

Logging Versus Fire: How Does Disturbance Type Influence the Abundance of *Pinus strobus* Regeneration?

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Eastern white pine (*Pinus strobus*) has decreased in abundance over the past century throughout the Great Lakes Region of North America, but the relative constraints placed on recruitment under contrasting disturbance regimes are not well understood. The objectives of this study were to determine the extent to which white pine could invade areas recently disturbed by fire or logging (within 10–28 years), and assess the relative limitations placed on recruitment by seed supply, microsite habitat, and competition. We compared white pine regeneration on 61 sites disturbed by fire or logging that were adjacent to intact mature stands that provided a seed source. White pine seedling and sapling densities declined with increasing distance from a seed source, and the rate of decrease was determined by the interaction between seed supply and variation in number and quality of safe sites. For a given combination of seed source and site, white pine seedlings were three times more abundant on burned than logged sites. White pine seedlings grew into the sapling size class more often on burned than logged sites due to lower shrub cover on burned sites. At 25 years after disturbance, regeneration densities of white pine sufficient to achieve eventual future dominance occurred up to 80 m and 20 m from the edge of mature white pine stands after fire and logging, respectively. To attain a similar level of white pine stocking after disturbance, three to four times as many patches of mature white pine need to be left after logging than after fire.

Keywords disturbance refugia, interspecific competition, Minnesota, seedling dispersion, seed source, white pine

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1 Introduction

Prior to European settlement eastern white pine (*Pinus strobus* L.) occupied approximately 4 million hectares in the northern Lake States, USA region of Michigan, Wisconsin, and Minnesota (Frelich 1995). White pine represented 20% of the forest basal area in presettlement northeastern Minnesota (Friedman et al. 2001). Currently it covers less than 2% of its former area in the Lake States (Miles and Chen 1990, Frelich 1995). The reduction in coverage can be explained by changes in the disturbance regime brought about by European settlement of the Lake States during the late 1800s and early 1900s. White pine is a mid-successional species, mid-tolerant of shade (Horton and Brown 1960, Wendel and Smith 1990). With European settlement came a wave of very severe disturbance, consisting of logging followed by slash fire, that essentially eliminated white pine seed source over vast tracts of the landscape, and allowed former white pine forests to be replaced by early successional hardwoods that can sprout from the stump or roots and have widely dispersed seeds, such as aspen (*Populus tremuloides* [Michx]), *Populus grandidentata* [Michx]), and paper birch (*Betula papyrifera* [Marsh.]) (Heinselman 1973). (Nomenclature follows Gleason and Cronquist [1991].)

Those white pine forests that were not removed by this early wave of severe disturbance faced another change in the disturbance regime: suppression of fire. In the presettlement forest ground fires every 20–40 years maintained and regenerated mid-successional species such as white pine by preparing seedbeds and eliminating invasion by late-successional species, while killing few mature white pine seed trees. The mature white pines have thick bark that can insulate the cambium from a fire for 10–15 minutes or more (Van Wagner 1963, Frissell 1973, Heinselman 1973, 1981, Johnson 1992). In the 20th century, the fire cycle increased to one of essentially no fires of significant size (Frissell 1973, Heinselman 1973, Frelich and Reich 1995). Without fire many white pine stands are now succeeding to late-successional species such as balsam fir (*Abies balsamea* [L.] Miller), black spruce (*Picea mariana* [Mill.] B.S.P.), and white spruce (*Picea*

glauca [Moench] Voss) in the northern part of its range, or red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* L.) and hemlock (*Tsuga canadensis* [L.] Carr.) in the southern and eastern parts of its range.

White pine is known to regenerate well after several types of disturbances, including even-aged stands after severe fire, uneven-aged stands maintained by surface fire, and white pine as a cohort within other forest types following partial natural disturbance or cutting (Abrams 2001). In the northern part of its range, including our study area, white pine historically grew in even-aged stands after severe fires, and in multi-aged stands with periodic recruitment after surface fires (Heinselman 1981, Quinby 1991). White pine can also invade old-field sites in New England although it rarely did so in the Lake States (Lutz and Cline 1947, Gill and Marks 1991, Abrams 2001) until very recently (Frelich, personal observation). White pine has been successfully regenerated using harvest systems like the shelterwood (Lutz and Cline 1956, Lancaster and Leak 1978, Heckman et al. 1985), but again success has been limited in the Lake States.

Therefore, we undertook this study to test the hypothesis that disturbance type – namely the absence of fire – is the limiting factor for white pine regeneration in the Great Lakes part of the range. Now that logging has replaced fire as the major agent of disturbance over the landscape, it is important to study the implications for successional trajectories of the forest. Recent interest in regenerating white pine for lumber, aesthetics and maintenance of biodiversity has spurred a need for more research on ways to promote and expand the white pine type, which may be limited by the current disturbance regime. A few studies have looked at the invasion of white pine into areas cleared by fires or logging (Lutz and Cline 1956, Sharik et al. 1989, Ahlgren 1976, Carleton and MacLellan 1994, Carleton et al. 1996). None of these studies, however, has done a direct, detailed comparison of regeneration and stocking levels over time after the presettlement disturbance type that we know perpetuated white pine (fire) and the current dominant disturbance type (logging). Here we accomplish that by means of a ‘found’ experiment in northeastern Minnesota that, although not intentionally set up, includes several examples of

logged and burned forests of similar age classes, on the same landform and soil types, with remnant sources of white pine seed trees adjacent to the disturbed areas.

