Thinning in mature eastern white pine: 43-year case study

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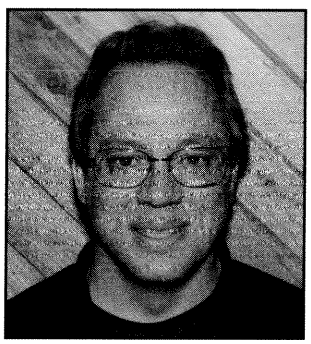
A white pine (*Pinus strobus* L.) stand at the western margin of the species range, approximately 125 years of age at present, was thinned in 1953 from 33.5 m^2 ha^{-1} to target residual basal areas of 18.4, 23.0, 27.5, and 32.1 m^2 ha^{-1}. Repeated measurement over the following 43-years indicated that the greatest total volume production and the greatest number of large diameter trees occurred in the unit of highest residual density. Over time, the distribution of stems was predominantly random although mortality between 1979 and 1996 resulted in a tendency for clumping in the 23.0 and 27.5 m^2 ha^{-1} treatments. DNA analysis indicated that thinning intensity had little effect on the genetic diversity of residual white pine. This study suggests that mature white pine stands in northern Minnesota may be managed at relatively high densities without loss of productivity. However, regardless of overstory density, there was little or no white pine regeneration occurring in this stand.

Key words: thinning, growth, genetic diversity, molecular markers, spatial pattern, regeneration

Un peuplement de pin blanc (*Pinus strobus* L.) stand à la limite occidentale de la distribution de l'espèce, âgé actuellement d'environ 125 ans, a été éclairci en 1953 passant de 33,5 m^2 ha^{-1} à des surfaces terrières résiduelles visées de 18,4, 23,0, 27.5 et de 32,1 m^2 ha^{-1}. Le remesurage répété effectué au cours des 43 années suivantes a indiqué que la plus importante production en terme de volume et le plus fort nombre d'arbres de gros diamètre sont survenus sur le site à la densité résiduelle était la plus forte. Au cours de cette période, la distribution des tiges a été principalement aléatoire même si la mortalité entre 1979 et 1996 a entraîné une tendance au regroupement dans les sites traités à 23,0 et 27,5 m^2 ha^{-1}. L'analyse de l'AND a démontré que l'intensité de l'éclaircie a eu peu d'effet sur la diversité génétique des pins blancs résiduels. Cette étude laisse entendre que les pinèdes blanches à maturité du nord du Minnesota pourraient être aménagées à des densités relativement élevées sans perte de productivité. Cependant, peu importe la densité du couvert forestier, il y a eu peu ou pas de régénération pour le pin blanc de ce peuplement.

Mots-clés : éclaircie, croissance, diversité génétique, marqueurs moléculaires, distribution spatiale, régénération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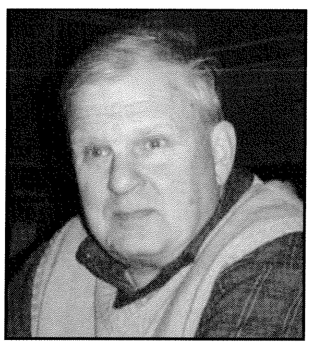
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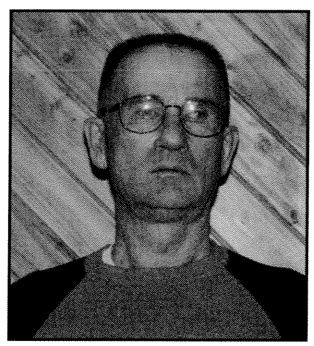
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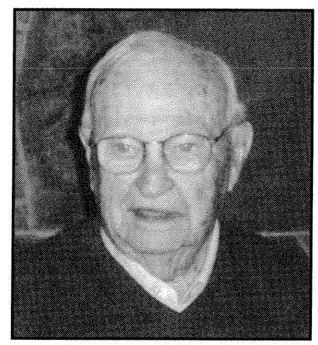
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Introduction

Interest in white pine (*Pinus strobus* L.) in Minnesota is greater now than it has been for several decades, perhaps since the presettlement forests were being exploited at the beginning of this century. Its importance as a component of Minnesota forests had always been recognized, but because of blister rust (*Cronartium ribicola* Fisch.) and white pine weevil (*Pissodes strobi* Peck), white pine was more or less ignored as a management option (Stine and Baughman 1992, White Pine Regeneration Strategies Work Group 1996, Chippewa National Forest 1997, Rajala 1998). Because of these problems, there was little formal research conducted on stand growth and development and little effort to encourage natural regeneration or artificially regenerate the species, at least relative to red pine, which was established on several hundred thousand hectares in the northern Great Lakes region.

Long-term information on white pine stand development is not readily available. In this paper, we report on some aspects of the development of thinned white pine stands over a 43-year period. Early results from this study were reported by Buckman and Zasada (1960) and by Schlaegel (1971). At the time the study began, this stand was dominated by white pine and this dominance has been accentuated by the thinning treatments. In its present condition, the overstory is essentially pure white pine. This stand represents the least common condition for white pine in Minnesota (White Pine Regeneration Strategies Work Group 1996). On the Chippewa National Forest, the white pine type occupies about 2200 ha and 32% of the stands are greater than 100 years old (Chippewa National Forest1997).

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Materials and Methods

Study Site

The study site is located on the Pike Bay Experimental Forest, Chippewa National Forest near Cass Lake, Minnesota (lat. 47° 25′ N, long 94° 30′ W). The white pine appears to be essentially even-aged and about 125 years old; however there are scattered individual red pines that are 170 to 200 years old and there may be older white pines. The largest white pine in the study area (89 cm dbh, 38 m tall) is 125 years old. Prior to thinning, the stand was 91% white pine by basal area with a minor amount of red pine (*Pinus resinosa* Ait.); hardwoods were present throughout the area but were generally in the intermediate or suppressed crown classes. The site is on the Guthrie till plain in land type 45 (described as fire-dependent mixed pine-hardwood) phase of the Chippewa National Forest ecosystem classification system (Shadis *et al.* 1995). Buckman and Zasada (1960) reported that the apparent site index was 17 m (base age 50). They stated that the pine developed under an aspen overstory (release occurred in 1934 at about age 60) and site index may be somewhat higher. Site index for aspen on these sites is generally 21 to 24 m (base age 50 years). These sites are among the most productive for aspen in northern Minnesota.

Although forests of the Guthrie till plain were historically mixed pine–northern hardwood types, much of this forest area converted to aspen following extensive logging in the early twentieth century. On the Pike Bay Experimental Forest, white pine has persisted in small stands surrounded predominantly by aspen stands, and a lesser number of small northern hardwood stands. The study described here was conducted in the largest mature stand of white pine on the experimental forest. The nearest stand of mature white pine is located approximately 0.8 km south of the study site.

Thinning Treatments and Vegetation Measurements

Permanent plots were established in 1953 before the first thinning. The stand was divided into four blocks, each approximately 2.4 ha. Within each block, six to eight 0.08 ha plots were established (Buckman and Zasada 1960, Schlaegel 1971). A map showing the location of each tree was developed for each plot when the study was established in 1953; these maps were used to identify trees in subsequent remeasurements (e.g., Fig. 1). Prior to 1996 only trees 8.9 cm dbh (diameter at 1.37 m) and greater were measured and mapped at each remeasurement.

Four residual basal area treatments, 18.4, 23.0, 27.5, and 32.1 $m^2 ha^{-1}$ (referred to subsequently as 18, 23, 28, and 32 treatments), were randomly assigned to each of the four blocks. There was no control and the treatments were not replicated, but the six to eight measurement plots in each treatment provided an estimate of stand-level variation within each treatment. The first thinning occurred in 1954 with subsequent thinnings to assigned basal areas in 1959 and1964. Thinning was mainly from below. Treatments were not maintained between 1964 and 1996 (Buckman and Zasada 1960, Schlaegel 1971).

The plots were measured every five years from 1954 to 1979 and in 1996. Trees removed by harvesting and those dying from undetermined natural causes were recorded. At each remeasurement, dbh was determined at a permanently marked height of 1.37 m, and total height of three to five of the tallest trees estimated with an abney level or clinometer. In late fall of 1997, total height, height to base of live crown, and height to top of live crown of all white pine was measured with a laser range finder (Impulse Laser Hypsometer, Laser Tech, Inc.).

