Effects of Intensity and Frequency of Harvesting on Abundance, Stocking and Composition of Natural Regeneration in the Acadian Forest of Eastern North America

John C. Brissette

Brissette, J.C. 1996. Effects of intensity and frequency of harvesting on abundance, stocking and composition of natural regeneration in the Acadian Forest of eastern North America. Silva Fennica 30(2–3): 301–314.

In a silviculture experiment in east-central Maine, USA, natural regeneration was sampled to measure the effects of: (1) a range of partial harvest intensities, and (2) repeated partial harvest at one intensity. Under the first objective, five treatments were compared with residual basal areas ranging from 15 to 24 m^2 ha^{-1} for trees ≥1.3 cm diameter at breast height. For the second objective, regeneration was evaluated after four harvests at 5 year intervals. Prior to harvests, the overstory of all the treated stands was dominated by *Tsuga canadensis* (L.) Carr., *Picea* spp. A. Dietr., and *Abies balsamea* (L.) Mill. Eleven species or species groups were identified among the regeneration: *A. balsamea*, *T. canadensis*, *Picea* spp., *Thuja occidentalis* L., *Pinus* spp. L., *Betula papyrifera* Marsh., *Acer rubrum* L., *Betula populifolia* Marsh., *Populus* spp. L., *Fagus grandifolia* Ehrh. and *Prunus serotina* Ehrh. Regeneration abundance was measured as counts of seedlings or sprouts taller than 15 cm but with diameters less than 1.3 cm at breast height (1.37 m). Regardless of harvest treatment, total regeneration was profuse, ranging from over 25 000 to nearly 80 000 trees ha^{-1}. Regeneration was dominated by conifers with a total angiosperm component of 10 to 52 percent approximately 5 years after harvest and 11 to 33 percent after 10 years. Consequently, in forests of similar species composition, tree regeneration following partial harvests should be sufficiently abundant with an array of species to meet a variety of future management objectives.

Keywords natural regeneration, harvest intensity, partial harvest, repeated harvests, silviculture
Author's address USDA Forest Service, Northeastern Forest Experiment Station, 5 Godfrey Drive, Orono, Maine 04473, USA **Fax** +1 207 866 7262
Accepted June 13, 1996

1 Introduction

In eastern Canada the boreal forest extends south to about latitude 47°N. In the northeastern United States the northern boundary of the broadleaf forest is at about 42°N. Between is a mixed-species forest dominated by conifers. Gymnosperms include boreal species such as balsam fir (*Abies balsamea* (L.) Mill.) and a number of spruces (*Picea* spp. A. Dietr.). Also included are species at the northern limit of their ranges, like eastern hemlock (*Tsuga canadensis* (L.) Carr.) and pines (*Pinus* spp. L.). East of the Great Lakes, this region is termed the Acadian Forest (Rowe 1972). Here stand-replacing fires are less frequent than in other boreal and temperate forests (Wein and Moore 1977, 1979). Other common natural disturbances are insect epidemics and wind storms that often cause sporadic, partial mortality. Such disturbances may occur only once during the life of the relatively short-lived fir, but several times during the life of spruce, hemlock or pine.

Selective logging for high value products was common during the 18th and 19th centuries. The rate of harvesting accelerated in the early 20th century as the pulp and paper industry expanded in the region. Following a severe outbreak of spruce budworm (*Choristoneura fumiferana* Clemens) that started in the mid-1970s, clearcut harvesting has become a common silvicultural practice (Seymour 1992). In recent years, however, impacts of production silviculture on forest ecosystems have been questioned from a number of perspectives, including diversity (Hunter 1990) and sustainability (Rowe 1994). Alternative approaches to forest management have been proposed which recommend patterning silvicultural systems after natural disturbance regimes, placing a greater emphasis on species and age class diversity (Seymour and Hunter 1992), and exploring a broad range of silvicultural options (Burton et al. 1992). Such strategies rely on partial harvests to provide needed wood products while retaining a more or less continuous forest canopy.

A critical question for today's forest manager is: What are the impacts of partial harvesting on natural regeneration? A number of attributes of regeneration are important. Abundance is a count by species or of the total. Stocking is the proportion of the site occupied by a species or in total. Both of these measures are meaningful, abundance indicates how many seedlings or sprouts there are in the area of interest, while stocking expresses how well they are distributed throughout that area. Composition gives an indication of what species will likely be in the future stand.

What is certain about the Acadia Forest is that natural reproduction is prolific (Smith 1991), although not always of the species most desired by managers; and that advance regeneration is essential to ensure timely stand establishment following cutting (Seymour 1995). However, little is known about how the intensity and frequency of partial harvesting affects natural regeneration. The objectives of this paper are to: (1) describe impacts of a range of partial harvest intensities on abundance, stocking and species composition of natural regeneration, and (2) examine effects of repeated partial harvesting on those attributes of regeneration.