What mechanisms could explain any differences in white pine regeneration success that may exist after logging and fire? The amount of seed coming from mature trees adjacent to a disturbed area and the distance those seeds travel is important for white pine (Palik and Pregitzer 1994, Dovciak et al. 2001), but is not expected to vary systematically with disturbance type. Seed dispersal curves are expected to be negative exponential with distance from seed source, with a maximum distance of about 210 m in the open (Wendel and Smith 1990, Greene and Johnson 1989). However, the seeds must land on a safe site for germination and early survival. We hypothesized that burning would increase numbers of suitable seedbeds and reduce competition more so than logging (Buckman 1964, Carleton and MacLellan 1994, McRae et al. 1994). Therefore, burned areas may have a higher percentage of seeds that germinate and survive, resulting in dispersion of seedlings that reaches further away from seed sources, and with higher numbers of seedlings at a given distance from seed source, as compared to logged areas. There is also a temporal component to these mechanisms. As a new stand develops after disturbance competition for resources from other species will increase and limit the ability of white pine to continue to grow and survive. We hypothesize that fire will set back the competition more than logging, thus giving white pine a longer period of time to regenerate and grow.

This paper has three objectives. Objective one is to address the overall hypothesis that disturbance type limits white pine regeneration during the current era with logging as the dominant disturbance type. Objective two is to address the hypotheses on mechanisms mentioned in the previous paragraph, regarding differential availability of safe sites and reduced competition after logging and fire. Objective three is to demonstrate the differences in stocking levels that would occur under given conditions, such as equal seed source and distance from seed source, after the two disturbance types. Such information could be useful for restoration and management of white pine forests.

2 Methods

2.1 Study Area

Our study was conducted in northeastern Minnesota, USA during the summer and early fall of 1999 (Fig. 1). All sites were located within the Superior National Forest. This region is part of the Canadian Shield where most soils are thin and overlie bedrock (Heinselman 1996), however, deeper soils are common on moraine features. The climate is continental with approximately 100 frost-free days per year and about 62 cm of annual precipitation. Average daily maximum and minimum temperatures for the summer are 24°C and 11°C, and -9°C and -20°C for the winter. The forests are considered sub-boreal, and the major tree species include white pine, red pine (*Pinus resinosa* [Aiton]), jack pine (*Pinus banksiana* [Lambert]), white spruce, black spruce, balsam fir, red maple, aspen, and birch.

2.2 Site layout

All sites included a white pine seed source (refuge) and an adjacent area cleared by fire or logging (disturbed area). The refuges had a minimum of three large (>65 cm diameter at 1.4 m above ground, or dbh) trees, or >0.25 ha of smaller white pines (>25 cm dbh). The stand age of refuges ranged from 50 to 170 years and the average basal area was 25 m²/ha. Sampling plots

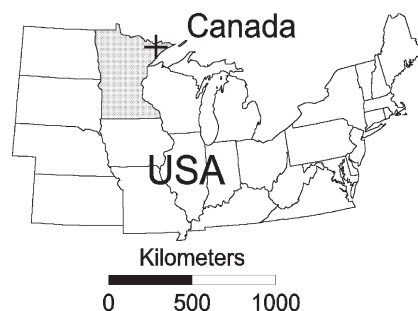


Fig. 1. Location map. The northeastern quadrant of the USA is shown, Minnesota is shaded and the plus (+) in northeastern Minnesota marks the location of the study area.

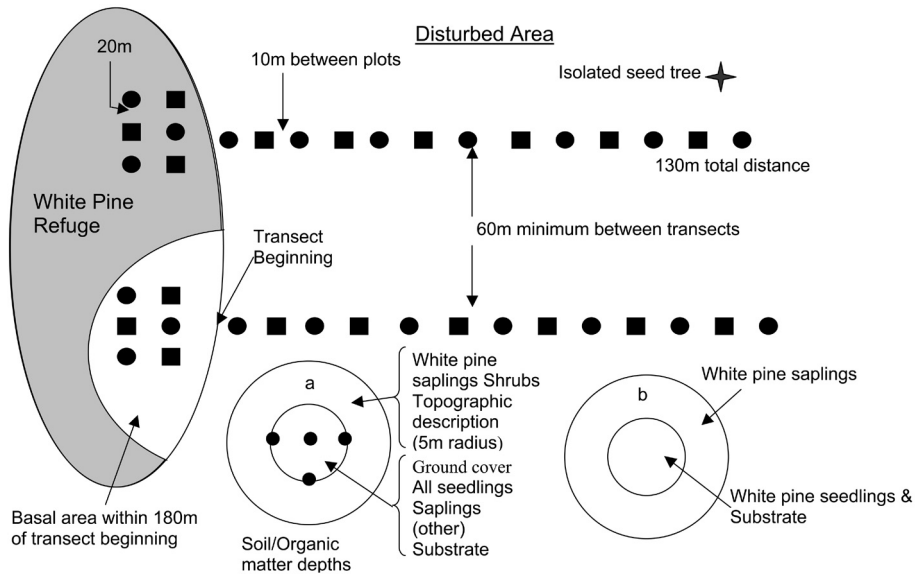


Fig. 2. Schematic diagram of a typical site (not to scale). The refuge is a mature forest of white pine seed trees and the disturbed area was cleared by fire or logging. Each of the two transects has alternating plot types (represented by squares and circles) at a 10 m spacing. All data types were collected on plots represented by circles (a), and only white pine seedling, sapling and substrate data were collected on the plots represented by squares (b).

were located within the refuge and on transects running outward from the edge of the seed source (Fig. 2). Typically, sites contained two transects 130 m in length at least 60 m apart and two accompanying sets of refuge plots. Plots were 20 m apart in the refuge and 10 m apart along transects in the disturbance. White pine data and substrate data were collected on every plot, and seed source strength was calculated for every plot, whereas data for tree species other than white pine, shrubs, herbaceous plants, and physical site properties were collected on every other plot along the transects (Fig. 2, details of data collection given below in section 2.4).