During 1996–97, understory density and composition were determined. Ingrowth trees (stems greater than 8.9 cm dbh) were mapped and advanced regeneration (stems greater than 2.5 cm but less than 8.9 cm dbh) was tallied by species on each 0.08-ha plot. Seedling density was characterized in two ways. First, the number of trees less than 2.5 cm dbh but greater than 1.37 m tall were tallied by species on each 0.08 ha plot. In addition, the number of tree seedlings less than 2.5 cm dbh but greater than 15 cm tall and shrubs greater than 15 cm tall were tallied by species on four 0.0005 ha subplots within each 0.08-ha plot.

The spatial arrangement of white pine in each plot was reconstructed from the original 1953 stem location maps and subsequent inventories in 1954, 1959, 1964, 1969, 1974, and 1996. For each thinning treatment, the spatial pattern of the overstory stems was characterized using Distance Index of Dispersion (*ID*; Johnson and Zimmer 1985, Ludwig and Reynolds 1988). For each treatment and inventory, *ID* was estimated from 30 to 32 random point-to-nearest individual distances. *ID* is based on the ratio between the sum of squared nearest neighbour distances and the sum of nearest neighbour distances. Compared to several other simple point-to-nearest neighbour or individual-to-nearest neighbour dispersion indices, *ID* tends to be more powerful and is independent of stand density (Ludwig and Reynolds 1988). Expected values of *ID* for random patterns is 2 while clumped patterns have values in excess of 2 and uniform patterns have values less than 2. The significance of departures from randomness was determined from a z-test statistic, as compared to the standard normal distribution.

Genetic Characterization

In the winter of 1999, dormant bud samples were collected from three mature white pines on each of five plots within each of the four thinning units. DNA was extracted from these buds and used to genotype the individuals using genetic markers (seven simple sequence repeat, SSR, loci) according to procedures of Echt *et al.* (1996). Genetic diversity was characterized for each treatment and over all treatments by calculation of allele frequencies for the seven marker loci. Genetic diversity was measured in terms of the number of polymorphic loci, the total number of alleles and the mean number of alleles per locus, and average heterozygosity. Allele frequencies and diversity parameters were calculated using POPGENE Version 1.31 software (Yeh *et al.* 1999).

Analyses

We present means and standard deviations for the plot means within each treatment for each morphological variable. Frequency of occurrence estimates are calculated as the proportion of the total number of sampled plots on which a species occurred. The diameter and height distributions for the white pine overstory are presented; these 0.08-ha plots covered a combined area of 0.49 to 0.65 ha or between 20 to 25% of the stand area for each treatment and represented 17 to 25% of the estimated number of trees in each treatment.

Results

White Pine Growth and Development Response to Thinning

Prior to establishment of the treatments (stand age about 80 years), average stand density (all species) varied from 556 to

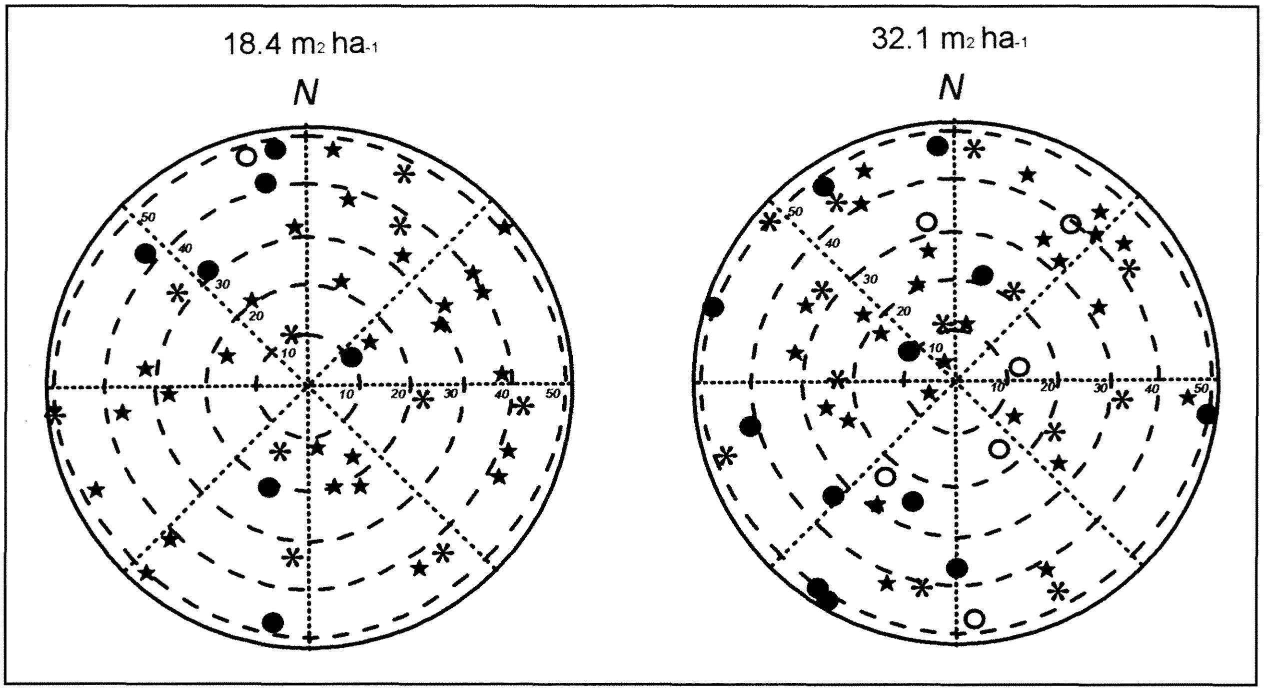

Fig. 1. Examples of stem maps available for each of the 28, 0.08-hectare plots in the study area. Distances along radial axes are in feet (the original units of measurement). Symbols indicate the following: ∗ living crop trees in1996; ★ trees removed in thinnings; ○ dead from natural causes; ● hardwoods removed in 1954 thinning. The basal area in 1953, before thinning, for the 18 treatment was 34.0 m^2 ha^{-1} and in 1996 it was 31.7 m^2 ha^{-1}. For the 32 treatment, the basal area in 1953, prior to thinning, was 41.1 m^2 ha^{-1} and in 1996 it was 45.0 m^2 ha^{-1}. The 1953 stand includes all of the symbols. The 1996 stand is represented by the crop tree symbols.

656 trees/ha (Table 1). White pine comprised more than 85% of the initial basal area with red pine contributing 3 to 11% and various northern hardwoods contributing 2 to 10%. The initial low thinning in 1954 removed the hardwood tree component and most of the red pine component, leaving stands comprised almost exclusively of white pine (Table 2). In total, the three thinnings removed on average 78, 71, 68, and 62% of the pretreatment stand in the 18, 23, 28, and 32 treatments respectively. Mortality, over the 43-year study tended to be less in the 18 (5%) treatment than in the 23 (9%), 28 (9%), and 32 (9%) treatments. Average density in 1996 ranged from 102 to 195 trees/ha (Table 1), representing 17, 20, 23, and 30%, respectively, of the 1953 density for the 18, 23, 28, and 32 treatments. There was essentially no white pine ingrowth from trees < 8.9 cm over the study period.

Average white pine diameter in 1996 varied among treatments from 52 to 62 cm and was 132, 96, 108, and 109% greater than the average diameter in 1953 before the first thinning for the 18, 23, 28, and 32 treatments, respectively (Table 1). The diameter distribution for each density before thinning, after the first thinning and in 1996 is shown in Fig. 2. Note that prior to the first thinning, less than 1% of the trees were greater than 60 cm, while more than 80% of the trees were less than 38 cm. (Fig. 2). In 1996, trees 76 cm or larger in diameter occurred in all treatments except 28. The greatest number of trees 60 cm or larger dbh occurred in the 32 treatment (59 per hectare compared to 53, 44, and 58 per hectare in the 18, 23, and 28 treatments, respectively). Trees 60 cm or greater dbh comprised 57, 37, 41, and 31% of all trees in the 18, 23, 28, and 32 treatments, respectively (Fig. 2).

