a similar effect. Although slower to act, ever-expanding (2-10 feet per year) pockets of dwarf mistletoe cause the demise of canopy black spruce and tamarack to regenerate APn81 forests.

Widely mentioned is the connection between windthrown/diseased timber and fire in forested peatlands. The argument is that dead-and-down spruce and tamarack greatly add to the available fuel for a catastrophic fire, thus increasing greatly the likelihood of that event. Increased intensity in diseased and windthrown timber is our experience in burning peatlands by prescription, but the effect of available fuel on frequency is debatable. Most students of disturbance ecology would argue that severe drought is by far the stronger correlate with fire frequency than available fuel. Most APn81 forests tend to occur in large peatlands with incredible amounts of stored water, meaning that severe and sustained drought is required to make them vulnerable to catastrophic fire. Based upon our calculations, such drought and fire was a rare event.

Mature Growth-stage: >55 years

About 65% of the historic APn81 landscape was mature forest (PLS-1). Stands in this stage were more often monotypic (67%) than mixed (33%). Monotypic conditions were represented mostly by survey corners where all bearing trees were tamarack (78%). At survey corners with mixed composition tamarack and black spruce were predominant (82%), but northern white cedar was also important at 8% of mixed survey corners.

Although APn81 forests follow the usual trend of mature forests being more mixed than young ones, it is unusual for mature forests to be remain mostly monotypic as is the case for this community (67%). This pattern is restricted to communities where tamarack is the dominant tree in mature forests. This pattern is partially due to the fact that there are just two species are present in most situations. However, other wetland trees able to form young monotypes – black spruce, northern white cedar, and black ash – have mature growth stages that are far more likely to be mixed. Most ecologists believe that mixing is the result of several things that add to the variety of habitats as stands mature: enough time for seeds of most trees to reach the site after a disturbance, a shift from species-specific mortality to age-dependent mortality, the formation of multiple strata of woody plants favoring shade-tolerant species over pioneers, increased abundance and variety of organic seedbeds, and maintenance disturbances that create a variety of sizes of canopy gaps. Mature APn81 tamarack swamps are lacking in most of these categories: they are remote from the seed sources of many tree species, mortality of canopy trees is attributed mostly to species-specific insects and diseases, they become structurally simple in maturity and sunlight on the forest floor maintains a continuous carpet of mosses, there are no mineral soil seedbeds, and variety in canopy gap size is not important because there is no solid canopy. Several hypothesis might explain the slight tendency of black spruce to become more important in older APn81 forests historically. First, APn81 forests have at least some shade, which favors black spruce over tamarack in the understory. Silvics manuals describe tamarack as totally intolerant; however, our assessment of its ability to develop advance regeneration beneath the usual APn81 canopy show it to be just slightly less able than black spruce **(R-2)**. Also, the fact that tamarack is deciduous might favor understory black spruce by giving them a slightly longer growing season. Finally, our perception of greater black spruce abundance in mature stands is based upon a landscape summary **(PLS-1)**. If the cycles of species-specific, canopy-purifying diseases/pests affecting mature trees are shorter for tamarack than black spruce, we would see the same results.

Releves preferentially sample modern, mature APn81 forests and they shed some light on our perceptions from the historic PLS data. Canopy mixture is a matter of scale. It is unusual to look at a large APn81 peatland on an air photo and not consider it to be mixed. It is incredibly easy to place point samples like PLS corners or FIA subplots where all adjacent trees are the same species. It is also easy to place 20x20m releve plots where it is highly likely for the canopy to be monotypic. Groundlayer mixture is also a matter of scale. It differs from the canopy in that it is usually mixed within the bounds of a releve (72%). That is, the rather even distribution of tamarack and black spruce advance regeneration is often not reflected in the canopy. The opportunity for trees to recruit beneath a partial canopy seems common. The historic rotation of partial canopy loss was just 85 years, and modern forests rarely have more than 50% cover. If mature APn81 forests are maintained by disturbances that are largely species-independent (e.g. partial windthrow), it is hard to imagine why older forests are not usually mixed. If canopy gaps are formed by species-specific diseases or pests, they would need to affect both the canopy trees and advance regeneration leaving pure patches of residual tamarack or black spruce trees and their advance regeneration. Thus, tamarack and black spruce would alternate occupancy of canopy gaps. For this to work, we should see releves with mixed advance regeneration and an overstory of residual tamarack at least as often as we see black spruce because APn81 stands are more often tamarack in the canopy. This in not true, as releves with a mixed understory almost always have a canopy of black spruce.