2.3 Site Selection

Thirty previously burned sites and 31 previously logged sites were sampled for this study. U.S. Forest Service records were available to identify disturbance history for these sites. All the burned sites were within seven wildfires. Five fires occurred in the late spring, and two in the

late summer. Their sizes range from 2 to 5,821 hectares. Fire severity was not considered when selecting sites for this study except that the severity must have been sufficient to cause nearly complete stand mortality. All logged sites but one were clearcuts. Whole tree harvest methods were used with the slash piled and burned (Ralph Bonde and Dean Seitz, personal communication). Preharvest stands typically consisted of a mix of aspen, birch, and white pine. The stand that was not clearcut was selectively harvested leaving white pine seed trees on the site. This site was omitted from all analyses except for seedling substrate. On nearly all sites, the disturbed area had no residual live overstory remaining after the disturbance, although a few sites had a few single stems or small clumps of trees remaining. Time since burning or logging ranged from 10 to 28 years, and the stands were not physically altered after the disturbance. There was no artificial seeding or planting of white pine.

2.4 Site Descriptors

2.4.1 Stand Age

The variable stand age was defined as the time since logging or fire of the disturbed area. The 61 sites were separated into two stand age classes, 10–17 and 21–28 years old, at a natural break point in the data.

2.4.2 White Pine

White pine densities were sampled for several size classes. Seedlings (defined as stems less than 1.4 m tall) were counted on all plots within a 3.5 m radius of plot center in three height classes (0–50 cm, 51–100 cm, and 101–137 cm). Saplings and small trees were counted at all plots within 5 m of the plot center in three dbh classes (0.1–5 cm, 5.1–15 cm, and 15.1–24.9 cm, with the latter very rare). Trees ≥ 25 cm dbh were considered seed trees (Weyenberg, personal observation), and their basal area was determined using a variable radius prism for three dbh classes (25–40 cm, 40.1–64.9 cm and > 65 cm). The influence of sporadic white pine seed trees found within the disturbance was taken into account by measuring their size and location with respect to the nearest plot. Dead trees were not recorded.

2.4.3 Substrate Type

The percent cover by substrate type was recorded within the 3.5 m radius seedling plots. Also, the substrate on which each seedling < 100 cm in height was growing was recorded. Seedlings in this small size class are likely < 10 years old, and thus their substrate type still reflects that on which germination occurred. Thirteen different substrate types were identified, eight of which were later eliminated in the analysis due to inadequate sample sizes (these 8 had a total of 4% of all plot area). The remaining types used in the analyses were: hardwood litter, rotten log, feather mosses (*Pleurozium*, *Hylocomium*, and *Thuidium*), conifer litter, and mixed conifer/hardwood litter.

2.4.4 Seed Source Strength

Seed source strength, an index of seed availability, was calculated for each transect plot using two factors: basal area of seed trees in the refuge area, and distance from the seed trees. Basal area of pine trees was assumed to be proportional to number of seeds produced by trees within the refuge (Graber 1970). To get seed source strength for each plot, the basal area of seed trees was weighted by the proportion of seeds expected to reach the plot, given the plot's distance from the seed trees and the Weibull seed dispersal curves of Greene and Johnson (1989, 1996), using a seed dispersal distance of 30 m and Weibull shape parameter of 1.3 (Eq. 1). On a few of the study sites, there were scattered white pine seed trees within the disturbed area, and these were also added to the seed source strength, since their basal area and distance to each plot was known.

$$\text{Total seed source strength/plot} = (\text{BA}_{\text{Ref}})(\exp(-(\text{Dist}_{\text{Ref}} / 30\text{m})^{1.3})) + (\text{BA}_{\text{Dstrb}})(\exp(-(\text{Dist}_{\text{Dstrb}} / 30\text{m})^{1.3})) \quad (1)$$

BA_{Ref} = Basal area of seed trees in the refuge
 BA_{Dstrb} = Basal of a seed tree in the disturbed area
 Dist_{Ref} = Distance from the refuge.
 $\text{Dist}_{\text{Dstrb}}$ = Distance from a seed tree found in the disturbed area.

The basal area within 180 m of the transect beginning was used for the refuge (Fig. 2). This area was assumed to capture the majority of trees contributing seed to a transect of plots. Weighted basal areas for sporadic seed trees were added to a plot only if they were within 60 m of the plot. The adequacy of the parameters chosen was tested using Ordinary Least Squares regression (JMP-IN v. 3.2.6, SAS Inst., Cary, NC). A variety of parameters were tested without any appreciable change in the r^2 value.

2.4.5 Other Tree Species

Trees species other than white pine (other trees) were recorded on all transect and refuge plots in three size classes, < 1.4 m tall, 1.4 m tall – 4.9 cm dbh, and > 5 cm dbh. Seedlings (< 1.4 m tall)

were recorded as a total percent cover for all species but were excluded from the analysis due to a lack of a large range in the data. Saplings (other saplings) (1.4 m tall – 4.9 cm dbh) were counted in density classes of 10 stem increments within a 3.5 m radius plot. Trees >5 cm dbh were counted using a variable radius prism and average diameters were recorded for each species.

2.4.6 Shrubs and Forbs

Density, height and distribution of tall shrubs, mainly beaked hazel (*Corylus cornuta* [Marshall]) and mountain maple (*Acer spicatum* [Lam.]), were assessed for transect and refuge plots in a 5 m radius plot. Density and height were recorded as low, medium or high and spatial distribution was uniform or clumped. Shrub measures were later combined into one ordered variable. Orders were ranked by density then by height. Low density by low, medium and high heights represented orders 1, 2, and 3, respectively. Medium and high densities by the three height classes represented orders 4 through 9. To scale patchy and uniform coverages within the same variable; the order remained as is (1–9) if the plot was patchy, if uniform, the order was doubled. Therefore, all the possible combinations of the original 3 measures are represented; 19 ordered levels in all, including 0 for no shrubs. In the end, ordered levels 3, 9, and 15 corresponded to low, medium, and high shrub coverage respectively. Herbaceous ground cover and low shrubs were assessed together as percent cover on each 3.5 m radius plot.