The assigned basal areas were maintained by the three thinnings mentioned above. From 1964 (following the last thinning) through 1996, the net increase in basal area, as a per cent of the average basal area after thinning in 1964, was 53, 40, 31, and 41% for the 18, 23, 28, and 32 treatments, respectively (Table 1). Average basal area growth for the 32-year period was 0.31, 0.28, 0.26, and 0.40 m^2 ha^{-1} y^{-1} for the 18, 23, 28, and 32 treatments respectively; maximum basal area growth for individual plots in these treatments was 0.40, 0.57, 0.37 and 0.60 m^2 ha^{-1} y^{-1}. Because of the variation in mortality, there was a substantial difference among the plots in both total basal area and basal area growth (Table 1), this was particularly true in the 28 treatment where blow-down significantly affected two plots; there was no blow-down in the other plots.

The total gross volume removed in three thinnings ranged from approximately 125 m^3 ha^{-1} in the 32 treatment to 202 m^3 ha^{-1} in the 18 treatment (Table 3). As expected, the volume removed in the 1953 thinning was greatest in the 18 treatment and least in the 32 treatment as the different residual basal areas were established (Table 3). Gross volume yield of the 1959 and 1964 thinnings were less than those of 1953 and more similar among treatments. However, between 1979 and 1996, the greatest volume production occurred in the 28 and 32 treatments (Table 3). The potential gross volume production (total volume removed in thinning plus the 1996 standing volume) was increased with increasing residual density from 526 m^3 ha^{-1} for the 18 treatment to 707 m^3 ha^{-1} for the (38 400 to 51 500 bf ac^{-1}, respectively). Volume production relationships were similar when calculated as cubic meters per hectare (the total main stem) or board feet per acre (the main stem to a 15 cm top diameter) (Table 3).

Table 1. Stand density, diameter and basal area of thinned mature white pine stands in the Pike Bay Experimental Forest. Values are means, standard deviations, and ranges of n = 6 to 8, 0.08-hectare plots per treatment unit

		$18\ m^2\ ha^{-1}$			$23\ m^2\ ha^{-1}$			$28\ m^2\ ha^{-1}$			$32\ m^2\ ha^{-1}$		
Year	**Thin**	**Mean**	**S.D.**	**Range**	**Mean**	**S.D.**	**Range**	**Mean**	**S.D.**	**Range**	**Mean**	**S.D.**	**Range**
					Stand Density (Number of Trees per Hectare)								
1953	Before	556	(59)	457 – 642	614	(110)	482 – 791	623	(136)	420 – 778	656	(96)	507 – 766
	After	185	(21)	161 – 210	261	(32)	210 – 309	297	(32)	259 – 346	391	(78)	272 – 469
1954		185	(19)	161 – 210	261	(32)	210 – 309	297	(32)	259 – 346	388	(75)	272 – 469
1959	Before	184	(24)	148 – 210	259	(35)	210 – 309	299	(29)	272 – 346	386	(75)	272 – 481
	After	139	(18)	111 – 161	203	(19)	173 – 235	243	(48)	185 –321	297	(55)	222 – 383
1964	Before	139	(18)	111 – 161	198	(17)	173 – 222	257	(53)	185 – 334	293	(54)	222 – 395
	After	115	(14)	99 – 136	162	(24)	124 – 198	192	(37)	148 – 247	235	(44)	173 – 321
1969		115	(14)	99 – 136	162	(24)	124 – 198	192	(37)	148 – 247	224	(31)	173 – 272
1974		111	(17)	86 – 136	161	(23)	124 – 198	183	(31)	148 – 222	212	(30)	173 – 272
1979		102	(15)	86 – 124	155	(22)	124 – 198	171	(37)	124 – 222	208	(32)	173 – 272
1996		94	(20)	62 – 124	131	(16)	111 – 148	144	(36)	86 – 185	195	(39)	161 – 272
					Diameter Breast Height (Centimetres)								
1953	Before	26.7	(1.0)	25.4 – 28.4	26.3	(1.2)	24.0 – 27.6	26.6	(2.1)	24.0 – 30.2	25.5	(1.7)	23.6 – 28.5
	After	34.3	(2.3)	31.1 – 37.2	32.6	(1.8)	31.1 – 36.0	33.7	(1.7)	31.3 – 35.9	31.4	(4.0)	26.2 – 37.4
1954		35.4	(1.9)	33.5 – 38.2	32.9	(1.8)	31.5 – 36.5	34.2	(1.9)	31.4 – 36.4	31.7	(3.7)	27.5 – 37.2
1959	Before	38.7	(2.2)	36.7 – 42.4	35.6	(1.7)	34.3 – 39.1	36.2	(1.8)	33.4 – 38.8	33.8	(4.1)	28.1 – 39.7
	After	40.0	(2.4)	36.8 – 43.0	37.7	(1.7)	35.9 – 41.1	38.2	(3.5)	33.5 – 42.7	36.6	(3.6)	31.5 – 42.3
1964	Before	43.5	(2.3)	40.9 – 46.9	40.7	(1.7)	38.5 – 43.7	38.9	(4.9)	31.7 – 45.9	39.2	(3.9)	33.5 – 45.0
	After	45.0	(2.2)	41.4 – 47.1	41.9	(2.3)	38.4 – 45.2	42.5	(4.1)	36.9 – 47.4	41.4	(4.2)	34.8 – 47.8
1969		47.6	(2.2)	44.1 – 50.0	44.3	(2.6)	40.3 – 48.1	44.7	(4.3)	38.7 – 49.8	43.2	(4.2)	37.8 – 49.9
1974		50.1	(2.5)	45.8 – 52.3	46.4	(2.6)	42.1 – 50.4	46.7	(4.3)	40.9 – 51.4	45.5	(4.4)	39.4 – 51.6
1979		52.7	(2.4)	49.5 – 55.2	48.3	(2.7)	43.7 – 52.3	49.0	(4.8)	42.6 – 53.8	46.9	(4.5)	40.8 – 53.0
1996		61.9	(2.7)	57.5 – 64.7	51.5	(10.8)	28.8 – 62.3	55.4	(3.4)	51.2 – 59.6	53.3	(4.3)	47.2 – 59.6
					Basal Area (Metres Squared per Hectare)								
1953	Before	34.7	(2.3)	32.1 – 37.6	37.0	(4.2)	30.9 – 42.3	38.0	(2.9)	33.4 – 41.2	39.4	(3.7)	35.0 – 44.6
	After	17.8	(0.5)	16.7 – 18.4	22.4	(1.1)	21.1 – 24.2	27.3	(0.5)	26.5 – 27.8	31.9	(0.9)	30.0 – 33.0
1954		18.8	(0.3)	18.4 – 19.3	22.8	(1.1)	21.7 – 24.9	28.0	(0.8)	26.9 – 29.1	32.2	(0.7)	30.9 – 32.8
1959	Before	22.1	(0.8)	21.5 – 23.4	26.8	(1.8)	24.6 – 29.8	32.2	(1.8)	29.1 – 33.8	36.6	(1.1)	35.0 – 38.1
	After	17.9	(1.1)	16.2 – 18.8	23.1	(0.6)	22.5 – 24.2	28.2	(0.8)	27.4 – 29.2	32.3	(0.5)	31.4 – 32.8
1964	Before	21.1	(1.1)	19.7 – 22.0	26.3	(0.5)	25.6 – 26.7	31.9	(1.3)	30.1 – 34.1	36.5	(0.9)	34.9 – 37.6
	After	18.5	(0.6)	17.5 – 18.9	22.5	(1.1)	20.2 – 23.4	27.3	(0.3)	26.9 – 27.7	32.2	(0.6)	30.8 – 33.0
1969		20.6	(0.8)	19.4 – 21.5	25.2	(1.2)	22.9 – 26.4	30.1	(0.3)	29.7 – 30.6	33.9	(1.8)	30.4 – 35.7
1974		22.1	(1.8)	18.8 – 24.2	27.4	(1.2)	25.2 – 28.7	31.6	(0.9)	30.1 – 32.6	35.2	(3.0)	28.4 – 38.6
1979		22.6	(2.6)	19.5 – 26.6	28.8	(1.5)	26.9 – 30.5	32.1	(1.9)	28.5 – 33.7	36.9	(3.0)	30.5 – 39.7
1996		28.3	(4.2)	19.8 – 33.0	31.4	(6.3)	21.1 – 38.6	35.7	(6.1)	24.0 – 39.5	45.1	(5.6)	33.6 – 51.5