Contemplating both the historic and modern data leads to yet another, but simpler, explanation of succession in APn81 forests. It is possible that all canopy trees recruit after a major disturbance and succession is just a matter of black spruce outliving tamarack. This is the usual explanation for communities where the rotation of catastrophic disturbance is shorter than the life-expectancy of the pioneer trees. Combined, the rotation of catastrophic fire or windthrow on APn81 sites is estimated to be about 250 years. Do most black spruce and some tamarack live that long in these peatlands? Perhaps – field estimates of tree age from APn81 forests are notoriously poor and usually underestimated, but beneath the microscope there are examples of 300 year-old black spruce and tamarack. Explaining the lack of recruitment is more difficult, but does fit our field observations. By the time APn81 forests reach maturity, stagnant growth is the rule and radial growth is nearly at a standstill regardless of tree diameter. Canopy removal might result in some release of understory seedlings but by maturity, there may be very little nutrient capital available for growth that would bring those seedlings into the canopy or into diameter classes suitable for bearing 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?

Black Spruce

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

Identification Problems

The PLS surveyors did not distinguish between black and white spruce. In this case, black spruce is so prevalent on APn81 peatlands that it is fairly safe to assume that surveyor references are to black spruce. APn81 releve samples show that for plots with spruce present: 2% have both species present; 98% are black spruce without white spruce.

Suitability

APn81 sites provide ***excellent habitat*** for black spruce trees. The near perfect ***suitability ranking*** of 4.8 for black spruce is influenced mostly by its high presence (65%) as trees on these sites in modern forests **(R-1)**. When present, black spruce is an important co-dominant and sometimes dominant tree, contributing 26% mean cover in mature stands. No other tree has a higher presence and cover on APn81 sites as sampled by releves. In general, all northern acid peatlands are dominated by black spruce. Among these, APn81 is the most likely to have less black spruce than tamarack, but this community offers the best commercial opportunities for black spruce because the spruce trees on other APn communities are stunted and of poor quality.

Young Growth-stage: 0-55 years

Historically, black spruce was an important tree in young (0-55 years) APn81 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young black spruce represented 14% of the trees at survey corners described as burned **(PLS-3)**. By virtue of their semi-serotinous cones, black spruce are well-adapted to seeding onto burned peatlands after fires. Black spruce was also important following windthrow, representing 16% of the trees at such survey corners. Young APn81 corners with black spruce trees present were mostly monotypic (92%) with all attending bearing trees being black spruce. Small-diameter, black spruce regeneration was most often observed coming in among larger trees about 30-50 years after disturbance **(PLS-5)**. Most often (80%) smaller-diameter black spruce seemed to be recruiting beneath larger black spruce, and less often beneath larger tamarack. We doubt that this is true establishment and recruitment relating to canopy development or other stand maturation events. In this stark environment, we believe their is enough variation in radial growth relating to nutrient availability to explain the variety of diameters at young survey corners. Smaller-diameter black spruce could just be individuals starting to show signs of stunting or stagnation before others. Alternatively, APn81 forests were slow to stock (see Natural Stand Dynamics) . Standing dead spruce can hold, and periodically shed viable seed from semi-serotinous cones for up to 20 years or so. This might explain their ability to slowly fill available growing space and seem to recruit below initial-cohort trees. Also, recruitment late in the young growth-stage could be the result of initial-cohort trees reaching sexual maturity at about age 30 and establishing a second generation.