2 Study Site

This study is part of a silviculture experiment at the Penobscot Experimental Forest (PEF) located in the towns of Bradley and Eddington, in Penobscot County, Maine. The PEF is 1540 ha in size and its center is at approximately 44°52'N, 68°38'W. It was established in 1950 for the purpose of conducting timber management research in the northeastern spruce-fir forest type. History of the PEF prior to 1950 is not well documented. What is known is that only a small portion was ever cleared for agriculture or grazing and that most of the area was cut lightly in the recent past (perhaps 20 to 40 years before 1950) for pine, hemlock and spruce sawlogs. Earlier cutting may have been heavier; presence of charcoal and old burned stumps in some areas indicate fires following cutting of pine stands (Safford et al. 1969). In 1950, stands on the PEF were 60 to 100 years old with a few older individual trees scattered throughout the area.

Under a recent ecological land classification, the PEF is located in the Central Maine Coastal and Interior Section of the Laurentian Mixed Forest Province (McNab and Avers 1994). Prevailing winds are from the west, but the Atlantic Ocean is less than 100 km east; consequently, weather is influenced by both continental and maritime air masses. The highest elevations between the PEF and the ocean are highlands less than 400 m, so orographic lifting has little influence on weather in the area. The elevation of the PEF itself is less than 75 m above sea level.

The 30-year (1951–1980) normal (i.e. mean annual) temperature for nearby Bangor, Maine, is 6.6 °C. The warmest month is July with a normal temperature of 20.0 °C; this is higher than the 18 °C mean July isotherm that Kuusela (1990) used to define the southern boundary of the boreal coniferous forest. The coldest month in Bangor is January with a normal temperature of –7.7 °C. Normal precipitation is 1060 mm per year, with 48 percent of that falling from May through October.

Glacial till is the principal soil parent material on the PEF. Soil types vary from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams and silt loams in flat areas between these low-profile ridges. Along water courses are deposits of marine sediments. Very few sand and gravel deposits are present. A few organic deposits also occur. Till ridges, flats and streams are often in close proximity, resulting in extremely variable site conditions on relatively small areas.

A list of woody plants (trees and shrubs) of the PEF includes 103 species in 60 genera (Safford et al. 1969). Of those, 41 are trees, 13 of which grow to become large trees; i.e., >61 cm diameter breast height (DBH measured at 1.37 m).

The silviculture experiment that is the focus of this research occupies about 160 ha in the most conifer-dominated part of the experimental forest, none of it in that portion that had been cleared for agriculture or grazing. The experiment is concentrated on somewhat well-drained to somewhat poorly-drained soils; however, even within the study, soil type and drainage class can vary markedly.

The forest canopy within the silvicultural experiment is dominated by a mixture of species. Gymnosperms include: eastern hemlock; spruce, mostly red (Picea rubens Sarg.) with some white (*P. glauca* (Moench) Voss); balsam fir; northern white-cedar (*Thuja occidentalis* L.); eastern white pine (*Pinus strobus* L.); and, infrequently, tamarack (*Larix laricina* (Du Roi) K. Koch) or red pine (*P. resinosa* Ait.). The most common angiosperms are: red maple (*Acer rubrum* L.); paper birch (*Betula papyrifera* Marsh.); gray birch (*B. populifolia* Marsh.) and aspen, both quaking (*Populus tremuloides* Michx.) and bigtooth (*P. grandidentata* Michx.). Individuals of sugar maple (*Acer saccharum* Marsh.), yellow birch (*B. alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.,) and American basswood (*Tilia americana* L.) are scattered throughout the study area.

3 Methods

The silviculture experiment was established between 1952 and 1957. A number of treatments were imposed, including both even-age and uneven-age regimes. The treatments were assigned to compartments at random and replicated twice, each replicate or compartment averaging 10 ha. The experiment has eight treatments; this paper focuses on five that incorporate partial harvests: fixed and modified diameter limit cutting, and selection silviculture with 5-, 10-, and 20-year harvest intervals; FDL, MDL, S05, S10 and S20, respectively (Table 1).

In the diameter limit treatments, trees are harvested when they reach specified diameters and those diameters vary with species (Table 1). The most commercially valuable species have the largest diameter limits. In FDL compartments, the diameter limits are strictly adhered to and the harvest interval varies, depending on when a compartment regrows to its initial volume. Harvesting has occurred at 21-year intervals so far. Under the MDL treatment, diameter limits are guides, allowing the research forester to adjust for density and tree quality. Furthermore, the harvest interval does not vary, instead periodic growth is harvested every 20 years.