Table 2. Overstory species composition prior to initial thinning, following the first thinning, and 43-years post-initial thinning

		Percent of Total Basal Area			
Year	**Species**	$18\ m^2\ ha^{-1}$	$23\ m^2\ ha^{-1}$	$28\ m^2\ ha^{-1}$	$32\ m^2\ ha^{-1}$
1953	White pine	90.8	85.8	90.0	86.7
	Red pine	7.1	11.1	3.8	3.4
	*Others	2.1	3.1	6.2	9.9
1954 (After-thin)	White pine	100.0	97.0	100.0	100.0
	Red pine	0.0	3.0	0.0	0.0
	Others	0.0	0.0	0.0	0.0
1996	White pine	100.0	100.0	100.0	100.0
	Red pine	0.0	0.0	0.0	0.0
	Others	0.0	0.0	0.0	0.0

*Other species include trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* L.), red maple (*A. rubrum* L.), red oak (*Quercus rubra* L.), elm (*Ulmus americana* L.), black ash (*F. nigra* Marsh.), basswood (*T. americana* L.), and white spruce (*Picea glauca* (Moench) Voss).

Throughout the study, white pine occupied dominant and co-dominant canopy positions in all the treatments. By 1996, crown condition varied greatly as white pine tree heights ranged from 5.1 to 38.7 m and live crown ratios ranged from 1 to 91%, but differences among treatment means were slight (Fig. 3 and Table 4). Damage to crowns from white pine blister rust, lightening strikes, and other climatic and biological agents were evident as spiked (lacking foliage in terminal portion of crown), broken, or forked crowns on approximately 16% of the standing live white pine. Stand density effects on crown damage were not apparent as the percent of trees with obvious crown damage was 21, 14, 16, and 17%, for the 18, 23, 28, and 32 treatments, respectively (Table 4).

Spatial pattern of the white pine stems changed over time (Fig. 4). Prior to the initial thinning, stems in all treatments were distributed randomly. Thinning in 1959 resulted in a clumped

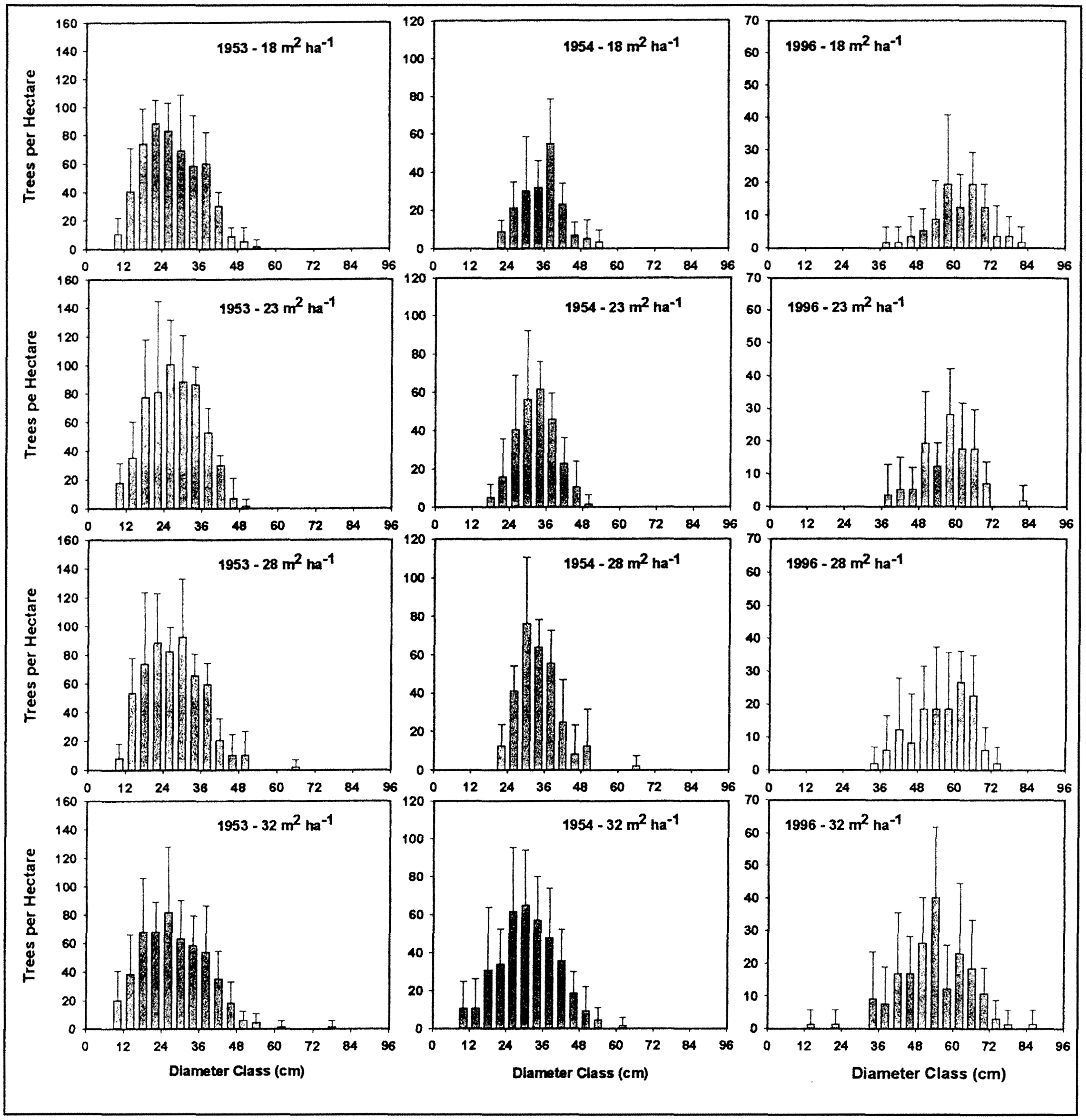

Fig. 2. Mean density of white pine by dbh class in 1953 before the first thinning, in 1954 after the first thinning, and in 1996 for units thinned to target residual basal areas of 18.4, 23.0, 27.5, and 32.1 m2 ha–1 in1954, 1959, and 1964. Values are means ± 1 standard deviation for n = 6-to-8 plots per treatment.

distribution in the 18 treatment; following the subsequent thinning in 1964 the stand reverted to a random pattern that was maintained through 1996. Although demonstrating a random pattern from 1953 through 1979, subsequent mortality in the 23 treatment resulted in a clumped pattern in 1996. Following the initial thinning, stems in the 28 treatment were uniformly distributed and remained so through 1964. Subsequently, the distribution of stems in the 28 treatment transformed to a random pattern through 1979 and a clumped pattern by 1996.

Understory Composition

Although the overstory species composition was biased towards pure white pine by thinning from below, understory species diversity was evident in 1996 as ingrowth and advanced tree regeneration measured 1.37 m above the ground, and as seedling and shrub cover measured 15 cm above the ground. Ingrowth (trees > 8.9 cm dbh) density ranged from 156 to 511 stems per hectare with the density of the 18 treatment being two to three times greater than that of the other treatments (Table 5).