Mature Growth-stage: >55 years

In the mature growth-stage (>55 years), black spruce abundance slowly increases but does not become more frequent than tamarack **(PLS-1, PLS-2)**. The tendency of black spruce to increase relative to tamarack as stands age is the reason we consider it to be ***late-successional*** in APn81 forests. Mature survey corners with spruce were still more likely to be monotypic (66%), but this is a significant trend towards mixture as compared to the young growth-stage where 92% of the corners were monotypic. Because of its ability to establish and recruit seedlings beneath the canopy **(R-2)**, its ability to vegetatively layer as Sphagnum grows up around the tree, and its great longevity on these sites – black spruce is well-adapted to indefinitely dominating APn81 sites. Although black spruce regeneration coming in among larger trees peaks late in the young growth-stage, it maintains a poor, but consistent ability to recruit throughout the mature growth-stage

(PLS-5). At this time, spruce was mostly recruiting under older black spruce (54%), but often (28%) it was apparently replacing older tamarack.

Regeneration Strategies
On APn81 sites, black spruce is a successful initial-cohort tree. It is capable of competing with tamarack in the ***open*** after a stand-regenerating event, and its positive reaction to fire is well documented in the literature. It is important to remember that our assessment of regeneration strategies is relative among the set of trees commonly found in a native plant community. Thus within this 2-species set, black spruce has all the earmarks of a late-successional, ***small-gap*** species when compared to tamarack. In the historic PLS data this interpretation is supported by: the fact that black spruce steadily increases in abundance as stands age (PLS-1, PLS-2), (2) its abundance is highest in undisturbed forest (PLS-3), it has excellent ability to establish and recruit beneath a canopy (R-2), and the most common situation for black spruce today is to be subordinate beneath the canopy (situation 12, FIA-1). Left undisturbed, APn81 sites will eventually be dominated by black spruce. The fact that this happens slowly and at a time when growth is at a standstill, makes the significance of black spruce replacing tamarack trivial from the perspective of commercial silviculture.

Historic Change in Abundance
Today, black spruce has far greater importance on APn81 sites than it did historically (PLS/FIA-1). The relative dominance of tamarack and black spruce have reversed in all growth-stages since these peatlands were surveyed in the late 1800s. Pollen diagrams and other means of reconstructing the vegetation history of APn81 and similar peatlands clearly show a recent shift from tamarack to black spruce. Unfortunately, the time resolution of these investigations are not adequate for separating the possibility that the shift to black spruce was a natural response of vegetation to Little Ice Age cooling or the reaction of peatlands to settlement and logging. Better documented are historic outbreaks of larch sawfly, beginning as early as 1900 in Minnesota. Defoliation by these insects left thousands of acres of stressed tamarack to die from prolonged drought (e.g. 1930’s), larch beetle infestations, or disease. It is unlikely that exploitation is the proximal cause for the loss of tamarack and success of black spruce. Although there was widespread use of tamarack for fence posts, rot-resistant siding, and railroad ties, the properties of black spruce are similar. Also, given the tools and technology of that time, it seems unlikely that there could have been enough preferential removal of tamarack from these remote and treacherous mires to explain our observations. The timber industry has probably contributed to the increase of black spruce. On APn81 sites and almost any other FPn or APn peatland, the standard practice is to clear-cut and seed black spruce. This is done for no better reason than it is simply easier to collect black spruce cones and for now, black spruce has higher market value. This is done in spite of tamarack’s obvious dominance on these sites and in spite of its proven ability to naturally seed and colonize logged sites.

Tamarack

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

Suitability

APn81 sites provide ***excellent habitat*** for tamarack trees. The ***suitability ranking*** of 4.5 for tamarack is influenced mostly by its presence (41%) as trees on these sites in modern forests **(R-1)**. When present, tamarack is an important co-dominant and sometimes dominant tree, contributing 21% mean cover in mature stands. Tamarack is second only to black spruce with regard to presence and cover on APn81 sites as sampled by releves. In general, tamarack dominates richer FPn peatlands more so than APn sites.

