Northern White-Cedar Regeneration Dynamics on the Penobscot Experimental Forest in Maine: 40-Year Results

Catherine Larouche, Laura S. Kenefic, and Jean-Claude Ruel

ABSTRACT

The objective of this study was to assess the long-term dynamics of northern white-cedar (*Thuja occidentalis* L.) seedling and sapling growth and mortality on the Penobscot Experimental Forest in Maine. Data collected between 1965 and 2005 in four twice-replicated partial cutting treatments were analyzed. White-cedar seedlings established in all treatments despite relatively high white tailed-deer (*Odocoileus virginianus* Zimmerman) population densities. However, although it appears that regeneration cohorts of associated softwoods increased in size over time, the white-cedar cohort did not. Ingrowth of white-cedar from the seedling to sapling stage was lower than the combined rates of sapling mortality and recruitment to the pole stage; sapling density of this species in 2005 was >80% less than it was at the start of the measurement period. Sapling mortality was high, and recruitment to larger size classes was low, although mortality decreased and recruitment increased as sapling size increased. Browsing was prolific; 90% of white-cedar seedlings and small saplings showed signs of browse in 2005. Overall, white-cedar sapling growth was slow, with an estimated 100 years needed to grow from small sapling to merchantable size in the study stands. Efforts to release white-cedar saplings through precommercial treatment and control of browsing pressure are recommended.

Keywords: partial cutting, recruitment, browsing, growth, eastern white cedar

Northern white-cedar (*Thuja occidentalis* L.) is a commercial species present between the 44th and 48th parallels (Johnston 1990) in many forest types of northeastern United States and southeastern Canada, including the Acadian Forest. White-cedar grows in pure stands on wet and dry sites, but growth is best on mesic sites in the southern portion of its range, where it shares growing space with many other tree species (Johnston 1990). In mixedwood stands, natural reproduction is generally prolific after natural disturbances and harvesting activities (Smith et al. 1997), but species differ in silvics and reproduction adaptations. Consequently, silviculture system and timing of entry may favor one species over the others (Seymour 1995). Key elements for white-cedar seedling establishment and early survival are partial shading and constant humidity of the forest floor, proximity of white-cedar seed trees, and availability of receptive seedbeds, such as disturbed soil or decayed wood (Larouche 2009). However, these favorable microsites are largely colonized by other mid- and shade-tolerant tree species having a faster growth rate (e.g., balsam fir [*Abies balsamea* (L.) Mill.], red spruce [*Picea rubens* Sarg.], eastern hemlock [*Tsuga canadensis* (L.) Carrière], and yellow birch [*Betula alleghaniensis* Britt.]) (Larouche 2009). This leads to competition for growing space and resources, followed by stratification and self-thinning of the regeneration cohort (Oliver and Larson 1996, Smith et al. 1997).

Natural dynamics of Acadian Forest mixedwood stands are based on sporadic partial disturbances, mostly gaps created by mortality of individual stems or a small group of trees (Seymour et al. 2002). Stand-replacing perturbations, such as fire and catastrophic windthrow, are less frequent than in naturally even-aged, single-species stands (Wein and Moore 1977, 1979). Successful management of mixedwood stands is difficult, because development of cohorts is difficult to predict compared with single-cohort systems (Moores et al. 2007). Silvicultural systems inspired by natural disturbances in mixedwood stands emphasize diversity of species and development of cohorts (Seymour and Hunter 1992). At the stand scale, a growing interest in ecosystem-based management brings into question current silvicultural practices and how they can maintain ecological values and functions of ecosystems (Guldin 1996, Puettmann and Ammer 2007). The white-cedar component is often small in mixedwood stands, but it is important to maintain natural dynamics, conserve wildlife habitats and food resources, and sustain the forest industry.

Many studies have investigated the impact of partial harvesting on the abundance and stocking of natural regeneration in mixedwood stands (e.g., Brissette 1996, Archambault et al. 2003). The

Manuscript received June 17, 2009; accepted December 8, 2009.

Catherine Larouche (catherine.larouche@mrnf.gouv.qc.ca), Ministry of Natural Resources Québec, Direction de la recherche forestière, 2700 rue Einstein, bur. B.1.150, Québec, QC G1P 3W8, Canada. Laura S. Kenefic, US Forest Service, Northern Station, 686 Government Rd., Bradley, ME 04411. Jean-Claude Ruel, Départment des sciences du bois et de forêt, Université Laval, Québec, QC G1K 7P4, Canada. *This study was funded by the Fonds québécois de la recherche sur la nature et les technologies (FQRNT), and was made possible through support from the U.S. Forest Service, Northern Research Station. The authors thank John C. Brissette from the U.S. Forest Service for his support. They also thank Mathieu Fortin and Isabelle Auger from the Ministère des Ressources naturelle et de la Faune du Québec (MRNF)—Direction de la recherche forestière (DRF) and Aaron Weiskittel from the University of Maine for their help with statistical analyses. Catherine Larouche was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), the CFS, the CEF, the Fonds F.K. Morrow, and the MRNF (DRF). We are grateful to all those persons who contributed to the project.*

This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; square kilometers (km^2): 1 km^2 = 0.3861 mi^2; hectares (ha): 1 ha = 2.47 ac.

focus of such studies is often the composition of the newly established cohort and the proportion of the site occupied by each species. However, few studies have analyzed the stratification of regeneration cohorts that occurs because of differential height and diameter increments among species, or the rates of recruitment and causes of mortality of individual saplings over the long-term. This information is essential to understand the development of a population of trees and better assess long-term sustainability of species and stand structure (Kenefic et al. 2005). Long-term experiments, including repeated measurement and monitoring of individual stems, offer a great opportunity to better understand the dynamics of mixedwood stands (Sendak et al. 2006).