Table 3. White pine gross volume* production in cubic meters per hectare and Scribner board feet per acre including yield from thinnings, loss to mortality, and standing volume in 1996. Values are means (± standard deviation) of n = 6-8, 0.08-hectare plots per treatment unit

		18 m^2 ha^{-1}		23 m^2 ha^{-1}		**28 m^2 ha^{-1}		32 m^2 ha^{-1}	
Year		m^3 ha^{-1}	bf ac^{-1}	m^3 ha^{-1}	bf ac^{-1}	m^3 ha^{-1}	bf ac^{-1}	m^3 ha^{-1}	bf ac^{-1}
1953	Mean	136.6	9960	103.6	7550	84.5	6160	42.0	3047
Thinning	S.D.	(28.9)	(2111)	(47.4)	(3456)	(27.7)	(2003)	(29.7)	(2173)
1959	Mean	41.7	3031	34.4	2516	37.7	2756	39.3	2861
Thinning	S.D.	(12.4)	(902)	(21.2)	(1528)	(18.7)	(1355)	(17.9)	(1297)
1964	Mean	24.1	1757	39.1	2855	43.3	3169	44.0	3207
Thinning	S.D.	(8.7)	(640)	(12.1)	(872)	(9.3)	(653)	(6.8)	(486)
1996	Mean	324.0	23630	391.7	28560	470.3	34290	581.8	42410
Standing	S.D.	(81.6)	(5951)	(108.5)	(7931)	(75.6)	(5498)	(75.8)	(5514)
1953-96	Mean	134.1	685	282.9	1443	267.0	1362	204.0	1041
Mortality	S.D.	(91.3)	(465.2)	(161.9)	(826)	(119.7)	(612)	(173)	(884)
Total	Mean	660.4	39060	851.7	42930	903.0	47740	910.8	52560
	S.D.	(159.7)	(8846)	(137.6)	(7390)	(54.0)	(5300)	(96.3)	(7152)

*Volume estimated according to Buckman (1962): board feet (main stem to a 15-cm top) = 2.084(basal area × height); cubic feet (total main stem) = 0.4085(basal area × height); cubic meters = cubic feet × 0.0283

**Does not include two plots having extensive wind throw.

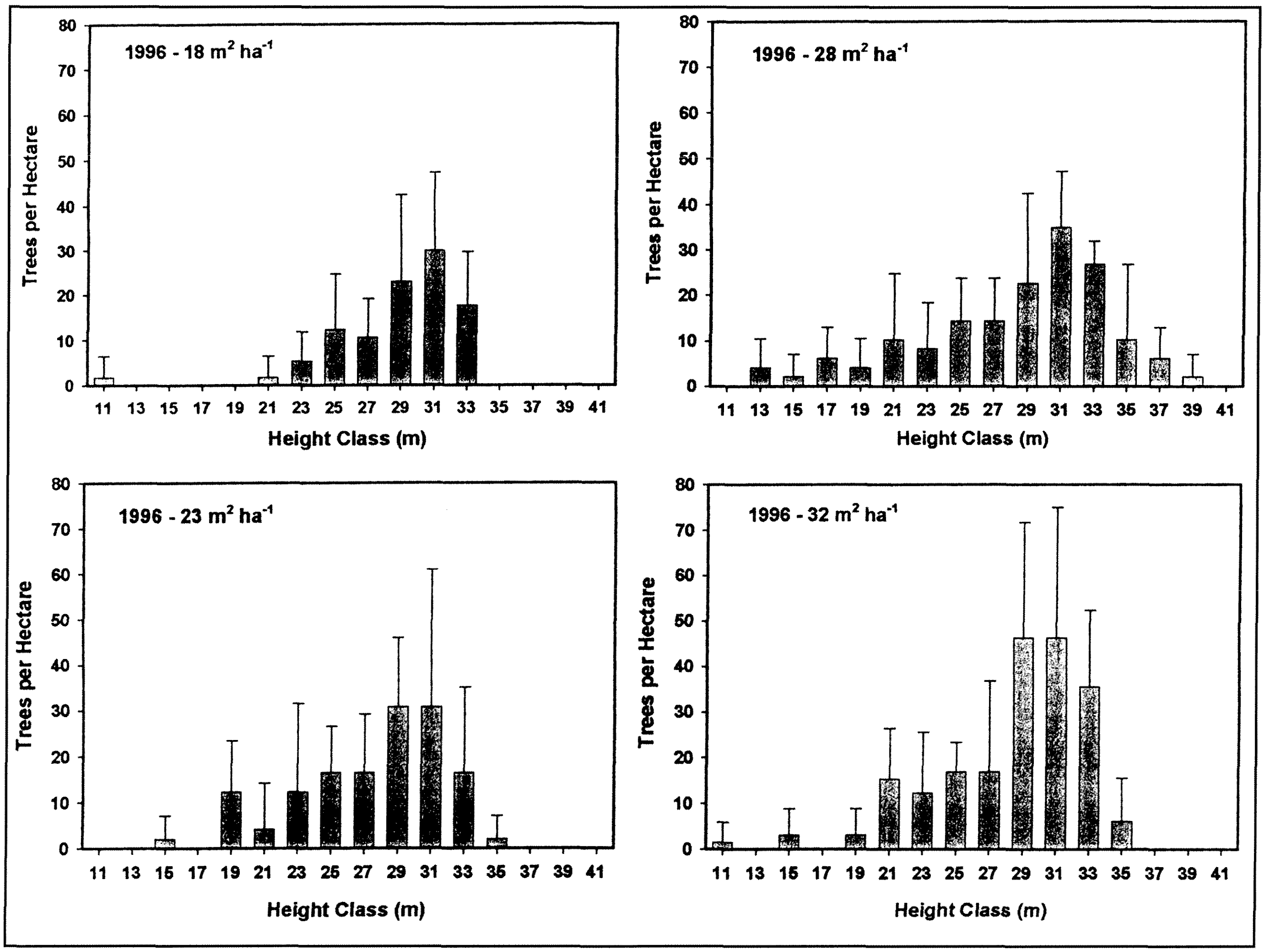

Fig. 3. Mean density of white pine by height class in 1996 for units thinned to target residual basal areas of 18.1, 23.0, 27.5, and 32.1 m^2 ha^{-1} in1954, 1959, and 1964. Values are means ± 1 standard deviation for n = 6-to-8 plots per treatment.

Table 4. 1996 canopy and crown characteristics of white pine in the Pike Bay Experimental Forest thinned to four density levels. Values are means and standard deviations for n = 6-8, 0.08-hectare plots per treatment

Density Treatment	Tree Height (m)		Live Crown Ratio (%)		Damaged Crowns (%)		Standing Dead Trees (%)	
(m^2 ha^{-1})	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
18	29.2	(2.1)	51.9	(11.4)	20.8	(12.1)	10.2	(6.0)
23	28.3	(4.4)	50.7	(19.1)	14.1	(8.8)	8.6	(4.8)
**28	29.6	(6.2)	48.3	(16.1)	15.9	(9.9)	14.8	(7.1)
32	28.8	(4.9)	55.2	(19.2)	16.5	(8.3)	9.7	(6.4)

*Height, Live Crown Ratio, and Damage estimates are for live trees; Standing Dead estimates are percentages of the total live and dead standing stems.
**Does not include two plots having extensive wind throw.