Young Growth-stage: 0-55 years

Historically, tamarack was dominant in young (0-55 years) APn81 stands recovering from stand-regenerating disturbance **(PLS-1, PLS-2)**. Young tamarack represented 86% of the trees at survey corners described as burned **(PLS-3)**. Tamarack was also important following windthrow, representing 84% of the trees at such survey corners. Virtually any kind of disturbance favored tamarack over black spruce. Nearly all young APn81 corners with tamarack trees present were monotypic (93%). Small-diameter, tamarack regeneration was most often observed coming in immediately after disturbance until about age 30 **(PLS-5)**. Nearly all smaller-diameter tamarack were recruiting beneath larger tamarack. We interpret this as tamarack slowly filling all available growing space after a catastrophic disturbance as APn81 forests seemed slow to stock (see Natural Stand Dynamics).

Mature Growth-stage: >55 years

In the mature growth-stage (>55 years), the abundance of tamarack slowly decreases but it remained the most abundant tree **(PLS-1, PLS-2)**. The tendency of tamarack to steadily decrease as stands age is the reason we consider it to be ***early-successional*** in APn81 forests. Mature survey corners with tamarack were still more likely to be monotypic (66%), but this is a significant trend towards mixture as compared to the young growth-stage where 93% of the corners were monotypic. Silvics manuals describe tamarack as very intolerant, and beneath any kind of hardwood canopy seedlings are non-existent. Beneath a canopy of older tamarack or black spruce on APn81 sites, tamarack appears to do rather well at establishing and recruiting seedlings **(R-2)**. We are uncertain as to whether sapling-sized tamarack are usually recruiting seedlings or just stunted, suppressed individuals. True seedlings are common and appear in releves of mature forests more often than not (71%, **R-2**). Tamarack regeneration and recruitment was poor in the mature growth-stage, but not absent **(PLS-5)**. At this time, small-diameter tamarack were apparently recruiting under older tamarack (86%), but sometimes (10%) it was replacing older black spruce.

Regeneration Strategy

Tamarack's primary regenerative strategy on APn81 sites is to out-compete black spruce in the ***open***, post-disturbance environment. It was successful following any type of disturbance, including fire. This is a bit surprising, given black spruce's highly touted abilities following prescribed burning. Our interpretation of tamarack as an ***open*** regeneration strategist is supported by: (1) the tendency of tamarack abundance to decrease as stands age **(PLS-1, PLS-2)**, (2) the high abundance of tamarack at disturbed PLS survey corners **(PLS-3)**, (3) its peak recruitment in the post-disturbance window **(PLS-5)**, and (4) higher presence in canopy situations at FIA subplots **(FIA-1)**. Most open regeneration strategists are intolerant species, and tamarack is considered highly intolerant in silvics manuals. However, in our releves it shows good ability to establish seedlings, and its seedling and sapling indices (4.0-4.5, **R-2**) are in line with those of tolerant species in terrestrial environments. We believe that on APn81 sites, light is not an important driver of succession as it is in richer habitats. Tree cover is short and sparse in mature

APn81 forests. Tamarack may be favored during the post-disturbance years because it is a window of time where mineral nutrients are slightly more available due to ash or modest increases in decomposition. This is consistent with the tendency of tamarack to dominate black spruce in all growth-stages of slightly richer, FPn peatlands.

Historic Change in Abundance

Today, tamarack seems to be losing its dominant grip on APn81 sites **(PLS/FIA-1)**. The relative dominance of tamarack and black spruce have reversed in all growth-stages since these peatlands were surveyed in the late 1800s. Pollen diagrams and other means of reconstructing the vegetation history of APn81 and similar peatlands clearly show a recent shift from tamarack to black spruce. Unfortunately, the time resolution of these investigations are not adequate for separating the possibility that the shift to black spruce was a natural response of vegetation to Little Ice Age cooling or the reaction of peatlands to settlement and logging. Better documented are historic outbreaks of larch sawfly, beginning as early as 1900 in Minnesota. Defoliation by these insects left thousands of acres of stressed tamarack to die from prolonged drought (e.g. 1930's), larch beetle infestations, or disease. It is unlikely that exploitation is the proximal cause for the loss of tamarack and success of black spruce. Although there was widespread use of tamarack for fence posts, rot-resistant siding, and railroad ties, the properties of black spruce are similar. Also, given the tools and technology of that time, it seems unlikely that there could have been enough preferential removal of tamarack from these remote and treacherous mires to explain our observations.