The selection compartments are managed with goals for species composition, density and diameter-class distribution (Table 1). *Picea* spp. is

Table 1. Experimental prescriptions for five partial harvest treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Treatment	Harvest interval	Experimental prescription
FDL	When regrowth volume reaches stand volume before first harvest (i.e. 148 $m^3 ha^{-1}$)	At harvest trees are cut if DBH exceeds: *Pinus* spp., 29 cm *Picea* spp. and *Tsuga canadensis*, 24 cm *Betula papyrifera*, 22 cm *Thuja occidentalis*, 19 cm all other species, 16 cm
MDL	Every 20 years, harvest not to exceed periodic growth	At harvest most trees are cut if DBH exceeds: *Pinus* spp. and *Picea* spp., 37 cm *Tsuga canadensis*, 32 cm *Betula papyrifera*, 24 cm *Thuja occidentalis*, 19 cm *Abies balsamea*, 16 cm all other species, 14 cm These limits are modified to capture mortality or to leave trees as seed sources or to provide wind protection.
S05	Every 5 years	*Stand structural goals*: post-harvest basal area, 26.4 $m^2 ha^{-1}$; maximum diameter before harvesting, 51 cm; quotient (q) between 2.54 cm diameter classes, 1.4. *Species composition goals* (percent basal area of trees ≥1.3 cm DBH): *Picea* spp., 35–55; *Tsuga canadensis* and *Abies balsamea*, 15–25; *Pinus* spp., *Thuja occidentalis*, *Betula papyrifera*, and all other species combined, each 5–10. *In practice*, cutting has emphasized capturing mortality, improving stand quality and species composition over strict adherence to residual basal area, maximum diameter and q goals.
S10	Every 10 years	Same as S05 except post-harvest basal area goal is 23.0 $m^2 ha^{-1}$.
S20	Every 20 years	Same as S05 except post-harvest basal area goal is 18.4 $m^2 ha^{-1}$.

favored over all other trees. Density goals for the beginning of an operating interval (i.e. following harvest) are highest for S05, lowest for S20, and intermediate for S10. From the maximum DBH goal of 51 cm for all selection treatments, the desired number of trees in each successively smaller 2.54 cm DBH class is defined by a multiplier, or "q", of 1.4.

These five treatments differ in two major respects, harvest intensity and harvest frequency (Table 1). Because S05 is harvested at 5-year intervals, S10 at 10-year intervals and the other treatments at or near 20-year intervals, there have been two periods when all the compartments were harvested over relatively short time spans: at the start of the experiment in the mid-1950s and 20 years later in the mid-1970s (Fig. 1). A third such period is underway at present but will not be complete until after the 1997 growing season.

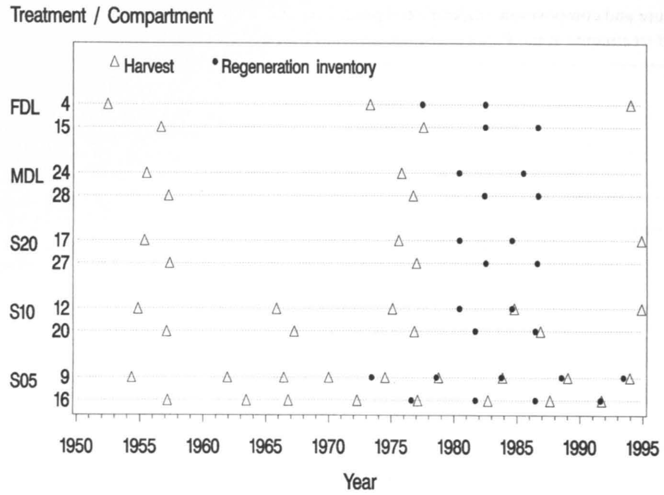

Fig. 1. History of partial harvest and regeneration inventories for selected treatments and their replicates at the Penobscot Experimental Forest, east-central Maine, USA.

Periodic measurements of stand composition and structure are taken on a series of permanent plots established in each compartment on a grid with a random start. These plots are a series of two concentric circles of different sizes with the same plot center. All trees with DBH ≥ 1.3 cm are measured on 0.20 ha plots. All trees with DBH ≥ 11.4 cm are measured on 0.81 ha plots. The number of such plots ranges from 13 to 23 per compartment with the 0.81 ha plots representing an average 15.2 percent sample and the 0.20 ha plots an average 3.8 percent of the compartment area.

Regeneration inventories did not begin until the 1960s, when three 4.05 m^2 plots were established on the circumference of the 0.20 ha plots (an average 0.23 percent sample of the compartment). On each regeneration plot, counts are made by species of each tree ≥15 cm tall but with a DBH < 1.3 cm. In treatment S05, regeneration plots are measured pre- and post-harvest. In other treatments, plots are measured before and after cutting and at about 5-year intervals between harvests.