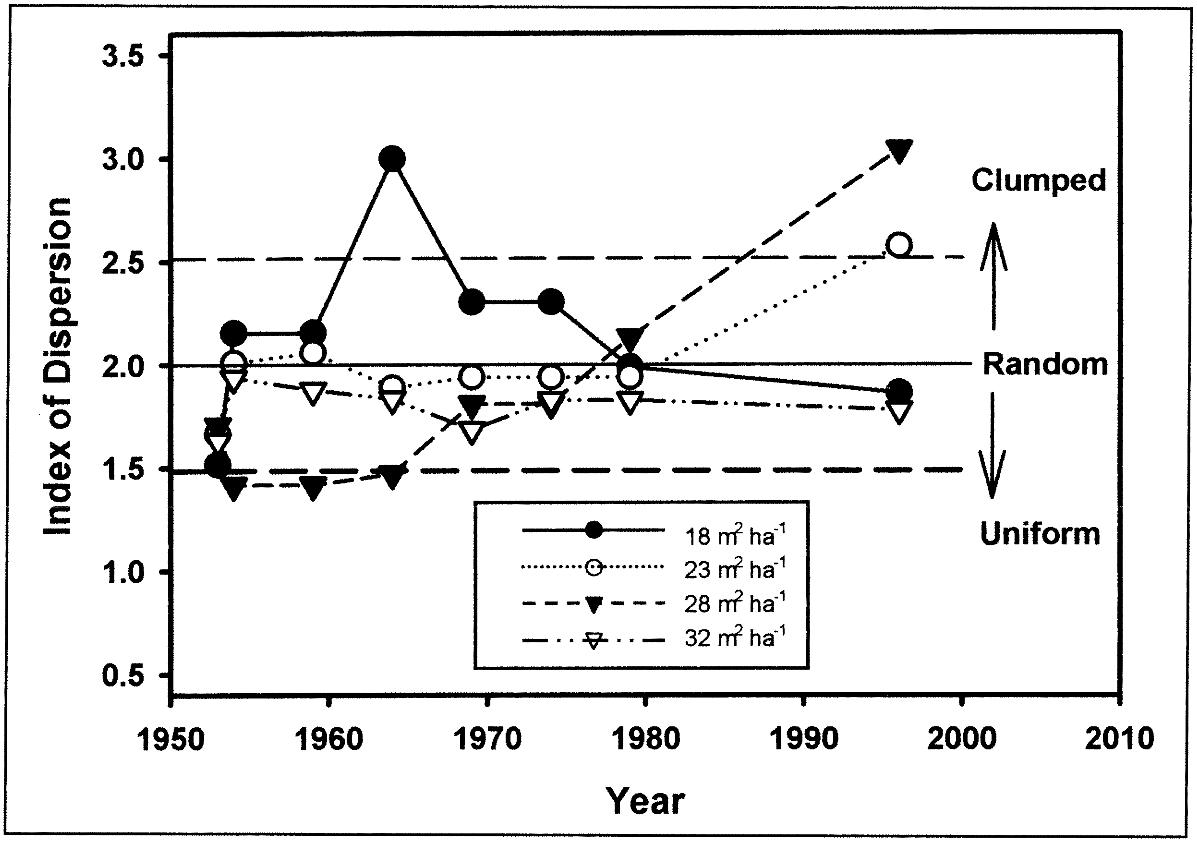

Fig. 4. Temporal variation in the spatial pattern of white pine thinned to target residual basal areas of 18.4, 23.0, 27.5, and 32.1 m^2 ha^{-1} in1954, 1959, and 1964. Index of dispersion (*ID*) values near 2 indicate a random spatial arrangement; values significantly in excess of 2 indicate a clumped arrangement and values significantly less than 2 indicate a uniform arrangement. The horizontal dashed lines indicate $p = 0.05$ thresholds for significant departure from randomness.

Red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), and basswood (*Tilia americana* L.) were the most common species, accounting for 76% of the ingrowth stems across all treatments.

Advanced regeneration (trees 2.5 to 8.9 cm dbh) density was fairly uniform across treatments, ranging from 1280 to 1920 stems per hectare (Table 5). Red maple and sugar maple dominated, accounting for 77, 57, 70, and 39% of the advanced regeneration stems in the 18, 23, 28, and 32 treatments, respectively. Although accounting for only about 9% of the density, bur oak (*Quercus macrocarpa* Michx.) was present at 64% of the sample locations across all treatments. In the 23, 28 and 32 treatments, black ash (*Fraxinus nigra* Marsh.) accounted for 17, 10 and 16% of the advanced regeneration (Table 5).

The density of seedlings less than 2.5 cm dbh and greater than 1.37 m tall was less than the density of advanced regeneration (Table 6). Only the 18 treatment had a substantial number (447 per hectare) and 95% of these were either red maple or sugar maple. Densities in the 23, 28 and 32 treatments were only 42, 111, and 47 stems per hectare (Table 6). In contrast, the densities of tree seedlings less than 2.5 cm dbh and greater than 15 cm tall was approximately 11 570, 4750, 2950, and 7000 trees per acre for the 18, 23, 28, and 32 treatments respectively (Table 6). As with advanced regeneration, red maple and sugar maple were the most common tree species accounting for 50 to 79% of tree seedlings greater than 15 cm tall. Shrub densities were 13 220, 24 830, 22 525, and 15 290 stems per hectare for the 18, 23, 28, and 32

Table 5. **Density and stocking of ingrowth (>8.9 cm DBH) and advanced regeneration (2.5-8.9 cm DBH). Densities are means ± (standard deviation) over all 0.08-hectare plots per thinning treatment (n = 6 to 8). Frequency values represent the percentage of 0.08-hectare plots or 0.0005-hectare quadrants on which ingrowth and advanced regeneration, respectively, occurred**

	18 m^2 ha^{-1}			23 m^2 ha^{-1}			28 m^2 ha^{-1}			32 m^2 ha^{-1}			All		
	Density (trees/ha)		Frequency	Density (trees/ha)		Frequency	Density (trees/ha)		Frequency	Density (trees/ha)		Frequency	Density (trees/ha)		Frequency
Species	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)
							Ingrowth (>8.9 cm DBH)								
F. nigra	0	(0)	0	20	(40)	33	7	(20)	17	25	(30)	50	15	(15)	26
T. americana	67	(77)	86	5	(10)	17	74	(99)	100	77	(54)	75	57	(57)	70
Q. macrocarpa	2	(10)	14	12	(30)	17	20	(20)	67	0	(0)	0	7	(12)	22
U. americana	2	(10)	14	7	(12)	33	17	(30)	33	15	(17)	50	10	(20)	33
Ostrya virginiana	7	(20)	14	0	(0)	0	5	(10)	17	0	(0)	0	2	(12)	7
B. papyrifera	20	(12)	57	12	(15)	50	7	(12)	33	12	(27)	25	12	(17)	41
A. rubrum	245	(96)	100	86	(59)	83	69	(62)	83	15	(17)	50	104	(114)	78
Q. rubra	49	(62)	57	25	(32)	50	12	(20)	33	32	(10)	13	22	(42)	37
A. saccharum	124	(54)	100	54	(30)	83	49	(47)	67	7	(12)	25	57	(59)	67
All	511	(168)	100	227	(143)	100	264	(128)	100	156	(67)	100	287	(195)	100
							Advanced Regeneration (2.5–8.9 cm DBH)								
F. nigra	32	(64)	14	222	(413)	50	128	(264)	33	225	(267)	72	153	(272)	44
T. americana	64	(47)	32	12	(20)	8	74	(158)	25	109	(94)	53	67	(94)	32
Prunus sp.	0	(0)	0	37	(27)	29	5	(10)	4	20	(22)	16	15	(22)	12
Q. macrocarpa	146	(69)	79	166	(64)	83	94	(72)	50	138	(173)	47	136	(106)	64
U. americana	0	(0)	0	20	(40)	13	30	(47)	17	111	(128)	47	44	(86)	20
O. virginiana	82	(72)	36	0	(0)	0	12	(30)	8	15	(44)	6	30	(54)	13
A. spicatum	0	(0)	0	74	(183)	17	12	(20)	8	217	(299)	50	84	(198)	20
B. papyrifera	47	(74)	11	17	(30)	17	20	(40)	13	40	(62)	28	32	(54)	18
A. rubrum	867	(361)	93	642	(366)	96	709	(178)	100	408	(257)	91	645	(334)	94
Q. rubra	77	(104)	43	12	(15)	13	7	(12)	8	10	(17)	6	27	(59)	18
A. saccharum	608	(255)	100	99	(111)	29	190	(166)	63	146	(121)	53	264	(264)	62
P. tremuloides	0	(0)	0	5	(10)	4	0	(0)	0	0	(0)	0	1	(5)	1
All	1920	(641)	100	1305	(716)	100	1281	(483)	100	1436	(472)	100	1498	(606)	100

treatments respectively (Table 6). The most common shrubs were beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*A. spicatum* Lam.) (Table 6). Although a minor amount of conifer regeneration less than 2.5 cm diameter and greater than 15 cm tall was present, there was none greater than 1.37 m tall (Table 6).

White Pine Genetic Diversity

The genetic diversity of the residual mature white pine was evaluated based on the variation in alleles present over seven marker genes (loci). White pine, as with most plant species found in the forest, is diploid; genetic conformation is coded by corresponding nucleic acid sequences (genes) located on pairs of chromosomes. Thus, for each coding region on the chromosomes of an individual tree, there are two alleles, or forms of the gene present, one each contributed by the paternal and maternal parents. The particular alleles present in a population of trees will vary with the diversity and frequency of alleles in the parental population and with other factors such as the spatial and temporal patterns of mating between individuals in the stand (mating system), and the influx of pollen and seed from other stands (gene flow). In addition, for those genes that are linked to adaptation, natural selection can influence the likelihood of tree survival under the environmental and biotic stresses posed by a site, and, therefore, genetic diversity.