2.4.7 Physical Site Properties

A number of soil and topographic factors were measured to characterize the physical site properties on all plots. Soil stoniness, which is the depth to a large rock or bedrock, was measured at 4 locations per plot via a soil probe. Organic matter depths were measured at the same locations as soil stoniness. Physiographic class for each plot was assessed on a five-point scale including xeric, xeromesic, mesic, hydromesic, and hydric. Hydromesic and hydric levels were later omitted from the analysis due to small sample sizes.

Topographic characteristics such as position on the hillside, land configuration, slope percent and aspect direction were documented for each plot. Five levels of position: top, shoulder, middle, toe, and bottom were observed but were later combined to form two levels, upland and lowland.

2.5 Statistical Analyses

2.5.1 Distance From Seed Source and White Pine Regeneration

Standard least squares regressions were used to characterize the mean trend in white pine seedling and sapling densities with distance from refuge seed source, using the mean densities among all plots at each 10 m distance class.

2.5.2 Environmental Factors and White Pine Regeneration

The site descriptors stand age, seed source strength, other tree species, shrubs and forbs, and physical site properties are all considered part of the environment for white pine seedlings and saplings, and their impact was analyzed using ordinal logistic regression (JMP-IN 3.2.6, SAS Inst., Cary, NC). Ordinal logistic regression is capable of showing whether explanatory variables (in this case the measured environmental factors) explain the distribution of the response variable (white pine seedling or sapling density) among several ordered categorical levels of abundance. Thus, ordinal logistic regression differs from logistic regression, which has a binomial response variable (presence or absence in the case of seedling or sapling abundance). The significant ($p < 0.05$) main effects and two-way interactions were determined using a Wald Chi Squared test and a forward elimination procedure.

To facilitate the ordinal logistic regression, each plot was assigned to one of five density classes for seedlings and saplings: 0, 1–400, 401–1000, 1001–2000, and 2000+ seedlings/ha, and 0, 1–200, 201–500, 501–1000, and 1001+ saplings/ha.

Plots are considered independent with respect to the biotic and abiotic factors measured for two

reasons. First, spatial autocorrelation analyses on nearby similar sites shows that the measured factors on one plot should not effect white pine regeneration on another plot given their distance (Machado 1999). Second, the topography of the sites is very heterogeneous at a small spatial scale (i.e. 10–30 m), with many knobs of rock and intervening small valleys. This heterogeneity does affect white pine regeneration and abundance by modifying the local environment in many ways, but it occurs on all of the study sites, which were purposely located on areas with the same physiography, and it does not have any systematic relationship to the location of fire and logging disturbances, both of which are much larger than the scale of topographical variation. The topographical heterogeneity also has no systematic relationship to the locations of refuge populations of white pine. Thus, unmeasured factors have a low likelihood of affecting our data in any systematic fashion.

To interpret relationships (positive or negative) between significant predictors and white pine seedling or sapling densities we examined the means for each significant predictor by seedling or sapling density class. This method was simple and was in agreement with the associations indicated by the regression coefficients in most cases. When regression coefficient signs did not agree with means in the data, interactions terms were involved, and the sign of regression coefficients was in agreement with the data when the models were run without interactions.

2.5.3 *Substrate Type and White Pine Regeneration*

The distribution of seedling densities among plots on each substrate type was highly right-skewed due to a large number of zeros. In such cases the Poisson regression – a general linear model that assumes the Poisson distribution for the response variable – was used to analyze the odds that seedlings are more or less likely to be found on various substrates than by chance alone (Cook and Weisberg 1999). Seedling density was the response, and disturbance history, stand age, distance from the seed source, and substrate type were the predictors. Significant variables were based on a

p-value <0.05 using a Likelihood Ratio Test. Comparisons among substrates were done using odds ratios (Cook and Weisberg 1999).

2.5.4 *Disturbance Type and Stand Age*

The previous analyses show how environmental variables influence white pine seedling and sapling abundance directly. However, disturbance type (logging or fire) and time since disturbance are the variables of most interest to us and to forest managers. Therefore, the influence of disturbance type and stand age, and their interaction, on environmental variables was estimated using ordinary least squares regression. Variables used included distance from the seed source, white pine seed tree basal area, basal area of other trees, seed source strength, other saplings, forb and shrub cover, organic matter depth, soil stoniness, and percent slope. Some variables were transformed with a square root transformation to bring distributions closer to normal. White pine seedling and sapling density were also analyzed as continuous variables, with the expectation that the results will be consistent with those from the ordinal logistic regression.

3 Results

3.1 Distance from Seed Source

There was a slightly convex curvilinear decrease in white pine seedling and sapling densities with increasing distance from the seed source, when all plots within a distance class were averaged (Fig. 3a and 3b). Seedlings showed a steeper decrease in absolute numbers than saplings, but the trend was similar in proportion. The shape of the seedling dispersion curve was substantially different than that predicted for seed dispersal which is negative exponential (Figs. 3a and 3b).

The mean distance from a seed source for seedling-rich plots with 2000+ seedlings/ha was 51.8 m compared to 75.2 m for plots with <400 seedlings/ha. The mean distance from a seed source for plots with sapling densities >1000/ha was 60.4 m, compared with 70.3 m for plots with densities <200 saplings/ha.