(PLS-1) Historic Abundance of APn81 Trees in Natural Growth-stages

Table values are relative abundance (%) of Public Land Survey (PLS) bearing trees at corners modeled to represent the APn81 community by growth-stage*. Growth-stages are periods of compositional stability during stand maturation. Arrows indicate periods of compositional change during which tree abundances increase or decrease substantially. Yellow and purple shading groups trees with abundance peaks in the same growth-stage. Percents on the bottom row represent a snapshot of the balance of growth-stages across the landscape *ca.* 1846 and 1908 AD.

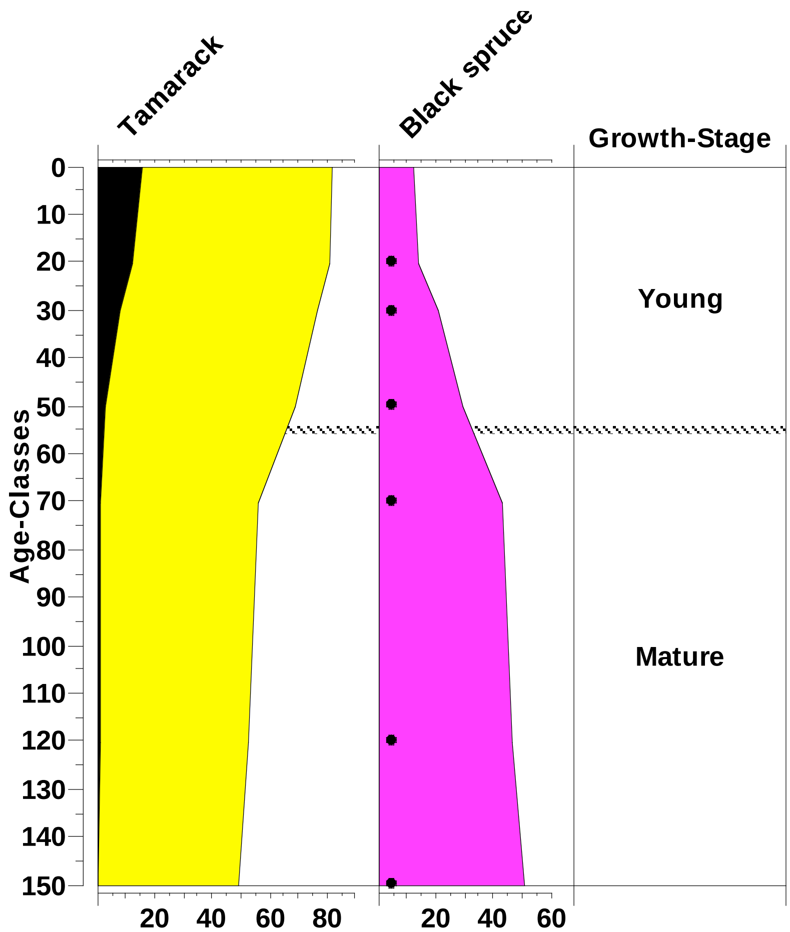
Dominant Trees	Forest Growth Stages* in Years		
	0-55	~55	>55
	Young		Mature
Tamarack	**77%**		**67%**
Black Spruce	**21%**		**27%**
Miscellaneous	**2%**		**3%**
Percent of Community in Growth Stage in Presettlement Landscape	**35%**		**65%**

***** APn81 does not have natural growth-stages as it is dominated by tamarack throughout succession. The break at 55 years was imposed to show slight increase in the relative abundance of black spruce in older forests.

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

(PLS-2) Abundance of trees throughout succession in APn81

Graphed for the individual species of APn81 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 inset for tamarack shows the proportion of bearing trees that were small-diameter trees that were presumably recruiting to bearing tree size (~4" dbh, see PLS-5). For black spruce, the presence of small-diameter trees is indicated by black dots rather than insets because the numbers are small.



APn81, J.C. Almendinger, April 2008

Note: for APn81 the growth-stage at 55 years was arbitrarily set. Here "succession" amounts only to having black spruce gradually replace tamarack as stands mature until the species are about evenly mixed.