In addition to interspecific competition, white-cedar seedlings and saplings may be disfavored by preferential browsing pressure. Many cases of browsing damage by white-tailed deer (*Odocoileus virginianus* Zimmerman), and to a lesser extent by snowshoe hare (*Lepus americanus* Erxleben), have been reported as compromising white-cedar regeneration (Johnston 1972, 1990, Davis et al. 1998). This pressure, added to harvesting treatments, can have a long-term effect on the composition of mixedwood stands (Frelich and Lorimer 1985, Cornett et al. 2000), depending on herbivore population levels (Larouche 2009).

Our objective was to examine the dynamics of white-cedar regeneration in managed mixedwood stands in the southern portion of the Acadian Forest. To achieve this objective, we analyzed the height class distribution of white-cedar seedlings and saplings over time in a number of partially cut stands and compared this distribution to those of associated softwoods (i.e., balsam fir, spruce species, and eastern hemlock). In addition, we determined rates of white-cedar recruitment, diameter growth, and mortality (as well as causes of mortality) from remeasurements of individual saplings made over a 30-year period. Implications of observed dynamics are discussed in light of concerns about white-cedar sustainability (e.g., Hofmeyer 2008).

Materials and Methods

Study Site

This study uses 40 years of data collected by the US Forest Service, Northern Research Station, as part of its stand-level silvicultural experiment at the Penobscot Experimental Forest (PEF) (44°52′N, 68°38′W). Although the history of the PEF prior to the Forest Service study is not well documented, it is known to have experienced repeated partial cutting (Safford et al. 1969, Kenefic et al. 2006). In 1950, the area used for the silvicultural experiment was softwood dominated and irregular to uneven-aged as a result of past cutting and natural disturbances (Sendak et al. 2003). The climate on the PEF is cool and humid with a mean annual temperature (±SD) of 6.7 ± 0.3°C (1971–2000). The normal annual precipitation is 1066 ± 137 mm; almost 50% of precipitation falls between May and October, and annual snowfall averages 289 ± 78 cm. The growing season is about 183 ± 15 days.

Average elevation of the PEF is less than 75 m above the sea level (Brissette 1996). Soils are the result of glacial influences and are variable in terms of texture, drainage, and depth of organic layer (Brissette 1996). The stands used in the present study have an organic layer of generally less then 16 cm developed on a 50–100-cm deep glacial till. Soil texture in the B-horizon ranges from silt-loam to sandy-loam with good to poor drainage (Safford et al. 1969).

The PEF is part of the Acadian Forest, and the study stands contained balsam fir, spruces (mostly red and white [*Picea glauca* (Moench) Voss]), eastern hemlock, white-cedar, eastern white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), sugar maple (*Acer saccharum* Marsh.), yellow birch, and white ash (*Fraxinus americana* L.). The mixture of species varies according to soil conditions and harvesting treatments. Understory tree species composition generally reflects the overstory and is softwood dominated. In mixedwood stands, arrangement of seedlings is determined by canopy composition, biophysical environment, interspecific competition, and browsing pressure.

It is difficult to get precise information about herbivore densities, because there have been no hare, moose (*Alces alces* Gray), or deer surveys on the PEF. However, scientific literature from the Lake States and hunting surveys in Maine indicate an increase in deer and hare populations during the last century (Grigal and Ohmann 1975, Chimner and Hart 1996, Rooney et al. 2002). According to the Maine Department of Inland Fisheries and Wildlife, deer populations tripled between 1960 and 2000, hare populations increased by 1.5 times, and moose abundance remained low. In 2008, there were between 5.8 and 9.7 deer/km^2, about 15.2 hare/km^2, and about 0.3 moose/km^2 in the region where the PEF is located (Maine Department of Inland Fisheries and Wildlife 2007).