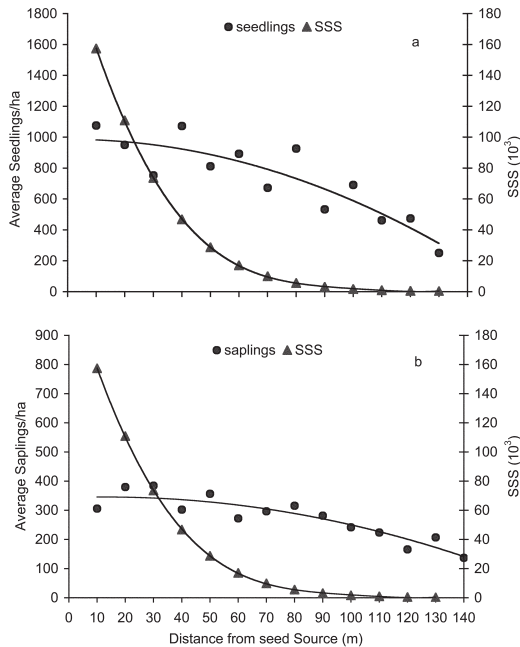


Fig. 3. Average white pine seedling (a) and sapling (b) densities versus distance from seed source. Note that y-axis scale differs between a and b. The ordinary least squares regressions equations that describe the mean trends for seedlings and saplings were: $y = 985.65 + 0.0444 D - 0.0402 D^2$ ($R^2 = 0.78$), and $y = 343.28 + 0.3396 D - 0.0127 D^2$ ($R^2 = 0.84$), respectively, where D = distance in meters. The expected curve for seed source strength (SSS) is shown for comparison. Its scale is relative but since it can be used as a surrogate for seed supply it is shown in thousands. Details for calculating seed source strength are given in the text.

3.2 Environmental Factors and White Pine Regeneration

Plots with high seedling and sapling densities tended to be close to the refuge, have high seed source strength, and lower shrub cover index and basal area of other tree species than plots with low seedling densities, and some environmental variables such as organic matter, soil stoniness had little trend with seedling density (Table 1). Disturbance history, stand age, seed source strength, and shrub cover all had a highly significant influence on white pine seedling abundance

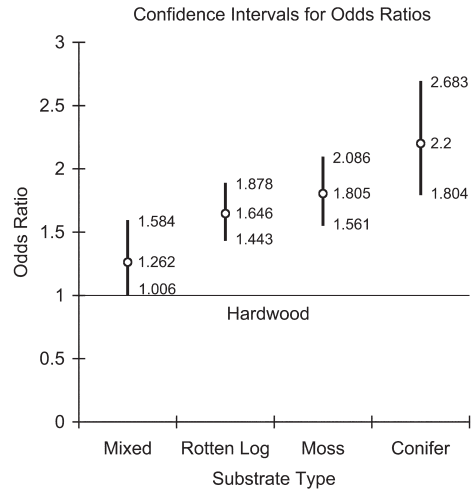


Fig. 4. Substrate comparisons based on confidence intervals of odds ratios. All substrates are compared to hardwood litter, which has an odds ratio of 1 in this case. The graph can be interpreted in this way: one is 2.2 times more likely to find a white pine seedling on conifer litter than on hardwood litter.

Table 3. Seedling densities by substrate type and percent of sampled area occupied by each substrate type.

Substrate	Seedlings/ha	%total area
Hardwood litter	360	70%
Conifer litter	600	4%
Mixed litter	310	9%
Moss	510	8%
Rotten log	480	8%
Average total	390	100%

in the ordinal logistic regression models (Table 2). The diameter of other trees, plot position, and physiographic class were not significant as a main effect, but were in significant interactions. Basal area of other trees and density of other saplings were not significant in the seedling model (Table 2). Disturbance history, stand age, seed source strength and shrub cover were also significantly related to sapling abundance as main effects, as were basal area of other trees, density and of other saplings, and several interaction terms (Table 2). Ground cover by forbs was also significant in this model but was considered a correlate rather than explanatory variable, since forbs have little influence on trees from 1.4 m tall to 24.9 cm dbh.

Table 1. Mean values for environmental variables among plots in each seedling and sapling density class.

	0	Density class – seedlings per ha			2000+
		1–400	401–1000	1001–2000	
Number of plots	589	237	259	193	138
Distance from refuge (m)	77.1	75.2	64.7	60.9	51.8
Seed source strength	0.854	0.875	1.286	1.470	1.646
Ground cover (%)	53.8	60.8	59.8	62.0	67.6
Organic matter depth (cm)	3.2	3.6	3.1	3.1	3.1
Shrub cover index	9.3	8.4	7.3	7.2	7.3
Soil stoniness (cm)	13.4	12.7	11.6	12.6	12.3
Basal area other trees m ² /ha	9.3	8.1	9.1	7.0	7.0
Other saplings/ha	2357	2546	2962	3066	3352
Dbh of other trees (cm)	11.7	11.7	11.3	12.8	15.7

	0	Density class – saplings per ha			1000+
		1–200	201–500	501–1000	
Number of plots	712	241	208	140	115
Distance from refuge (m)	73.1	73.2	63.8	63.5	60.4
Seed source strength	1.012	1.037	1.332	1.220	1.190
Ground cover (%)	53.6	57.8	61.4	70.7	71.7
Shrub cover index	10.4	6.7	6.9	5.2	4.4
Soil stoniness (cm)	13.2	12.1	11.6	11.6	14.4
Basal area other trees m ² /ha	9.4	8.9	7.3	7.5	6.7
Other saplings/ha	2754	2676	2780	2391	2754
Dbh of other trees (cm)	12.7	11.3	11.7	12.2	11.0

Table 2. Significant terms for ordinal logistic regression for white pine seedling and sapling densities (ordered categorical response variable with five levels) vs. environmental factors.

Predictors	Seedling model		Sapling model	
	χ^2	p-value	χ^2	p-value
Disturbance type	70.48	<0.001	11.75	<0.001
Stand age	14.94	<0.001	16.16	<0.001
Seed source strength	33.91	<0.001	8.89	0.003
Shrub cover index	9.96	0.002	98.69	<0.001
Dbh of other trees	0.035	0.851		
Physiographic class	3.02	0.221		
Position	0.84	0.361		
Ground cover			26.09	<0.001
Basal area other trees m ² /ha			13.25	<0.001
Other saplings/ha			20.62	<0.001
Dbh of other trees*shrub cover	4.14	0.042		
Dbh of other trees*position	7.19	0.007		
Disturbance type*stand age			41.00	<0.001
Disturbance type*ground cover			5.48	0.019
Stand age*seed source strength			5.81	0.016
Stand age*basal area other trees			4.39	0.036
Stand age*Other saplings			17.29	<0.001
Stand age*physiographic class	8.22	0.016		

White pine seedlings were influenced by two topographic features, whereas saplings were not influenced by any. Mean seedling densities were two times greater on uplands than lowlands (posi-

tion, 1057 versus 425 seedlings per ha, respectively), and mean seedling densities on xeromesic plots (1487/ha) were greater than those found on xeric (551/ha) or mesic (864/ha) plots.