The purpose of this paper is to examine post-harvest natural regeneration responses; consequently, I chose the most recent period, 1973 to 1977, when all the treatments were logged to compare the effects of harvest intensity on regeneration (Fig. 1). Treatment effects for both first and second inventories after harvest were compared, about 5 and 10 years post-harvest, respectively. To examine impacts of repeated partial cutting, four harvests between 1970 and 1987 in S05 were compared (Fig. 1).

Because a tree had to be at least 15 cm tall to be counted in this study, at the first inventory most would have been advanced regeneration; i.e., established seedlings at the time of harvest or developed from seed or sprouts from trees in the pre-harvest stand. At the second inventory, some of the smaller regeneration would likely have originated from trees in the post-harvest stand.

Besides differences in harvest intensity and frequency, there were differences among compartments in species composition and size structure prior to the mid-1970s harvest (Table 2). *Tsuga canadensis* and *Picea* spp. dominated the overstory of all the compartments. Thus, throughout the study area, they were the most likely seed

Table 2. Structure and composition of likely seed producing tree species or species groups prior to partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ DBH (cm)	Treatment[1)] / Compartment									
	FDL		MDL		S05		S10		S20	
	4	15	24	28	9	16	12	20	17	27
	Trees ha^{-1}									
Tsuga canadensis										
11–20	92	83	112	62	86	82	59	19	57	22
21–30	32	6	66	58	53	66	45	13	61	29
31–40	1	1	5	4	19	45	17	14	34	12
>40	1			1	10	1		1		
Picea spp.										
11–20	96	41	95	62	48	36	103	84	43	63
21–30	31	9	60	80	55	37	87	85	53	54
31–40			3	22	13	18	15	17	17	21
>40					1	1		1	1	<1
Abies balsamea										
11–20	113	104	68	112	136	66	227	107	59	111
21–30			1		2	3	13	6		
31–40										
>40										
Thuja occidentalis										
11–20	50	62	45	52	16	43	53	54	35	47
21–30	3	8	5	1	6	6	4	5	8	4
31–40			1					<1		
>40										
Pinus spp.										
11–20	1	1		4						
21–30	2	1	3	2	4	1	1	2		<1
31–40			3	4	4		1	1		<1
>40					9			<1	2	
Acer rubrum										
11–20	75	24	73	30	25	17	87	43	14	15
21–30	3	3	1	9	15	3	20	5	1	2
31–40				1		2				
>40				1						
Betula papyrifera										
11–20	71	4	16	13	27	2	32	3	10	6
21–30	1		5	3	20	5	7	4	3	1
31–40					1			<1		
>40										
Other angiosperms										
11–20	27	6	21	4	4	1	6	1	1	1
21–30		1	1		5		3			
31–40	1									
>40					1					

1) Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.

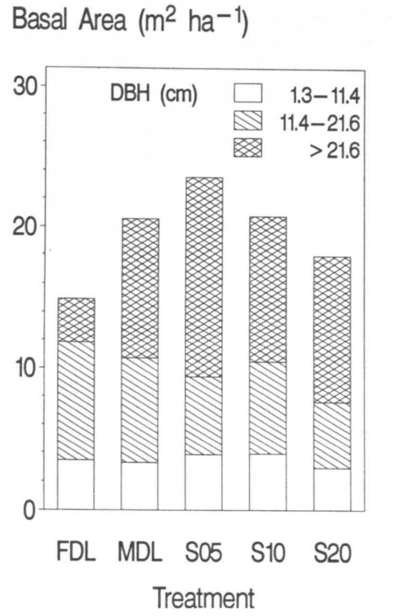

Fig. 2. Residual basal areas for three size classes of trees following harvesting stands under: fixed diameter limit cutting (FDL), modified diameter limit cutting (MDL), and selection silviculture with 5-(S05), 10-(S10), and 20- (S20) year harvest intervals.

producers contributing to regeneration that was present following harvest. However, the number of trees of various species in each size class differed markedly, even between compartments within a treatment.

Following the mid-1970s harvest, residual basal areas varied among treatments except between MDL and S10, which were nearly identical (Fig. 2). S05 had the greatest residual basal area and the most in large trees. FDL had the least total basal area and the least in large trees; in fact, basal area of trees larger than 21.6 cm DBH was less ($p = 0.01$) in FDL than in the other treatments. There were no differences among the smaller size classes, however.

Harvests were conducted by commercial logging crews that felled trees using chainsaws, delimbed them at the stump, and transported logs roadside with rubber-tired skidders. Harvesting in the various compartments occurred during different seasons of the year and permanent plots were treated no different than the rest of the stand.

3.1 Data Collection and Analyses

Comparisons among silvicultural treatments were made with analysis of variance (ANOVA) for a completely random experimental design. Treated compartments (replicates) were the experimental units and plots were sampling units. Treatment and inventory, first and second (except for S05) after harvest, were the independent variables. Response variables were abundance and stocking values by species or species groups. Separate analyses were conducted for each species or species group, and for total gymnosperms, total angiosperms and total regeneration. Differences among treatment means were evaluated using Duncan's New Multiple Range Test (Steel and Torrie 1980).