Design and Data Collection

The 240-ha experiment on the PEF includes even- and uneven-aged silvicultural systems and exploitative cutting. The long-term study includes 10 treatments initiated between 1952 and 1957, replicated twice, and randomly assigned to experimental units (hereafter called compartments) of about 10 ha (Brissette 1996, Kenefic et al. 2006). In this article, we focus on data from four of the partial harvest treatments; partial harvesting is common in mixedwood stands, and it has been suggested that such treatments create a biophysical environment favorable for the successful regeneration and recruitment of white-cedar (Schaffer 1996, Hofmeyer 2008). Treatments include selection cutting with 5-, 10-, and 20-year cutting cycles and fixed diameter-limit cutting with a harvest interval of about 20 years based on stand volume increment. All these treatments tend to maintain an irregular to uneven-aged stand structure, establish a new cohort of trees, and release regeneration at each entry (Kenefic et al. 2005). Harvest intensity in the selection treatments is a function of cutting cycle and a structural goal defined using the *BDq* method (where *B* is the residual basal area, *D* is the retained diameter class, and *q* is the negative exponential constant between diameter classes; Marquis 1978, Guldin 1991). The *q*-factor is 1.96 on 5-cm dbh classes and target residual basal area (for trees ≥1.3 cm dbh) is 26.4, 23.0, and 18.4 m^2/ha for the 5-, 10-, and 20-year cutting cycles, respectively (Seymour and Kenefic 1998). Fixed diameter-limit cutting is a commonly applied, exploitative form of partial cutting (Kenefic and Nyland 2005). The treatment on the PEF uses species-specific size thresholds above which merchantable trees are cut, allowing long-lived species to reach a larger dbh (Brissette 1996, Kenefic et al. 2005). In all treatments, felling is done with chainsaws and logs are transported with rubber-tired skidders. Season of harvest varies but is usually fall or winter.

Each compartment includes between 13 and 23 continuous forest inventory plots monitored every 5 years and before and after each stand entry. Treatments and inventories are not synchronized among compartments (Brissette 1996, Sendak et al. 2003), i.e., replicates of the same treatment are harvested and measured in different years per staggered dates of initial treatment application. Plots were established on a systematic grid according to compartment area to inventory about 15% of the productive area (Kenefic et al. 2005). These plots consist of two concentric circles measuring 0.02 and 0.08 ha. All trees with dbh $>$11.4 cm are measured on the larger plot, whereas trees with 1.3 cm $\leq$ dbh $\leq$ 11.4 cm (saplings) are measured on the smaller plot. Measurements were taken at different dates within the growing season for the different sampling periods, but time between two successive inventories is calculated accordingly. Since the 1970s, trees have been numbered, and dbh and condition (live, dead, and harvested) are recorded at each inventory.

Regeneration monitoring has been done since 1964 on the same time interval as saplings and merchantable trees, using three 4.05-m^2 subplots on the circumference of the 0.02-ha plots. Seedlings are counted by species and height classes (1 = 15–30 cm; 2 = 31–60 cm; 3 = 61–137 cm; 4 = $>$137 cm high with dbh $<$1.3 cm). Because young spruce seedlings are difficult to identify to species, they were pooled. However, on the basis of saplings and larger trees, it is clear that red spruce is the dominant spruce, with white spruce occasionally present and black spruce (*Picea mariana* [Mill.] B.S.P.) rarely found. In 2005, browsing on each seedling was monitored by the percentage of foliage consumed (0 = absence of browsing; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%).

Statistical Analyses

Abundance of Regeneration

Statistical analysis was not applied to data on white-cedar regeneration because the low abundance of this secondary species did not allow sufficient degrees of freedom for mixed analysis of variance (ANOVA) or enough observations for growth modeling. Consequently, descriptive statistics were used to illustrate changes in regeneration density over time.

Seedling Height Distribution

Chi-square test using exact *P* values was used to compare the height distributions of fir, hemlock, spruce species, and white-cedar seedlings at five moments during the last 40 years on the PEF (PROC FREQ, SAS 9.1, SAS Institute, Inc., Cary, NC). Pine species and tamarack (*Larix laricina* [Du Roi] K. Koch) occur rarely and were not included in the analysis. Every 10 years from 1965 to 2005, the distribution of each species by height class was compared with the overall expected distribution based on the 40-year average for all softwood species (Snedecor and Cochran 1967). This statistical analysis gave information about stratification by height class among softwood species over the entire measurement period, with the 40-year average used as reference base. If no inventory was available in a given compartment at a given year, the closest inventory was used ($\pm$2 years from the target year). Because the species-specific height-class distributions were undifferentiated among partial cutting treatments (data not shown), height distributions were computed for all treatments combined.

White-Cedar Sapling Dynamics

A total of 204 white-cedar saplings were numbered and monitored between 1973 and 2005 in the studied area. For the purpose of this analysis, these saplings were classed into three groups based on their dbh: small (1.3 cm $\leq$ dbh $\leq$ 4.6 cm), medium (4.7 cm $\leq$ dbh $\leq$ 8.0 cm), and large (8.1 cm $\leq$ dbh $\leq$ 11.4 cm). Trees with a dbh $>$11.4 cm are considered poletimber and were not included in this analysis. The 30-year period was split into three 10-year periods. During each period, a sapling may stay in the same group (dbh remaining between bounds during the entire period), grow into the next group, or die. No sapling had a sufficient diameter increment to grow through two groups during a 10-year period (i.e., a small sapling never grew to the large sapling group in 10 years). In addition, ingrowth into the small sapling class was counted at each period, as was the number of stems that recruited to the medium and large groups. The number of saplings at the beginning and end of each 10-year period and the distribution of saplings by dbh class were used to understand the development of the population. The low quantity of white-cedar saplings by compartment did not allow ANOVA on these data.