The total number of alleles observed across the seven genes ranged from 26 to 31 among thinning treatments (Tables 7 and 8). Over the trees sampled in all treatments, the total number of observed alleles was 39. Thus, none of the individual thinning treatments contained all the alleles present in the population. The average number of alleles present per locus ranged from 3.7 to 4.4 among treatments and averaged 5.6 across all treatments (Table 8). When adjustments are made for departures of the observed allele frequencies from theoretical expected frequencies, the resulting "effective" number of alleles per locus (Hartl and Clark 1989) ranged from 2.1 to 2.4 among treatments and was 2.3 for the population at large (Table 8). Heterozygosity, the proportion of genotypes having two different forms of a gene at a locus, averaged 0.43 over all treatments, and ranged from 0.41 to 0.46. The observed heterozygosity (0.48 over all treatments, and from 0.44 to 0.53 among treatments) was slightly lower than expected based on allele frequencies (Table 8). Of the alleles present, the proportion that occurred with intermediate or high frequency (greater than 0.25) was about 20% for all treatments combined but slightly greater for individual treatments (range of 32 to 36% across treatments) (Table 8). The number of unique alleles, those occurring in only one particular treatment unit, was 0, 3, 2, and 2 for the 18, 23, 28, and 32 treatments respectively.

Discussion

As a case history, this study provides a description of the changes in white pine stand characteristics resulting from planned commercial thinnings and from natural mortality. The treatments applied in this stand, including the 1934 removal of an aspen overstory for which there is no information, represent one scenario for intermediate treatments in the white pine type. The generalities that can be drawn from this study are limited because the treatments were not replicated, there was not a control, and it was confined to one ecological landtype.

The design of the study does provide insight, however, into the variation in response at the stand level and the development of the understory within each treatment. In terms of the current interest in extended rotations and the growth of large

Table 6. Density of seedlings greater than 1.37 m tall and seedlings and shrubs greater than 15 cm tall. Densities are means ± standard deviation over all 0.0005-hectare plots per thinning treatment. Frequency values represent the percentage of 0.0005-hectare plots in which the species occurred

	18 m^2 ha^{-1}			23 m^2 ha^{-1}			28 m^2 ha^{-1}			32 m^2 ha^{-1}			All		
	Density (tpa)		Frequency	Density (tpa)		Frequency	Density (tpa)		Frequency	Density (tpa)		Frequency	Density (tpa)		Frequency
Species	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)	Mean	S.D.	(%)
Seedling Regeneration (<2.5 cm DBH) greater than 1.37 m tall															
F. nigra	0	(0)	0	12	(20)	8	12	(30)	4	7	(12)	6	7	(17)	5
T. americana	17	(37)	11	0	(0)	0	5	(10)	4	10	(17)	9	7	(22)	7
Prunus sp.	0	(0)	0	0	(0)	0	5	(10)	4	2	(10)	3	2	(7)	2
Q. macrocarpa	2	(10)	4	7	(12)	8	0	(0)	0	2	(10)	3	5	(10)	4
U. americana	0	(0)	0	7	(12)	8	0	(0)	0	0	(0)	0	2	(7)	2
O. virginiana	2	(10)	4	0	(0)	0	0	(0)	0	0	(0)	0	1	(5)	1
A. spicatum	0	(0)	0	0	(0)	0	0	(0)	0	7	(17)	3	2	(10)	1
A. rubrum	114	(64)	50	12	(32)	8	54	(47)	29	10	(12)	9	47	(59)	24
A. saccharum	311	(284)	71	0	(0)	0	37	(35)	29	10	(17)	6	91	(190)	27
All	447	(297)	86	42	(67)	21	111	(69)	58	47	(40)	34	163	(230)	50
Seedling and Shrub Regeneration (<2.5 cm DBH) greater than 15 cm tall															
Viburnum rafinesquianum	287	(1181)	7	0	(0)	0	0	(0)	0	0	(0)	0	74	(610)	2
Corylus conuta	7858	(11416)	68	15417	(16934)	88	16870	(21799)	83	6874	(9434)	69	11196	(15481)	76
Vaccinium angustifolia	215	(833)	7	84	(408)	4	0	(0)	0	0	(0)	0	74	(469)	3
Diervilla lonicaera	0	(0)	0	1999	(3956)	29	1132	(3506)	17	563	(1777)	13	860	(2721)	14
Dirca palustris	0	(0)	0	166	(566)	8	0	(0)	0	126	(492)	6	74	(381)	4
A. spicatum	4500	(6877)	46	6000	(10163)	50	4260	(8849)	35	7438	(8876)	72	5664	(8691)	52
Cornus sp.	358	(1339)	7	1166	(1950)	33	262	(1250)	4	314	(1030)	10	504	(1431)	13
F. nigra	287	(1512)	4	166	(566)	8	86	(418)	4	687	(1490)	22	336	(1181)	10
T. americana	0	(0)	0	0	(0)	0	0	(0)	0	188	(781)	6	57	(430)	2
Q. macrocarpa	215	(630)	11	250	(897)	8	86	(418)	4	188	(593)	10	188	(647)	8
Prunus sp.	427	(1371)	11	1001	(3064)	17	956	(1989)	22	188	(1060)	3	598	(1947)	12
U. americana	0	(0)	0	168	(815)	4	87	(418)	4	1063	(3131)	19	373	(1804)	8
A. rubrum	5641	(9538)	64	2333	(3044)	54	870	(2545)	21	1626	(2708)	31	2674	(5664)	43
Q. rubra	786	(3786)	7	0	(0)	0	173	(576)	9	0	(0)	0	242	(1957)	4
A. saccharum	3714	(8426)	21	250	(897)	8	0	(0)	0	2436	(9756)	6	1757	(6958)	9
P. tremuloides	358	(1223)	11	418	(1317)	13	608	(2518)	9	625	(2511)	13	504	(1982)	11
P. strobus	427	(1574)	11	166	(815)	4	86	(418)	4	0	(0)	0	168	(917)	5
All	25071	(13645)	100	29583	(15560)	100	25478	(20522)	100	22313	(14794)	100	25345	(16071)	100

diameter white pine, these observations provide experience that is not readily available on permanent plots in northern Minnesota. Several results worth noting are discussed below.

The natural mortality of crop trees has not been of large proportion in any treatment, although there has been significant crown dieback on some trees. Thus, the dominant and co-dominant crop trees that were identified over 43 years ago have withstood the vagaries of nature during this time period. In addition to mortality from blister rust, we have observed porcupine damage. A relatively severe windstorm in 1995 broke the tops out of some trees and uprooted others, but the stand survived this wind fairly well. A severe windstorm in 1940 blew down entire stands over large areas in the general vicinity but apparently had little effect on this stand (Z.A. Zasada, personal observation).

The average diameter in 1996, 43 years after the first thinning, was somewhat greater for the 18 treatment, but the range in average plot diameter for all the treatments generally overlapped (Table 1). The number of trees greater than 60 cm dbh was greatest in the 32 treatment (Fig. 1, 4) and volume yield over the 1979 to 1996 period was greatest in the 28 and 32 treatments. This suggests that given the treatments evaluated in this study, white pine stands can be managed at relatively high residual basal areas for maximum volume production and still achieve goals of growing large trees; this finding is generally similar to that reported for white pine by Lancaster and Leak (1978) and Johnson (1994). However, even at the highest residual basal area treatment included in this study, there is an apparent lack of competitive stress given the low levels of observed mortality. In comparing an uncut white pine stand with an average basal area of approximately 45 m^2 ha^{-1} to a companion stand repeatedly thinned to average approximately 25 m^2 ha^{-1} basal area, both average stand diameter and the number of large diameter trees were greatly decreased in the uncut stand (Burgess and Robinson, 1998). This suggests that there are limits to the density that can be carried when a goal is the production of large-diameter, high-value trees. Aside from volume production, additional benefits of retaining more trees include insurance against future mortality from blister rust and other causes, and the tendency to reduce the invasion of hardwoods and therefore potentially reducing future competition when establishing pine regeneration.