To analyze the effect of repeated partial harvesting in S05, an ANOVA for each species, group or total was conducted with harvests as the independent variable, and number and stocking as response variables. For species or groups where the effect of harvest was significant ($p \le 0.05$), the relationship was examined by partitioning harvest sums of squares by orthogonal polynomials (Steel and Torrie 1980).

Eleven tree species or species groups are identified in this study: *Abies balsamea*, *Tsuga canadensis*, *Picea* spp., *Thuja occidentalis*, *Pinus* spp., *Betula papyrifera*, *Acer rubrum*, *Betula populifolia*, *Populus* spp., *Fagus grandifolia*, and *Prunus serotina*. Because young *Picea* seedlings can be difficult to identify to species, they were grouped. However, based on saplings and larger trees, it is clear that *P. rubens* is the dominate spruce with *P. glauca* occasionally present and *P. mariana* rarely found on the sites in this study. Although *Pinus* species are also grouped, *P. strobus* is the dominate pine with *P. resinosa* seedlings seldom present. Small *Populus* seedlings or sprouts can also be difficult to identify to species, so they too were grouped.

4 Results and Discussion

4.1 Treatment Effects on Tree Regeneration

Total regeneration was profuse (Table 3). There were over 27 000 trees ha^{-1} in the least abundant treatment (FDL) at the first inventory (Inv 1), and it increased to over 42 000 trees ha^{-1} at the second (Inv 2). At Inv 1, treatments S10 and S20 had significantly more regeneration than the other treatments. S20 and S10 still had the most regeneration at Inv 2, but S10 no longer differed from MDL. Not only was regeneration prolific, it was well distributed within the treated compartments (Table 4). Even in the poorest stocked treatment (MDL), 93 percent of the area was regenerated at Inv 2.

Coniferous species dominated regeneration in all treatments. With conifers comprising 90 percent of total regeneration, S05 had the most gymnosperms at Inv 1. Among the five treatments, only in S20 was the number of regenerating angiosperms greater than gymnosperms, 52 versus 48 percent of total regeneration. However, that was just at Inv 1, by Inv 2 conifers clearly dominated with 67 percent of the total. Treatment S20 had the lowest stocking of gymnosperms at Inv 1 (70 percent of the area), but the highest at Inv 2 (95 percent) (Table 4).

In total abundance of angiosperms, there were no differences among treatments with an average of 28 percent of all regeneration at Inv 1 and 23 percent at Inv 2 (Table 3). Yet, there were differences in stocking (Table 4). At Inv 1, S05, with 34 percent stocking of angiosperms, had less than other treatments except S10. S10 still had the least stocking of angiosperms (61 percent) at Inv 2, but differed only from S20, which had the most (84 percent).

Overall, *Abies balsamea* was the most abundant species and also had the greatest stocking at both inventories, although in MDL and S05 *Tsuga canadensis* was more prevalent (Tables 3 and 4). Among species or species groups, only *Thuja occidentalis* exhibited a difference in abundance with S05 having significantly more than the other treatments. Stocking of *T. occidentalis* at Inv 1 differed only between S05 and MDL. Treatments differed in stocking of *Betula papyrifera* and *B. populifolia* as well. S20 had the greatest stocking of both species at both inventories; however S20 only differed from the other selection treatments, not from the diameter limit treatments.

The three most common gymnosperms, *Abies balsamea*, *Tsuga canadensis* and *Picea* spp., accounted for an average of 71 percent of regeneration at Inv 1 and 75 percent at Inv 2 (Table 3). Availability of seed producing parent trees, site characteristics and seed attributes all contributed to the success of these species.

Abies balsamea, *Tsuga canadensis* and *Picea* spp. were the most common overstory species prior to the partial harvests, providing a ready seed source. However, *A. balsamea* trees were much smaller than the other two species, almost all in the 11–20 cm DBH size class (Table 2).

Seedlings of all three species are well adapted to growing in a shady, cool and moist understory; consequently, all of them are classified as very tolerant (Spurr and Barnes 1980). Shade provided by residual trees was apparently adequate to provide numerous germination sites, as there were no differences in abundance or stocking for these species among the treatments.

Seeds of *Abies balsamea* are 2 to 3 times heavier, on average, than those of *Picea rubens* or *Tsuga canadensis* (Franklin 1974, Safford 1974, Ruth 1974). Larger seeds provide greater reserves which may account for more rapid and deeper penetration of roots of *A. balsamea* seedlings compared to *P. rubens* (Frank 1990). Seeds of all three are wind disseminated and those of *A. balsamea* and *P. rubens* often disperse 100 m or more (Frank 1990, Blum 1990). However, because of their small wings, most seeds of *T. canadensis* fall within one tree height (i.e., 20 m or less at the study site) of the parent tree (Godman and Lancaster 1990). Thus, seed characteristics, which affect early seedling development, probably account for why *A. balsamea* was more common than *T. canadensis* or *Picea* spp.