The dynamics of a group of stems during a 10-year period was computed to elucidate increment and mortality using a transition matrix from one condition to another during two consecutive times (Ministère des Ressources naturelles 1998). Dynamics were computed for each sapling group individually because increment and mortality rates varied according to sapling size. Periodic diameter increment (PDI) of individual saplings was calculated for all stems living during the entire 10-year period:

$$PDI_i = (D_B - D_A)/(Y_B - Y_A) \times 10, \quad (1)$$

where PDI_i = periodic diameter increment of period *i* (cm/10 years); D_B = diameter at the end of period *i* (cm); D_A = diameter at the beginning of period *i* (cm); Y_B = last year of period *i*; and Y_A = first year of period *i*. Years are corrected for month of monitoring.

Saplings that died during a given period were excluded from PDI calculation, but they were classified as killed by cutting or undetermined causes and used to estimate mortality rates. Because growth increment and mortality were undifferentiated by time period, data were pooled across the entire measurement period to increase the number of observations and the robustness of predictions for each diameter group.

Results

In the mid-1950s, all studied compartments had a canopy with mixedwood composition dominated by hemlock, fir, and spruces. On average, hemlock accounted for 31.0% of total basal area, fir for 20.7%, spruces for 20.5%, and white-cedar for 13.7%. About 40 years later, all compartments were still softwood-dominated, but the composition of the overstory was slightly different; it was still dominated by hemlock (31.0%), spruces (22.9%), and fir (22.0%), but white-cedar was reduced by half, to 6.7% (US Forest Service, unpublished data).

The understory has also been dominated by conifers since the beginning of monitoring. In the mid-1960s, 83.6% of regeneration was softwood species: fir (47.2% of all seedlings), hemlock (24.9%), spruces (8.3%), and white-cedar (1.5%). After 40 years of partial cutting, the abundance of conifers increased slightly, to 87.5%: hemlock, spruces, and white-cedar increased to 32.2%, 15.6%, and 3.4% respectively, and fir decreased to 35.7% (US Forest Service, unpublished data).

During the 40-year measurement period, fir seedlings taller than 15 cm were present on 66.8% of subplots, hemlock on 55.6%, spruces on 44.7%, and white-cedar on 10.5% (Table 1). All treatments had presence of all softwood species. Although density of

Table 1. Regeneration stocking (percentage of subplots with at least one seedling taller than 15 cm but with dbh <1.3 cm) by conifer species, treatment, and 10-year period, and mean density of stocked plots.

Treatment[a]	Year 1965	1975	1985	1995	2005	Mean density of stocked plots (seedlings/m^2)
	. . . .	. . .	.(%).	. . .	. . . .	
Balsam fir						
S05	59	69	73	65	65	1.4 ± 1.0
S10	66	74	87	81	81	2.8 ± 2.6
S20	38	40	81	75	74	2.0 ± 1.9
FDL	58	56	74	74	51	1.6 ± 1.1
Hemlock						
S05	49	63	70	70	74	2.2 ± 2.1
S10	24	44	53	42	37	2.3 ± 1.9
S20	12	41	86	85	78	2.9 ± 2.1
FDL	48	54	73	67	43	1.5 ± 2.0
Spruces						
S05	21	43	59	57	55	2.0 ± 1.0
S10	20	45	66	63	49	1.7 ± 2.7
S20	8	32	68	64	54	1.2 ± 1.4
FDL	28	38	64	43	19	0.8 ± 0.8
White-cedar						
S05	5	11	14	8	8	1.7 ± 1.8
S10	5	10	19	14	11	1.8 ± 1.9
S20	3	3	14	20	13	1.9 ± 2.0
FDL	7	10	15	14	6	1.4 ± 1.1

[a] S05, selection cutting with 5-year cutting cycle; S10, selection cutting with 10-year cutting cycle; S20, selection cutting with 20-year cutting cycle; FDL, fixed diameter-limit cutting.

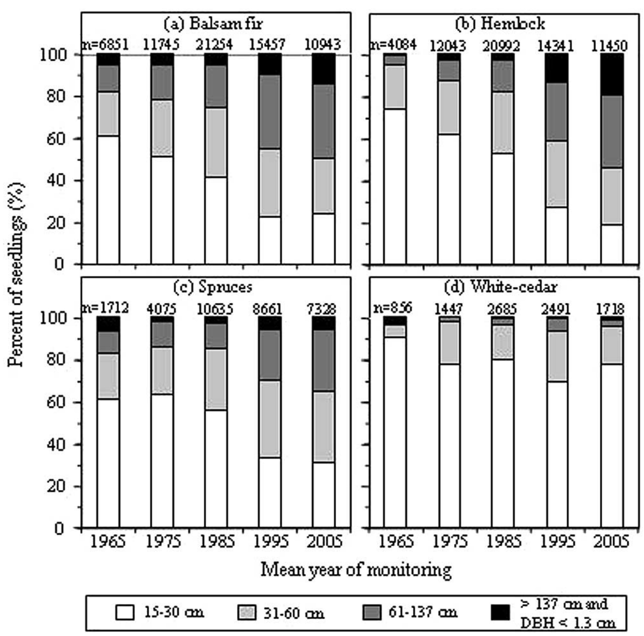

Figure 1. Distribution of seedlings by height class for balsam fir, hemlock, spruce species, and white-cedar. *n* values show the mean number of seedlings by hectare found in all partial cutting treatments by 10-year period.

seedlings on stocked plots (i.e., plots with ≥1 seedling) was similar for all species studied, lower stocking of white-cedar resulted in a mean density of fewer than 3 000 seedlings/ha. Mean densities of seedlings per hectare in the studied treatments are shown in Figure 1.