Hardwood litter was the most abundant litter type, occupying 70% of the total area sampled (Table 3). Percentages for all other types ranged from 4–9%. There were no significant differences of substrates between logged and burned plots. Poisson regression results show that the odds of finding a white pine seedling did not differ between rotten log, moss and conifer substrates, that these three substrates as a group were significantly different from hardwood litter, and the mixed litter type was intermediate (Fig. 4). Compared to hardwood litter the odds of finding a white pine seedling on other substrates were ~1.7 times greater for rotten log or moss and 2.2 times greater for conifer litter (Fig. 4).

3.3 Disturbance History, Stand Age, and White Pine Regeneration

Burned sites had at least three times the average white pine seedling density of logged sites for a given age class ($p < 0.001$), even though the mean basal area of white pine seed trees in the refuges and seed source strength were significantly lower on burned sites than on logged sites (Table 4). This trend also holds across distance classes and time since disturbance (age class). A greater percentage of burned plots had white pine seedlings

present and they were greater in density than on logged plots at a variety of distances from the seed source for 10–17 and 21–28 year age classes (Fig. 5a and b, Fig. 6a and b). There were consistently more seedlings at all distances and for both age classes after burning than after logging.

White pine sapling density shows a significant interaction with stand age and disturbance type (Table 4). Overall sapling densities are lower on burned plots than logged plots for the 10–17 year age class, but higher on burned than logged plots for the 21–28 year age class (Table 4). These trends and the disturbance type age interaction are also consistent across distance from the seed source for the percent of plots with saplings present and density of saplings (Fig. 5c and d, Fig. 6c and d).

Most environmental variables measured differed between burned and logged sites (Table 4). Densities of other saplings were greater on burned than on logged sites, while shrub cover was greater on logged than burned sites. Disturbance history was a significant predictor of diameter of other trees and organic matter depth. In contrast, disturbance history was not significantly related to differences in basal area of trees other than white pine or ground cover by forbs.

Significant differences existed between stand age classes for many environmental variables

Table 4. Means for variables as separated by disturbance type and stand age, p-values from ordinary least squares regression.

Variable	Means by disturbance type and age class				Disturbance type	P-values Stand age	Interaction
	Burned		Logged				
	10–17	21–28	10–17	21–28			
Number of samples	137	596	374	335			
Seedlings/ha	3789	645	650	223	<0.001	<0.001	<0.001
Saplings/ha	118.0	273.1	492.1	157.1	0.002	0.331	<0.001
Seed source strength	1.350	0.703	1.400	1.365	0.003	<0.001	<0.001
Distance from refuge (m)	61.8	72.4	70.5	67.7	0.413	0.006	0.110
White pine basal area in refuge (m ² /ha)	18.7	11.1	46.0	30.6	<0.001	<0.001	<0.001
Ground cover (%)	56	57	72	49	0.080	<0.001	<0.001
BA of other trees (m ² /ha)	3.7	11.4	4.6	9.6	0.386	<0.001	0.008
Other saplings/ha	4157	2339	3378	1819	<0.001	<0.001	0.595
Shrub cover index	7	6	11	10	<0.001	0.320	0.497
Dbh of other trees (cm)	25	11	10	12	<0.001	<0.001	<0.001
Organic matter (cm)	3	3	3	5	0.003	<0.001	<0.001
Soil stoniness (cm)	10	10	13	16	<0.001	0.454	0.109
Slope (%)	10	9	11	12	0.003	0.612	0.372

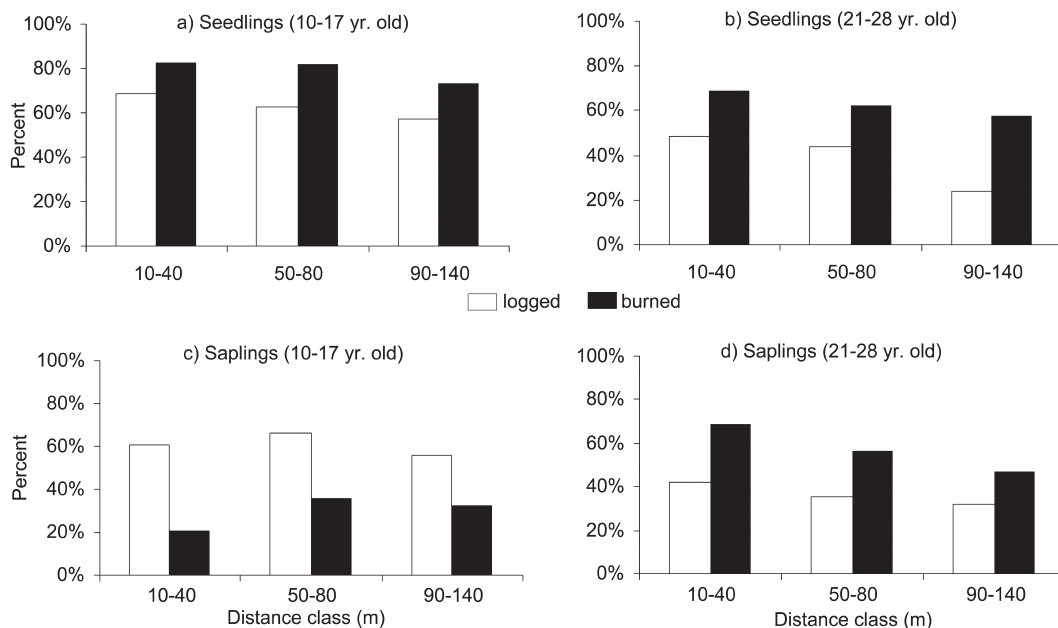


Fig. 5. Percentage of plots, by stand age class, with seedlings (a, b) and saplings (c, d) present for burned and logged sites. Percentages were calculated after plots were separated into 3 distance classes (meters from a refuge).