Among common regenerating angiosperm trees, understory tolerance ranges from very intolerant (*Betula papyrifera*, *Populus* spp.) to tolerant (*Acer rubrum*) (Spurr and Barnes 1980). It is notable that the very intolerant *B. papyrifera* and the tolerant *A. rubrum* were the most abundant angiosperms (Table 3) as well as those with

Table 3. Regeneration abundance following partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ Inventory	SE[2]	Treatment[1] FDL	MDL	S05	S10	S20	Mean[3]
		Trees ha^{-1}					
Abies balsamea							
1	5389	10131	9551	10129	27071	10535	13856
2	6539	14782	15404	[4]	32708	18227	20622
Tsuga canadensis							
1	4085	6014	10220	15636	11399	9537	10446
2	4817	9616	18059		15202	25723	16933
Picea spp.							
1	1782	2600	3822	4267	9233	4933	5061
2	1910	4563	6952		12596	8389	8208
Thuja occidentalis							
1	87	156b[5]	83b	1041a	392b	125b	351
2	385	536	672		1441	1037	934
Pinus spp.							
1	361	136	156	792	117	0	229
2	100	211	178		98	77	140
Total gymnosperms							
1	9518	19036	23831	31867	48214	25127	29944
2	9934	29739	41265		62044	53456	46845
Betula papyrifera							
1	6666	1976	5041	535	1932	17467	5324
2	6653	4460	4829		1078	16069	6434
Acer rubrum							
1	1097	3864	4878	2544	5234	3141	3968
2	991	4225	4640		5411	5417	4929
Betula populifolia							
1	526	1583	424	0	363	1706	833
2	1224	2801	588		667	2801	1723
Populus spp.							
1	1107	83	391	21	167	2440	612
2	683	62	166		99	1399	419
Fagus grandifolia							
1	719	475	697	73	0	1513	542
2	524	560	380		0	935	458
Prunus serotina							
1	55	21	83	0	59	170	66
2	134	84	378		69	105	151
Total angiosperms							
1	7649	8115	11660	3352	7753	26800	11501
2	8085	12430	11276		7322	26215	14119
Total regeneration							
1	3052	27153b	35490b	35218b	55968a	51928a	41446
2	4983	42170c	52539bc		69365ab	79671a	60964

[1] Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.
[2] Pooled standard error from analysis of variance.
[3] Weighted by area in each treatment.
[4] In this treatment, only one inventory is taken between harvest intervals.
[5] Within species and inventory, values with different letters are significantly different ($p \le 0.05$); if there are no letters, differences are not significant at that level.

Table 4. Regeneration stocking following partial harvest in selected treatments at the Penobscot Experimental Forest, east-central Maine, USA.

Species/ Inventory	SE[2]	Treatment[1] FDL	MDL	S05	S10	S20	Mean[3]
		percent stocking					
Abies balsamea							
1	13.43	70.6	54.8	77.2	76.6	56.5	67.4
2	8.11	76.1	69.6	[4]	89.7	78.7	79.0
Tsuga canadensis							
1	14.02	61.0	60.2	75.6	51.2	57.6	60.7
2	8.14	70.8	67.4		57.6	84.7	69.8
Picea spp.							
1	12.37	49.4	39.0	55.2	56.8	42.1	48.8
2	4.78	62.9	53.6		68.6	66.0	63.1
Thuja occidentalis							
1	2.16	4.6ab[5]	1.6b	11.4a	8.3ab	3.6ab	5.9
2	6.54	13.4	14.2		18.6	13.4	15.0
Pinus spp.							
1	5.84	4.2	6.3	11.6	4.8	0.0	5.2
2	2.96	6.0	5.9		4.0	1.9	4.4
Total gymnosperms							
1	11.53	82.8	70.4	90.0	82.2	70.2	79.2
2	3.24	92.0	86.9		92.1	94.6	91.5
Acer rubrum							
1	5.34	46.8	49.8	31.6	51.2	44.0	45.0
2	6.34	57.8	57.1		60.3	62.6	59.5
Betula papyrifera							
1	10.07	31.0ab	42.2ab	6.6b	17.1b	56.7a	30.6
2	10.03	43.4ab	48.5ab		11.9b	62.2a	40.5
Betula populifolia							
1	4.12	11.4ab	10.4ab	0.0b	5.2b	23.0a	10.0
2	5.25	16.0	10.4		5.6	24.4	14.1
Populus spp.							
1	9.23	2.5	2.5	0.8	3.2	20.2	5.8
2	7.45	1.6	3.0		2.8	16.2	5.8
Fagus grandifolia							
1	3.92	6.4	5.2	3.0	0.0	8.8	4.6
2	4.69	8.6	5.2		0.0	8.1	5.4
Prunus serotina							
1	1.71	0.8	2.5	0.0	2.4	5.7	2.3
2	1.99	2.2	8.9		2.0	1.9	3.6
Total angiosperms							
1	6.10	66.9a	63.2a	33.8b	56.0ab	76.2a	59.6
2	4.91	77.2ab	72.6ab		61.9b	83.6a	73.6
Total regeneration							
1	3.76	91.5	84.8	90.0	90.4	92.6	90.0
2	0.80	98.7ab	92.8c		96.0b	100.0a	97.0