Seedling Height Distributions

The distribution of softwood seedlings by height class reveals that the proportion of fir, hemlock, and spruce seedlings in the shortest class (15–30 cm) in 1995 and 2005 was lower than the expected value ($P < 0.01$; based on the 40-year average for all softwood species) (Table 2; Figure 1). In other words, they were underrepresented. However, the proportion of these species in the two tallest classes (61–137 cm and >137 cm with dbh <1.3 cm) was greater than expected during the same periods ($P < 0.05$ or 0.01); they were overrepresented. The distribution of seedlings by height class is very different for white-cedar; the proportion of seedlings in the shortest class was always greater than expected ($P < 0.05$ or 0.01) (Table 2), whereas the proportion in the 61–137-cm class was also always lower than expected ($P < 0.05$ or 0.01).

Between 1965 and 2005, the proportion of seedlings in the two tallest classes increased by 10.8 times for hemlock, 2.8 times for fir, 2.1 times for spruce, and stayed exactly the same for white-cedar. Moreover, only 1.4% of white-cedar seedlings were taller than 137 cm during the 40-year measurement period, compared with 7.8% of hemlock, 7.6% of fir, and 4.8% of spruces (Figure 1).

Table 2. Height distribution of individual species at each 10-year period (expected, or 40-year average distribution of all species combined, shown as a percentage).

	Height class[a] 15–30 cm	31–60 cm	61–137 cm	>137 cm with dbh <1.3 cm
General distribution of all species and periods combined	54%	25%	16%	5%
1965				
Balsam fir				
Hemlock	+ +		− −	
Spruces				
White-cedar	+ +	− −	− −	
1975				
Balsam fir				
Hemlock				
Spruces				
White-cedar	+ +		− −	−
1985				
Balsam fir				
Hemlock				
Spruces				
White-cedar	+ +		− −	
1995				
Balsam fir	− −		+ +	
Hemlock	− −		+ +	+ +
Spruces	− −	+	+	
White-cedar	+		−	
2005				
Balsam fir	− −		+ +	+ +
Hemlock	− −		+ +	+ +
Spruces	− −		+ +	
White-cedar	+ +		− −	

[a] + or − indicates a significant difference superior or inferior to the general distribution ($\chi^2 = 3.84$, $P < 0.05$); + + or − − indicates a very significant difference superior or inferior to the general distribution ($\chi^2 = 6.63$, $P < 0.01$).

White-Cedar Sapling Dynamics

There were 21 live small (1.3 cm ≤ dbh ≤ 4.6 cm) white-cedar saplings on the sample plots at the beginning of the first numbered-tree measurement period (year = 1975) (Figure 2a). During the next 10 years, 15 of these saplings died, and four recruited to the medium (4.7 cm ≤ dbh ≤ 8.0 cm) class. However, ingrowth from the seedling stage was only 10 saplings, so there were 12 live small saplings at the end of the period. Between 1985 and 1995, ingrowth from the seedling stage was nine saplings; density of small saplings

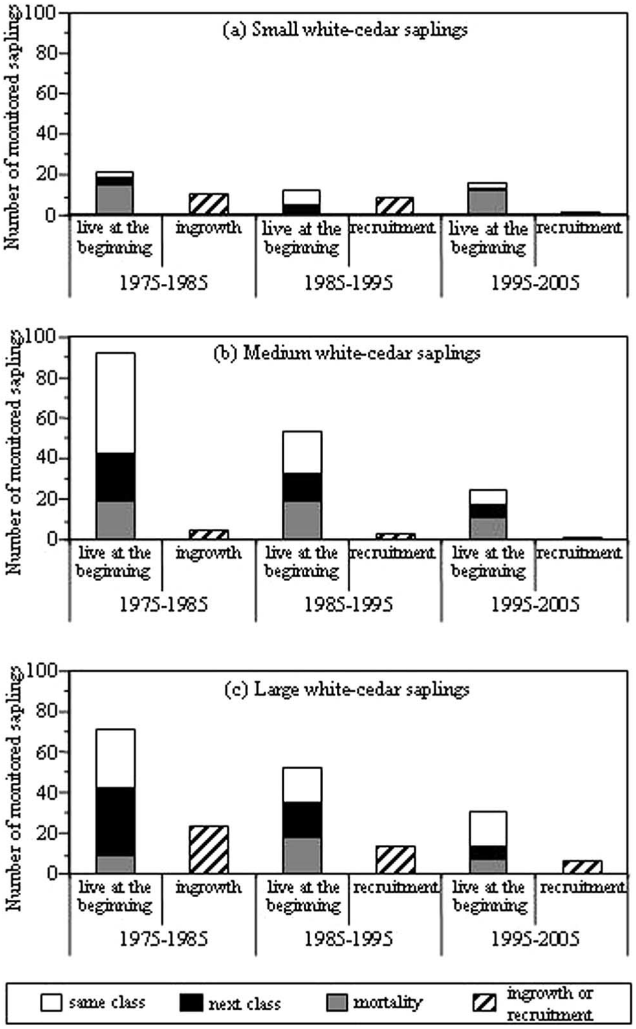

Figure 2. Dynamics of white-cedar saplings in 138 circular 0.02-ha plots over a 30-year period for small (1.3 cm ≤ dbh ≤ 4.6 cm), medium (4.7 cm ≤ dbh ≤ 8.0 cm), and large (8.1 cm ≤ dbh ≤ 11.4 cm) sapling size classes.

increased during that period because only two died and three recruited to the medium class. During the last period (1995 to 2005), 12 small saplings died, 1 recruited to the medium class, and there were 2 ingrowth saplings; there were thus only 3 live small saplings on the 138 sample plots in 2005.