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

(PLS-3) Historic Abundance of APn81 Trees Following Disturbance

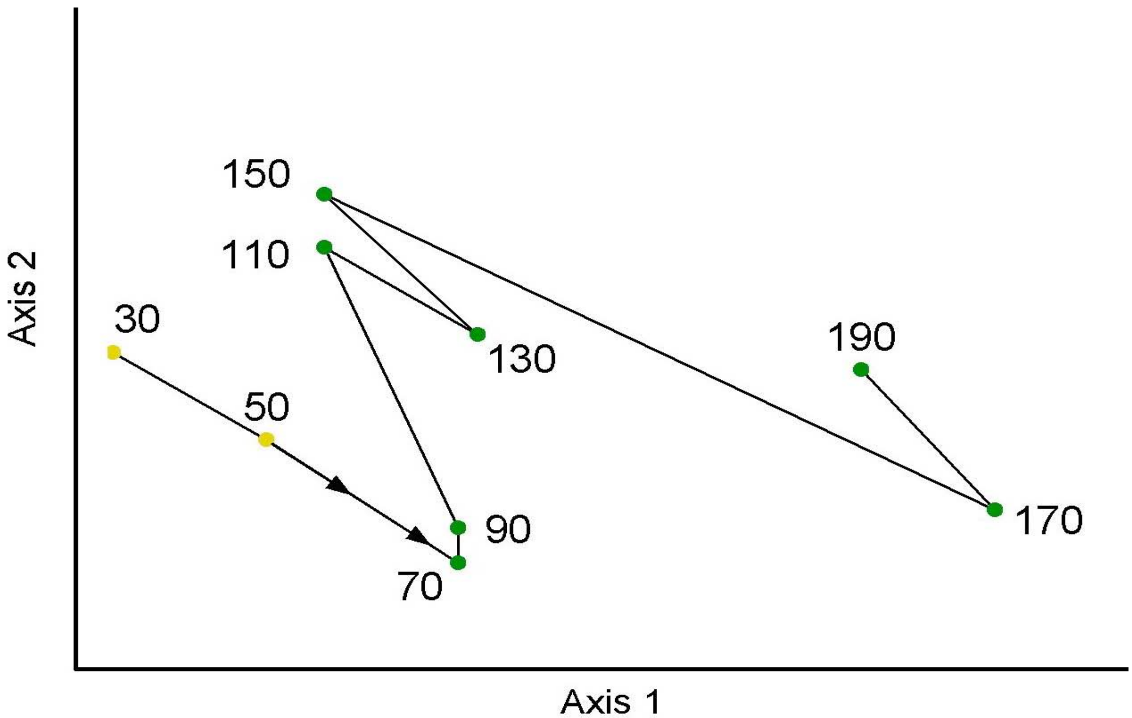
Table values are raw counts and (percentage) of Public Land Survey (PLS) bearing trees at survey corners likely to represent APn81 forests. The columns represent our interpretation of disturbance at the survey corners. Shading associates trees that peak in the same disturbance category.

Tree	Burned		Windthrown		Maintenance		Mature	
Tamarack	**61**	**86%**	**151**	**84%**	**351**	**79%**	**6203**	**73%**
Black spruce	**10**	**14%**	**28**	**16%**	**91**	**21%**	**2257**	**27%**
Total (% of grand total, 9152)	**71**	**1%**	**179**	**2%**	**442**	**5%**	**8460**	**92%**

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

(PLS-4) Ordination of Historic APn81 Age-classes

The distance between age-class points reflect change in composition from one age-class to another. Long distances between age-classes indicate some species mortality and replacement by other species. Short distances suggest little change in composition. For the APn81 community, this entire graphic is highly magnified as movement compared to communities that exhibit true succession is miniscule. If plotted at a comparable scale, the lines and points would be and indecipherable knot near the origin. For this reason there are no recognized growth-stages, rather age 55 was chosen as an arbitrary split to separate young and mature Apn81 forests at a time of silvicultural importance. The general wandering of the points to the right is caused by increased black spruce in older age-classes, and movement up is caused by increased abundance in white cedar.