[1] Treatments: FDL = fixed diameter limit; MDL = modified diameter limit; S05 = selection, 5-year harvest interval; S10 = selection, 10-year harvest interval; S20 = selection, 20-year harvest interval.
[2] Pooled standard error from analysis of variance.
[3] Weighted by area in each treatment.
[4] In this treatment, only one inventory is taken between harvest intervals.
[5] Within species and inventory, values with different letters are significantly different ($p \leq 0.05$); if there are no letters, differences are not significant at that level.

Table 5. Regeneration abundance following partial harvests repeated at about 5-year intervals at the Penobscot Experimental Forest, east-central Maine, USA.

Species	SE[2]	Harvest[1] 4	5	6	7	Mean	Trend[3]
		Trees ha^{-1}					
Tsuga canadensis	6542	11458	15636	19901	13608	15151	
Abies balsamea	609	9981	10130	10612	7294	9504	Quadratic
Picea spp.	774	2800	4267	6767	5582	4854	Linear
Thuja occidentalis	245	601	1041	1313	1465	1105	
Pinus spp.	595	664	792	476	348	570	
Total gymnosperms	6465	25505	31867	39068	28296	31184	
Acer rubrum	670	2690	2544	2228	2617	2520	
Betula papyrifera	536	1030	535	499	388	613	
Fraxinus americana	267	443	95	158	274	243	
Fagus grandifolia	26	251	73	73	115	128	Quadratic
Quercus spp.	21	21	21	21	21	21	
Total angiosperms	736	4497	3352	3031	3519	3599	
Total regeneration	6458	30002	35218	42099	31815	34783	

[1] Data following earlier harvests are not available.
[2] Pooled standard error from analysis of variance.
[3] When analysis of variance indicated significant ($p \leq 0.05$) differences among harvests, the relationship was determined by partitioning harvest sums of squares by orthogonal polynomials.

the greatest stocking (Table 4). *B. papyrifera* produces abundant, wind-disseminated seed (Safford et al. 1990). Therefore, it is well adapted to become established in any openings created by harvesting. *A. rubrum* probably grows on a wider range of site conditions than any other forest species in North America; furthermore, even small trees produce abundant seed and it sprouts vigorously from stumps (Walters and Yawney 1990). Thus, it is not surprising that it was so common in this study, or that there were no treatment effects on either abundance or stocking.

4.2 Repeated Harvesting Effects on Regeneration

Among the four harvests in S05 for which there were comparable regeneration inventories (Fig. 1), repeated harvesting resulted in few trends in abundance (Table 5), and even fewer in stocking (Table 6). Compared to after Harvest 4, abundance of *Abies balsamea* increased following Harvests 5 and 6, then declined sharply after Harvest 7. The trend for *Tsuga canadensis* was similar but not significant. Although the number of *Picea* seedlings also declined somewhat after Harvest 7, the overall trend was significantly positive. Among angiosperms, the abundance of *Fagus grandifolia* dropped to its lowest level after Harvests 5 and 6, then rebounded following Harvest 7. Nevertheless, stocking of *F. grandifolia* followed a declining trend across the four harvests.

Compared to their abundance after Harvest 6, the number of gymnosperm seedlings fell by over 10 000 ha^{-1} following Harvest 7. The reason for the decline is not clear. Since the harvests and inventories are staggered in time, it is not likely that either logging practices or climatic conditions affected the two replicate compartments the same. Some indication may be found by examining the inventory following Harvest 8 in Compartment 9 (Fig. 1). Except for *Pinus* spp., all other species or groups declined in abun-

Table 6. Regeneration stocking following partial harvests repeated at about 5-year intervals at the Penobscot Experimental Forest, east-central Maine, USA.