The abundance of white-cedar saplings also decreased in the medium and large classes (8.1 cm ≤ dbh ≤ 11.4 cm) during the 30-year measurement period (Figure 2 b and c). Recruitment from smaller classes was always less than the sum of the number of saplings growing into the next larger class and the number of saplings that died. Thus, density progressively decreased from 1975 to 2005. About one-fourth of saplings in the medium class grew to the large class during each 10-year period, whereas about one-third of large saplings grew to the poletimber class.

Increment and Mortality Rates

Diameter increments of small, medium, and large saplings were 0.85, 0.94, and 1.63 cm/10 years, respectively (Table 3). Mortality rates were inversely proportional to the size of saplings: 58%, 29%, and 21% of small, medium, and large saplings, respectively. Harvesting operations accounted for 62.5% of large-sapling mortality, 32.7% of medium-sapling mortality, and 21% of small-sapling mortality. Other causes of mortality included browsing, self-thinning (mortality induced by competition for light and resources), desiccation, insects, and diseases. Monitoring in 2005 revealed that 92% of seedlings and small saplings >30 cm tall were browsed. Most of them had more than 50% of their foliage consumed by deer, whereas 20% had more than 75% of their foliage consumed.

Diameter increment and mortality rate suggest that if we follow 100 small saplings for 10 years, 32 will still be in the small-sapling class, 10 will have grown to the medium class, and 58 will have died before the end of the period (Table 3). In the medium-sapling class, only 29 saplings will die during the 10-year period, allowing 52 to stay in the same class and 19 to grow to the large-sapling class. In the large-sapling class, higher diameter increment and lower mortality would allow 41 saplings to stay in the same class and 38 to grow to the poletimber, while 21 will die.

Discussion

There was a sharp decline (81.3%) in the abundance of white-cedar saplings between 1975 and 2005. In 1975, there were 182 live white-cedar saplings on the measurement plots (65.9 stems/ha); there were only 34 (12.3 stems/ha) in 2005 (30 years later). The proportion of overstory basal area in white-cedar also declined by 50% in the study area since the early 1960s, whereas the number of merchantable trees was reduced by about 90% across the entire Forest Service study area since the early 1950s (US Forest Service, unpublished data). The reduction of merchantable trees is partially due to logging activities (Brissette 1996) but also to low recruitment of saplings. These dynamics may compromise the sustainability of white-cedar and thus the maintenance of ecological values in ecosystem-based management, in which it is important to maintain each individual species.

According to Brissette (1996), total softwood regeneration in the PEF partial cut treatments is profuse. Proximity of seed trees, receptivity of seedbeds, and moist environmental conditions all contributed to increases in the abundance of softwood regeneration over 40 years. White-cedar is a long-lived, shade-tolerant species noted to increase in frequency during succession in the mixedwood boreal forest (Bergeron and Dubuc 1989, Bergeron 2000). Regeneration of hemlock, spruce, fir, and white-cedar are favored by uneven-aged systems on the PEF (Table 1; Figure 1). Hemlock, spruce, and fir are prolific and adapted to a broad range of site conditions (Brissette 1996), and they are the most common species in the canopy, providing an abundant seed rain (Godman and Mattson 1976). These shade-tolerant seedlings are well adapted to establish on shady and moist forest floor and to colonize microsites warmed by increased available light after partial harvesting (Raymond et al. 2000). Moreover, these conifer seedlings and saplings are more shade-tolerant than associated hardwood species (e.g., red maple, birches, aspens) and maintain height growth even under partial shading (Moores et al. 2007).

However, the success of regeneration depends not only on the establishment of seedlings but also on the development and stratification of the new cohort (Grassi et al. 2003). Since 1985, the density of tall hemlock, fir, and spruce seedlings has been greater that the density of small ones (Table 2; Figure 1), engendering the vertical stratification of the regeneration cohort and limiting the availability of light for suppressed stems (Oliver and Larson 1996, Smith et al. 1997). Seedlings of these species are getting larger, but white-cedar seedlings are not. They may be staying <30 cm tall

Table 3. Diameter increment and mortality rates of white-cedar by sapling dbh class during a 10-year period.