(Table 4). Seed source strength and the basal area of white pine seed trees in the refuge were greater on the 10–17 year age class than the 21–28 year age class. Stand age was a significant predictor for several other variables measured (Table 4): the 10–17 year old sites had a lower average basal area of other trees, higher mean density of other saplings and greater ground cover. Stand age did not significantly affect shrub cover, and was unrelated to physiographic measures such as soil stoniness and slope. Logged sites had higher seed source strength (for the 21–28 year age class) and higher white pine basal area (both age classes) than burned sites (Table 4).

The interaction between stand age and disturbance history was also significant for seed source strength, basal area of white pine and other trees, diameter of other trees, ground cover by forbs, and organic matter (Table 4). The fact that there were no interactions between stand age and disturbance types for physiographic measures and distance from seed source indicates that the sites studied were representative for these factors, with no systematic differences that could influence the results.

4 Discussion

4.1 Seedling Dispersion Relative to Seed Sources

Seed source strength had a clear positive effect on white pine seedling densities (Tables 1, 2 and 4). We did find a decrease in white pine seedling/sapling densities with distance from a seed source, but the shape was not the negative exponential shape expected based on other studies of seedling dispersion (Wood 1932, Rudis et al. 1978, Hughes and Bechtel 1997), or studies of tree seed dispersal in northern conifer forests (Greene and Johnson 1989, 1995, 1996, Okubo and Levin 1989, Hughes and Bechtel 1997). The relationship of seedling and sapling density versus distance was best fit by a polynomial with slightly convex curvature, which is almost linear (Fig. 3a and b). We don't know the reason for this, but there are two likely explanations. First, most of the safe sites within 50–70 m of the forest edge may have been filled by seedlings of white pine which are now undergoing self thinning, because 10–28 years have already passed since distur-

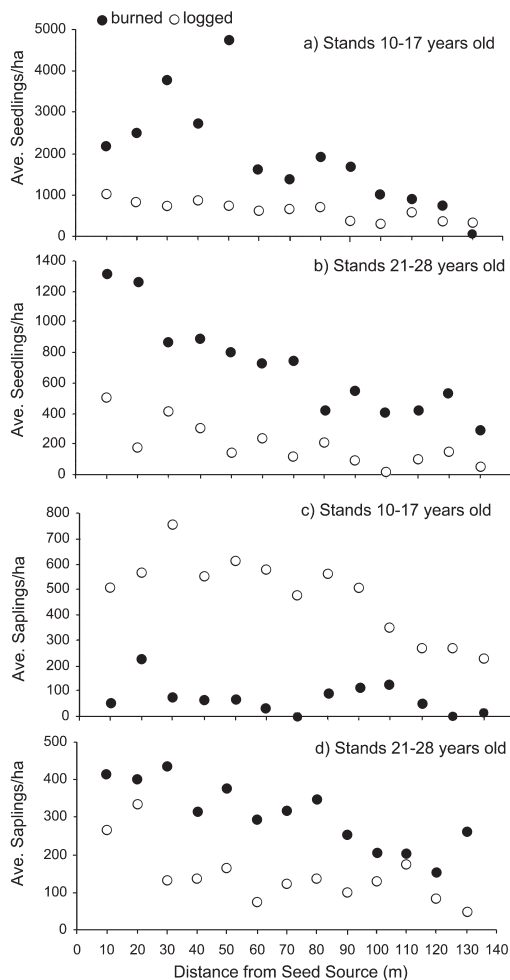


Fig. 6. Seedling (a, b) and sapling (c, d) density distributions with distance as separated by stand age and disturbance type.

bance on our study sites. It is possible that the density of seedlings near the forest edge might have been far higher in the first few years after disturbance, thus giving the seedling dispersion curve a negative exponential shape that would have more closely reflected the seed dispersal curve at that time. Second, seeds and seedlings may be at a relative disadvantage due to disease dynamics, adverse microenvironmental conditions, or more competition from other species of trees that may exist close to mature trees at the forest edge (Augsburger 1984, Dovciak et al.

2001). The extent to which spatial distribution of seedlings and saplings is far from negative exponential, and the mechanisms responsible, represent an important area for future research.

4.2 Disturbance Type and White Pine Regeneration

This study reveals positive evidence for the overall hypothesis that white pine regeneration in the Lake States is limited by the type of disturbance that predominates at this time. Overall, seedling densities were ~3 times greater on burned than on logged sites even though the basal area of seed trees was more than 3 times higher adjacent to logged than burned sites. There were more seedlings at almost all distance classes from the seed source after fire than logging. This was true for both age classes (10–17 and 21–28 years after disturbance), and for absolute numbers of seedlings as well as proportion of plots with seedlings present (Figs. 5 and 6). Seedlings are also more successful at growing into the sapling size class after fire than after logging. There were more saplings after fire than logging for all distance classes from the seed source (Fig. 6), and the proportion of plots with saplings present is higher 21–28 years after fire than logging (Fig. 5).