Table 7. Molecular DNA markers (SSR, simple sequence repeat loci) used to characterize genetic diversity of white pine thinned to four densities at Pike Bay Experimental Forest

Locus	No. Alleles Observed	Allele Size Range (base pairs)
RPS1b	4	195–213
RPS2	6	151–173
RPS6	5	160–186
RPS39	5	169–179
RPS50	11	153–185
RPS84	6	143–161
RPS127	2	192–196

Table 8. Genetic diversity and allele frequency of white pine thinned to four densities, by treatment and for all treatments combined as indicated by alleles at seven simple-sequence-repeat (SSR) loci. Values are absolute numbers, frequencies, or means ± (standard deviation) of n = 6-8 plots per treatment

	Measures of Genetic Diversity				
	All Treatments	**18 m^2 ha^{-1}**	**23 m^2 ha^{-1}**	**28 m^2 ha^{-1}**	**32 m^2 ha^{-1}**
# Trees Sampled	60	15	15	15	15
Total # Alleles over 7 Loci	39	26	31	30	28
Mean # Alleles per Locus	5.57 ± 0.20	3.71 ± 0.46	4.43 ± 0.35	4.29 ± 0.42	4.00 ± 0.41
Mean # Effective Alleles per locus	2.33 ± 0.12	2.08 ± 0.19	2.37 ± 0.23	2.25 ± 0.22	2.31 ± 0.24
# Polymorphic Loci	7	6	7	7	7
Observed Heterozygosity	0.43 ± 0.02	0.41 ± 0.05	0.46 ± 0.03	0.43 ± 0.05	0.44 ± 0.05
Expected Heterozygosity	0.48 ± 0.02	0.44 ± 0.05	0.53 ± 0.03	0.47 ± 0.05	0.48 ± 0.04

	Allele Frequency									
	All Treatments		**18 m^2 ha^{-1}**		**23 m^2 ha^{-1}**		**28 m^2 ha^{-1}**		**32 m^2 ha^{-1}**	
Frequency Class	**Number Of Alleles**	**% of Total Number**	**Number Of Alleles**	**% of Total Number**	**Number Of Alleles**	**% of Total Number**	**Number Of Alleles**	**% of Total Number**	**Number Of Alleles**	**% of Total Number**
High (P ≥ 0.75)	3	7.7	3	11.5	2	6.5	3	10.0	2	7.1
Intermediate (0.75 > P > 0.25)	5	12.8	6	23.1	9	29.0	7	23.3	7	25.0
Low (0.25 ≥ P > 0.01)	25	64.1	17	65.4	20	64.5	20	66.7	19	67.9
Rare (P < 0.01)	6	15.4	0	0.0	0	0.0	0	0.0	0	0.0
Unique	Not Applicable		0	0.0	3	7.7	2	5.1	2	5.1

Ingrowth of white pine did not occur in the 32 years following the last thinning and seedlings as defined in this study were rare. Future thinnings or regeneration cuts in this stand will tend to release the hardwood understory and midstory present in some parts of all treatments, making regeneration of white pine difficult without site preparation and removal of the hardwoods. In the study of Burgess and Robinson (1998), repeated thinning to 25 m^2 ha^{-1} basal area resulted in substantial white pine regeneration when understory hardwood competition was treated several times during the 70-year period of observation; pine regeneration was absent in their unthinned control stand.

The apparent trend toward replacement of white pine by more tolerant hardwood species in the understory confirms the results of studies on similar sites in Canada and the northeastern United States (Hibbs 1982, 1983; Frelich 1992; Lancaster and Leak 1978; Carleton *et al.* 1996; Johnson 1994). The maintenance of white pine on this particular site type has possibly been a function of disturbance history. Periodic fires that burned into these stands from the adjacent Bemidji sand plain, where fires were common (Shadis *et al.* 1995), may have retarded the development of fire-sensitive hardwood regeneration allowing the more fire-tolerant white pine to capture the site. The current canopy density, hardwood regeneration and shrub sub-canopies, and lack of recent seedbed disturbance are factors that may have contributed to the lack of white pine regeneration evident in 1996.

Although white pine were generally randomly distributed in all treatments through 1979, there was some evidence that thinning in the mid-1960s temporarily altered the spatial pattern of residual stems in the 18 m^2 ha^{-1} treatment. The significance of this alteration is unknown, as there was no evidence of unique diameter or basal area growth rate responses to the temporary clumped distribution. However, clumping in the 23 and 27 treatments as a result of mortality between 1979 and 1996 may affect regeneration in these treatments. Clumping is indicative of canopy gaps that may be conducive to understory development. The 1996 densities of two common shrubs, bush honeysuckle (*Diervilla lonicera* Mill.) and beaked hazel were nearly twice as great in the clumped 23 and 28 treatments compared to the 18 and 32 treatments that had random stem distributions (see Table 6). Continued monitoring will determine if the canopy spatial distribution influences regeneration of white pine and other tree and shrub species.

Measures of genetic variation (Table 8) suggest that the different intensities of thinning had little impact on the genetic diversity of the residual white pine. Although few comparable data exist, the levels of diversity present in the Pike Bay white pine are similar to those for old-growth white pine stands in Ontario, Canada and in uncut old-growth and shelterwood stands on Menominee tribal lands, Menominee, Wisconsin. Based on 13 SSR loci and a complete inventory rather than sampling, Rajora *et al.* (2000) found in two Ontario old-growth stands that 92% of the loci were polymorphic and mean heterozygosity was approximately 0.5 both before harvest and after removing approximately 75% of the stems. Echt (1999), screening 8 SSR loci, found heterozygosities of 0.57, 0.55 and 0.53 in uncut old growth, a 75% residual basal area shelterwood, and shelterwood progeny, respectively on the Menominee Reservation. As with our study, observed heterozygosities were slightly less than expected in the Menominee and Ontario stands. This is indicative of a tendency for inbreeding in these white pine populations. Echt (1999), however, found that white pine regeneration in the shelterwood stands had lower levels of inbreeding than the overstory, perhaps the result of pollen influx from outside the stand.

Rajora *et al.* (2000) contend that the distribution of alleles among frequency classes provides greater insight to the impacts of harvest on residual stand diversity. In the Ontario study, the preharvest stands had 87 and 90% of the alleles occurring with frequencies less than 0.25 (low and rare frequency). Of alleles lost through harvest, most were from the low and rare frequency classes and amounted to approximately 26% of the allele richness for both stands. In our study, of the 39 different alleles detected across all plots, the proportion present in the individual treatment units ranged from 67% to 77%. Thus, we observed an apparent decreased allele richness of 23 to 33%. However, in contrast to the complete census performed in the Ontario study, we sampled a limited number of trees and this would limit our detection of low-frequency alleles as well as lead to potentially low estimates of allele richness following thinning.

The importance of stand level genetic diversity arises from the interaction between the landscape distribution of white pine and ecological and genetic processes that operate at the population and stand levels. In isolated stands, non-random mating may lead to inbreeding, decreased fertility and reduced genetic diversity (Hartl 1988, Friedman 1996). Inbreeding may lead to slower growth rates within a couple of generations, while over several generations a loss of diversity may decrease the resilience of the stand to environmental or pest stresses. Loss of stand-level diversity is more rapid if stands are widely separated across the landscape and the influx of pollen or seed from other stands is limited. Loss of diversity due to isolation is more rapid the smaller the stand. If silvicultural treatments such as thinning decrease heterozygosity and allele richness, the detrimental effects of stand isolation are exacerbated. Throughout much of its range in Minnesota, past harvesting and subsequent management has resulted in white pine being left in small, dispersed residual stands that individually are potentially sensitive to isolation effects. It should be noted that even though the nearest white pine stands are more than 0.8 km distant from the study site, the allelic diversity data do not provide evidence that this stand is undergoing a reduction in diversity due to isolation.

Thinning in mature white pine is a silvicultural option that may become increasingly important as interest builds for managing this species over longer rotations. This study has demonstrated that large trees and high volume yields can be obtained while maintaining relatively high stand densities. The perpetuation of white pine on this site may be difficult because in the absence of fire, hardwood regeneration is dominant and is suggestive of transition to a northern hardwoods cover type. Relationships between silvicultural practices and stand-level genetic diversity are only recently quantifiable, and then only for species for which biochemical or molecular markers have been developed. The thinning regimes used in this study had little apparent effect on white pine residual genetic diversity; however, more robust genetic criteria will emerge as information regarding mating systems and gene flow between stands and between generations becomes available. An awareness of the potential impacts of silvicultural practices on genetic diversity will enable managers to take appropriate mitigating measures such as supplementing natural regeneration with planted seedlings when genetic diversity of natural seedling cohorts is in question.

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