Sapling dbh class	Bounds		Increment (cm/10 years)	n^a	Distribution			
	Minimum	Maximum			Same dbh class[b]	Next dbh class[c]	Mortality[d]	Total
	........(cm)........				....................(%)....................			
Small	1.3	4.6	0.85	50	32	10	58	100
Medium	4.7	8.0	0.94	167	52	19	29	100
Large	8.1	11.4	1.63	152	41	38	21	100

[a] Total number of saplings used to calculated the increment in each sapling dbh class.
[b] Saplings that stayed in the same dbh class.
[c] Saplings that recruited to the next dbh class.
[d] Saplings that died.

because light is limited, height growth may be limited by browsing, or they may be dying because of harvesting operations or other causes. Scott and Murphy (1987) found that 96% of white-cedar seedlings in their study did not reach a height of 25 cm or taller. Even if total abundance of white-cedar seedlings increased over 40 years, it is necessary to have new sapling ingrowth from the seedling stage to compensate for mortality and recruitment to the poletimber. To increase the density of saplings, ingrowth must be higher than recruitment and mortality rates. For white-cedar saplings, ingrowth is low and the mortality rate is high (Figure 2). This suggests that existing saplings that die (most of them) or grow to pole stage (few of them) are not replaced by seedlings growing into the sapling classes. This situation results in a white-cedar size structure biased toward merchantable stems.

White-cedar saplings may tolerate browsing pressure for many years by mortgaging height and diameter growth, but if browsing persists over a long period, they will die. Repeated browsing is more difficult to tolerate for slow-growing species, as white-cedar, than for fast-growing species (Côté et al. 2004). Browsing is often considered to be the primary factor contributing to the decline of white-cedar regeneration in regions with high deer densities (Alverson et al. 1988, Heitzman et al. 1997, Cornett et al. 2000). Field observations indicate that browsing of white-cedar seedlings is common on the PEF (US Forest Service, unpublished data; Larouche, unpublished data), whereas hemlock and fir are not consumed. Saunders and Puettmann (1999) found higher susceptibility to browsing for seedlings between 30 and 130 cm high in a study of eastern white pine in Minnesota; this may explain the higher abundance of unbrowsed white-cedar seedlings in the smallest height class compared with taller seedlings and saplings in the present study. The browsing pressure seems to be especially high on the PEF compared with the more northern regions of the Acadian Forest. It is possible to see more white-cedar regeneration in other parts of the region where deer populations are lower or topography is steep (personal observation). On the PEF, large saplings, mostly exempt from browsing pressure, are more often killed by cutting than medium and small saplings. Partial cutting generates damage to stems and roots of residual trees during logging and felling (Mitchell and Beese 2002). That may be an important problem for large saplings that are less flexible than small and medium saplings (Hannah 1988). Other possible causes of mortality may include interspecific competition for resources and self-thinning; drought of sites; winter desiccation; and physical damage by trampling, snow, and tree fall. Insects, such as mites (*Oligonychus* spp.) and leafminers (*Argyresthia* spp.), and diseases may attack mature white-cedar and also cause mortality (Rose et al. 2000), but few scientific studies have evaluated the impact of insects and diseases on white-cedar seedlings and saplings.

Considering the mean PDI of saplings, a small sapling needs 39 years to reach the medium-sapling class (Table 3). It takes about the same amount of time for medium saplings to reach the large-sapling class, whereas large saplings grow 3.3 cm dbh in only 20 years. This suggests that a sapling needs about 94 years at breast height to become merchantable in the PEF partial cuts. This result is very similar to that of Hofmeyer (2008), who found through stem analysis that it took 96 years for white-cedar trees to grow from sapling to poletimber size in northern Maine. Similarly, results from Larouche (2009) indicate that white-cedar stems of sexual origin need between 24 and 32 years to become 130 cm high in northern temperate forests without or with occasional browsing. That delay of recruitment to the pole stage is much higher than other associated tolerant softwood species (Hofmeyer 2008) and may be increased by preferential browsing pressure.

Management Implications

White-cedar sustainability is not the focus of silvicultural treatments on the PEF (Kenefic et al. 2005). Irregular to uneven-aged stand structures will persist because of partial cutting, but the composition of future stands will probably be different from that of current ones. There will be saplings and poles of hemlock, fir, and spruce, whereas white-cedar will be almost absent. It is not enough to maintain the stand structure and the vertical heterogeneity with multiple layers; the distribution of each individual species is also important to maintain.

This expected long-term change in composition creates an imbalance in the natural dynamics of the study stands and compromises the sustainability of the resource. It may be time to favor white-cedar through interventions such as keeping large, long-living white-cedar as seed trees; such trees are often cut because of internal decay (US Forest Service, unpublished silvicultural prescriptions). In addition, control of the deer population would limit browsing. It may also be possible to add precommercial thinning to increase available growing space and resources by cutting competitive species and controlling stand species composition (Brissette et al. 1999). White-cedar seedlings established under partial canopy and saplings may grow faster under high sunlight conditions (Larouche 2009) or stay suppressed by stratification or be killed by self-thinning (Oliver and Larson 1996). Suppressed stems must survive under a dominated position and maintain the capacity to react to canopy opening after many years to qualify for release (Schütz 2002); white-cedar demonstrates these characteristics after many years of suppression (Larouche et al. 2007, Hofmeyer 2008). Consequently, we recommend partial harvesting to encourage advance regeneration, browsing control to minimize seedling stress, and targeted release of white-cedar saplings in subsequent entries to promote height growth.

Subsequent partial harvest entries present an ideal opportunity to make sure that the most difficult-to-recruit species receive the needed follow-up release to preserve their continued presence in mixedwood stands.