An examination of the hypotheses on mechanisms presented in the Introduction sheds some light on the reasons that fire enables better reproduction success than logging. The first hypothesis is that the quantity and quality of safe sites for germination and early survival are more abundant after fire than logging. Thus we would expect more suitable substrate for white pine seedlings and less competition from other vegetation after fire. Contrary to our expectation, substrate differences between burned and logged sites did not seem to explain the differences in white pine seedling success. Regeneration was poorer on hardwood litter compared to other substrates, consistent with other studies (Simard et al. 1998, Smith 1951). In contrast to other studies for conifers other than white pine (Smith 1951, Cornett et al. 1997, Simard et al. 1998), rotten logs and moss did not favor regeneration in this study. However, the proportion of various substrates was not significantly different after the two disturbance

types, and therefore any differences in success of white pine among substrate types, and whether these differences follow expectation or not, likely cannot explain the greater success of white pine regeneration after fire as compared to logging. However, substrate is most important during the germination and early establishment phase, which is disconnected by time from our observations 10–28 years after disturbance, and it is likely that substrate conditions immediately after the disturbances differed from what we observed.

Competition from shrubs, on the other hand, probably does explain much of the differential success of white pine after logging and fire. Clearly, logging had a more positive effect on shrub densities than burning (Table 4). Shrub cover was significantly lower on burned sites and shrubs were negatively related to seedling densities and to sapling densities (Table 2). Competition from other trees and saplings cannot explain site differences in recruitment, since densities and basal area of saplings and other trees, respectively, were not consistently higher at logged sites. White pine sapling densities were influenced more by competition than were white pine seedlings. White pine is a mid-tolerant species and has a whole plant light compensation point between 2 and 6% of full sun (Bourdeau and Laverick 1958). Given this tolerance, white pine seedlings can establish despite intense competition and many will survive for several years under low light conditions. As seedlings age, only those in low competition areas will grow into saplings and survive, thus sapling densities become dependant on competition.

Differing shrub densities were likely what drove differences in white pine sapling densities between logged and burned sites. All of the other factors examined that could have affected safe sites or competition, such as ground cover by herbs, site moisture, organic matter depth, and topographical factors such as slope, aspect, and landscape position, did not vary systematically between logged and burned sites.

It is likely that burn severity on our study sites had high variability at fine spatial scales, and this variability is known to influence post-fire response of vegetation for several years (Schimmel and Granstrom 1996). It was not possible to measure these fine-scale variations during this study, which took place 10–28 years after the fires, and it is no

longer possible to assign variability in shrub cover to variability in the burn pattern. This variability is a likely explanation for the large amount of scatter in shrub and seedling density among plots in our data. However, the trends were still strong enough for a high level of confidence that shrub cover is different between logged and burned areas, and that shrub cover strongly influences white pine regeneration density.

The second hypothesis on mechanisms by which fire and logging have differential effects on white pine regeneration was that conditions that allow successful establishment last longer after fire than logging. There was strong positive evidence in favor of this hypothesis. The proportion of plots with seedlings present falls more between the 10–17 and 21–28 year age classes after logging than after fire (Fig. 5a and b). The proportion of plots with saplings decreases substantially as stands age from 10–17 to 21–28 years after logging, but increases substantially after fire (Fig. 5c and d). Thus, saplings that were in the understory prior to logging, that are generally left intact during logging operations, succumb due to stress from a changing environment or from competition with shrubs. Most pre-existing saplings are killed by fire, so fewer are present in young forests after fire. However, the seedlings that are established after fire are able to survive and grow into the sapling class by age 21–28. Ultimately, this leads to a greater number of saplings after fire as compared to logging, that are able to pass the hurdles of germination, establishment and recruitment, which are then free to grow into mature trees.

4.3 Implications

In our study, fire promoted white pine regeneration relative to logging. Burning likely reduced competition allowing white pine regeneration, while logging promoted coppice reproduction of brush and consequently reduced the presence of white pine overall.

Our results suggest that prescribed burning may be an effective tool to regenerate white pine if it inhibits competition for at least 10 years after the burn. The success of prescribed burning, however, will depend on the severity of the burn. Prescribed

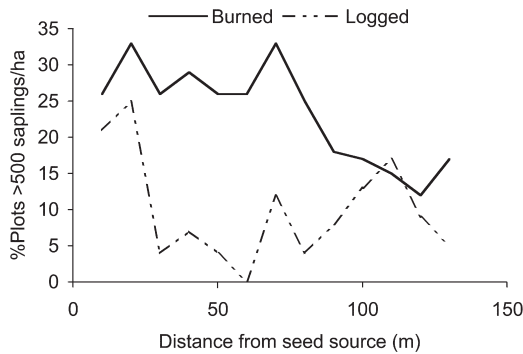


Fig. 7. Percent of plots with greater than 500 saplings/ha by distance and disturbance history for site 21–28 years after disturbance.

fires are often less severe than wildfires because the latter usually occur during droughts that are conducive to high severity, while the former are conducted when fire weather is not so extreme for safety reasons. Single low-severity prescribed burns often promote brush that competes with white pine, but repeated burning can reduce shrub densities significantly (Van Wagner 1963, Buckman 1964, Methven 1973, Methven and Murray 1974, Van Wagner and Methven 1978, Olson and Weyrick 1987, McRae et al. 1994).

The distance from a white pine seed source is an important consideration to the implementation of cutting or burning operations with expectations for white pine regeneration. On a landscape scale, subtle differences in white pine recruitment with distance can lead to dramatic long-term differences. To underscore this point we used our data to estimate how efficiently refuges, with an adequate white pine seed source of 25 m² / ha (equivalent to the average among the refuges in this study), would reforest a disturbed landscape with white pine. We will assume that a 25% chance of attaining a density of 500 saplings/ha for each 78 m² area (the size of one of our sapling regeneration plots) as adequate stocking to achieve a future stand of white pine. This stocking was achieved up to 80 m from a refuge for burned plots but only up to 20 m for logged plots by about 25 years after disturbance (Fig. 7). With these parameters, about 68% of a 1 km² area would be stocked by 25 years after disturbance if 10, 1-ha remnants of forest were left after fire,

but only 20% would be so stocked 25 years after logging. From another point of view, to achieve a fully stocked, 1 km² landscape within 25 years, about 15, 1-ha remnants would have to be left after fire, but 51 such remnants would have to be left after logging.

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