Species	SE[2)]	Harvest[1)] 4	5	6	7	Mean	Trend[3)]
		percent stocking					
Abies balsamea	2.77	70.9	77.2	79.8	73.0	75.2	
Tsuga canadensis	8.64	59.0	75.6	76.2	74.2	71.3	
Picea spp.	10.22	43.8	55.2	62.8	58.1	55.0	
Thuja occidentalis	2.82	13.9	11.4	13.0	11.0	12.3	
Pinus spp.	9.98	10.2	11.5	9.0	9.0	9.9	
Total gymnosperms	3.23	83.1	90.0	90.3	87.8	87.8	
Acer rubrum	8.23	29.4	31.6	29.9	39.4	32.6	
Betula papyrifera	6.26	12.2	6.6	11.8	11.0	10.4	
Fagus grandifolia	0.52	5.9	3.0	3.0	2.2	3.5	Linear
Fraxinus americana	1.41	1.3	1.3	1.3	3.4	1.8	
Quercus spp.	0.8	0.8	0.8	0.8	0.8	0.8	
Total angiosperms	9.36	39.2	33.8	35.4	47.0	38.8	
Total regeneration	3.56	84.4	90.0	92.0	92.8	89.8	

1) Data following earlier harvests are not available.
2) Pooled standard error from analysis of variance.
3) When analysis of variance indicated significant ($p \leq 0.05$) differences among harvests, the relationship was determined by partitioning harvest sums of squares by orthogonal polynomials.

dance after Harvest 8. Gymnosperm abundance fell by 17 percent while the total number of angiosperms was 50 percent less than after Harvest 7. Total regeneration stocking also declined somewhat, but still exceeded 92 percent and total stocking of conifers did not change from the previous inventory. Thus, the continued high level of regeneration stocking suggests that no serious problem has yet developed with regeneration in Compartment 9. Furthermore, until a comparable inventory is made in Compartment 16 following its eighth harvest, it is not possible to infer whether the decline in regeneration is a treatment or a site effect.

5 Summary and Conclusions

There were few statistically significant differences among the silvicultural treatments or among repeated harvests in this study. A number of explanations can be considered: with only two replicates the power of the experiment to detect differences between treatments is low; there is considerable site heterogeneity within each treated compartment; the species which occupy this forest type are prolific, robust and adapted to a broad range of site conditions; or, neither the abundance nor stocking of natural regeneration was impacted by the range of partial harvest treatments applied in this study. All these reasons are contributing factors.

Although power in this experiment was low making it difficult to detect differences, there are no trends among the five treatments to suggest that greater statistical power would make the results more clear. For example, prior to the mid-1970s harvest, S20 did not have a lot of overstory angiosperms. Nonetheless, following harvest it had the most regenerating angiosperms, suggesting that relatively heavy overstory removal opened up the stand and favored angiosperm seedlings and sprouts. However, even more open conditions existed in FDL following the harvest but angiosperm regeneration was not nearly as prolific. Furthermore, the experiment did detect rather subtle differences in stocking of total regeneration; a 3.2 percent difference was significant.

The magnitudes of standard errors compared with their respective means attest to the within-treatment heterogeneity in this study. Thus, although a diligent attempt was made to apply treatments uniformly to the replicates, the sites themselves were not uniform. Sites varied not only in drainage and soils but also in initial stand structure and composition. Repeated harvest entries should eventually result in more uniform structure and composition between treatment replicates. However, site will remain a major determinant of presence and abundance of a particular species. Even in S05 where there has been repeated harvests, the replicates differ; seedlings of *Pinus* spp. have, to this point in time, been found only in Compartment 9 while regenerating *Quercus* spp. are only in Compartment 16. Nevertheless, the overall high levels of stocking indicate that the principal regenerating species have broad site requirements for establishment.

The abundance of the major regenerating species in this study was far in excess of the numbers needed to ensure their presence in the future stands. As a management tool, stocking is a measure of how much regeneration is required. Each regeneration plot was 0.000405 ha. Consequently, to be fully stocked with a particular species, or in total regeneration, only 2469 uniformly distributed seedlings or sprouts were required per hectare. A number of both gymnosperm and angiosperm species or species groups far exceeded the numerical requirement. That stocking was not 100 percent for those abundant species or groups suggests some areas of unfavorable site or overstory conditions within the stands. However, 100 percent regeneration stocking is not necessary for managing a stand for forest products. Frank and Bjorkbom (1973) recommend just that stocking of *Picea* spp. and *Abies balsamea* seedlings combined be greater than 50 percent. All of the treatments in this study exceeded that goal.

These results demonstrate that, under the site conditions in this boreal ecotone forest, natural regeneration of trees is prolific across a broad range of intensities and frequencies of partial harvests. Most of the regeneration is from three taxa of understory tolerant conifers and two species of angiosperms. A number of other gymnosperms and angiosperms are also found, but in fewer numbers and at lower levels of stocking. Thus, for a range of partial harvest strategies in the Acadian Forest, tree regeneration will be sufficiently abundant and diverse to sustain a stand capable of meeting a variety of future management objectives.

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