See linked text on brief methods and silvicultural application for Table PLS-4, file ***NPC Figures and Tables***

(PLS-5) Historic Windows of Recruitment for APn81 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 and gap windows. Arguably, there is no ingress beneath a closed canopy on APn81 sites as the trees are often stunted and rarely form a tight canopy.

Initial Cohort	Species	Peak years	P-D 0-50 years	G-1 >50 years
Yes	**Tamarack**	**0-30**	**Excellent**	**Poor**
Yes	**Black spruce**	**30-50**	**Fair**	**Poor**

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 tamarack and black spruce, >50 years

Note: Black spruce exhibits stagnant growth in APn81 communities, meaning that there is little diameter variation among canopy trees of quite variable age, making it difficult to interpret recruitment. Tamarack shows enough diameter variation to distinguish its initial peak of recruitment, but such variation is small when compared to trees on terrestrial sites. Both species show poor, but consistent recruitment from about 50 years up to, and probably well beyond, 150 years.

Shading: light yellow = trees with peak regeneration immediately after disturbance; **gold =** trees with peak regeneration later in the P-D window

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

(R-1) Suitability Ratings of Trees on APn81 Sites

This table presents an index of suitability for trees in APn81 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 APn81			
Tree	**Percent Presence as Tree**	**Mean Percent Cover When Present**	**Suitability Index***
Black spruce (Picea mariana)	**65**	**26**	**4.8**
Tamarack (Larix laricina)	**41**	**21**	**4.5**
			*Suitability ratings: **excellent**, **good**, **fair**

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

(R-2) Natural Regeneration and Recruitment of Trees in Mature APn81 Stands

This table presents an index of regeneration for APn81 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 APn81 communities. Changes in the index values from one stratum to another can be used to estimate regenerative bottlenecks, whether establishment (R-index) or recruitment (SE-, SA-, or T-indices).

Natural regeneration indices for regenerants, seedlings, saplings, and trees common in the canopy of Northern Poor Conifer Swamp – APn81					
Trees in understory	**% presence R, SE, SA**	**R-index**	**SE-index**	**SA-index**	**T-index**
Black spruce (Picea mariana)	**93**	**5.0**	**5.0**	**5.0**	**4.8**
Tamarack (Larix laricina)	**71**	**3.3**	**4.0**	**4.5**	**4.3**

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

% presence: the percent of 68 APn81 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 ***NPC Figures and Tables***

(FIA-1) Structural Situations of Trees in Mature APn81 Stands

This table presents percentages of structural situations for trees as recorded in Forest Inventory Analysis (FIA) subplots that we modeled to be samples APn81 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. Note: the paucity of tree data (situations 13, 23, and 33) has to do with the fact that these trees often do not meet our arbitrary definition of a tree being taller than 10m.

Species	Tree Count	Structural Situations					
		11	22	12	23	13	33
Black spruce	**5962**	**30%**	**32%**	**34%**	**2%**	**1%**	**1%**
Tamarack	**2014**	**30%**	**39%**	**25%**	**2%**	**0%**	**3%**

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 ***NPC Figures and Tables***

(PLS/FIA-1) Abundance of APn81 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 APn81 community and estimated to fall within the young, and mature 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	>55	
	Young			Mature	
Black Spruce	**21%**	**59%**		**27%**	**66%**
Tamarack	**77%**	**29%**		**67%**	**24%**
Balsam Fir	**--**	**5%**		**1%**	**3%**
White Cedar	**--**	**2%**		**2%**	**3%**
Miscellaneous	**2%**	**5%**		**3%**	**4%**
Percent of Community in Growth Stage in Presettlement and Modern Landscapes	**35%**	**41%**		**65%**	**59%**

Natural growth-stage anal y sis and landscape summar y of historic conditions is based upon the anal y sis of 3,818 Public Land Surve y records for section and quarter-section corners. Comparable modern conditions were summari z ed from 4,961 FIA subplots that were modeled to be APn81sites.

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

Forest Health Considerations

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.

Tamarack

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

WATCHOUTS!

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

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

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

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

Public Land Survey

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

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

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

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

Modern Forest

Releve Samples

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

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

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

For more information on the releve method and NPC Classification:

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

FIA Samples

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

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

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

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

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

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

Link to the USFS website, north central