Conclusion

White-cedar seedlings have established in all partial cutting treatments studied on the PEF, even at relatively high deer population densities, but few have grown taller than 30 cm. Although it appears that the fir, spruce, and hemlock regeneration cohorts have increased in size over time, the white-cedar cohort has not. Consequently, there has been a progressive reduction in the density of white-cedar saplings. Ingrowth from the seedling to sapling stage has been lower than the combined rates of mortality and recruitment to the pole stage, and the number of white-cedar saplings is now >80% less than it was at the beginning of the measurement period. Sapling mortality is high and recruitment to larger size classes is low, although mortality decreases and recruitment increases as sapling size increases. Browsing is prolific; 90% of seedlings and small saplings showed signs of browse in 2005. Overall, white-cedar sapling growth is slow, taking almost 100 years to grow from small sapling to merchantable size. Efforts to release white-cedar saplings and control browsing pressure are recommended. Future research should address the impacts of a broader range of silvicultural treatments, site characteristics, and browsing pressures on white-cedar dynamics and further investigate the advantages and disadvantages of various silvicultural treatments for growth of white-cedar regeneration.

Literature Cited

ALVERSON, W.S., D.M. WALLER, AND S.L. SOLHEIM. 1988. Forests to deer: Edge effects in northern Wisconsin. *Biol. Conserv.* 2(4):348–358.

ARCHAMBAULT, L., J. BEGIN, C. DELISLE, AND M. FORTIN. 2003. Dynamique forestière après coupe partielle dans la Forêt expérimentale du Lac Édouard, Parc de la Mauricie, Québec. *For. Chron.* 79(3):672–684.

BERGERON, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* 81(6):1500–1516.

BERGERON, Y., AND M. DUBUC. 1989. Succession in the southern part of the Canadian boreal forest. *Vegetatio* 79(1–2):51–63.

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 Fenn.* 30(2–3):301–314.

BRISSETTE, J.C., R.M. FRANK, T.L. STONE, AND T.A. SKRATT. 1999. Precommercial thinning in a northern conifer stand: 18-year results. *For. Chron.* 75(6):967–972.

CHIMNER, R.A., AND J.B. HART. 1996. Hydrology and microtopography effects on northern white-cedar regeneration on Michigan's Upper Peninsula. *Can. J. For. Res.* 26(3):389–393.

CORNETT, M.W., L.E. FRELICH, K.J. PUETTMANN, AND P.B. REICH. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biol. Conserv.* 93(3):359–369.

CÔTÉ, S.D., T.P ROONEY, J.-P. TREMBLAY, C. DUSSAULT, AND. D.M. WALLER. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35(1):113–147.

DAVIS, A., K. PUETTMANN, AND D. PERALA. 1998. *Site preparation treatments and browse protection affect establishment and growth of northern white-cedar.* US For. Serv. Res. Pap. NC-330.12 p.

FRELICH, L.E., AND C.G. LORIMER. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Cons.* 34(2):99–120.

GODMAN, R.M., AND G.A. MATTSON. 1976. *Seed crops and regeneration problems of 19 species in Northeastern Wisconsin*. US For. Serv. Res. Pap. NC-123. 10 p.

GRASSI, G., G. MINOTTA, R. GIANNINI, AND U. BAGNARESI. 2003. The structural dynamics of managed uneven-aged conifer stands in the Italian eastern Alps. *For. Ecol. Manag.* 185(3):225–237.

GRIGAL, D.F., AND L.F. OHMANN. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecol. Monogr.* 45(4):389–407.

GULDIN, J.M. 1991. Uneven-aged BDq regulation of Sierra Nevada mixed conifers. *West. J. Appl. For.* 6(2):27–32.

GULDIN, J.M. 1996. The role of uneven-aged silviculture in the context of ecosystem management. *West. J. Appl. For.* 11(1):4–12.

HANNAH, P.R. 1988. The shelterwood method in the Northeastern forest types: A literature review. *North. J. Appl. For.* 5(1):70–77.

HEITZMAN, E., K.S. PREGITZER, AND R.O. MILLER. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Can. J. For. Res.* 27(12):1953–1961.

HOFMEYER, P.V. 2008. *Ecology and silviculture of northern white-cedar (Thuja occidentalis L.) in Maine.* PhD thesis, School of Forest Resources, University of Maine, Orono, ME. 160 p.

JOHNSTON, W.F. 1972. *Balsam fir dominant species under rethinned northern white-cedar.* US For. Serv. Res. Pap. NC-133. 4 p.

JOHNSTON, W.F. 1990. *Thuja occidentalis* L.—Northern white cedar. P. 1189–1209 in *Silvics of North America. Vol. 1: Conifers*, Burns, R.M., and B.H. Honkala (eds.). US For. Serv. Agricultural Handbook, Washington, DC.

KENEFIC, L.S., AND R.D. NYLAND. 2005. *Diameter-limit cutting and silviculture in northeastern forests: A primer for landowners, practitioners, and policy makers.* US For. Serv. Northeastern Area State and Private Forestry. NA-TP-02-05. 18 p.

KENEFIC, L.S., P.E. SENDAK, AND J.C. BRISSETTE. 2005. Fixed diameter-limit and selection cutting in northern conifers. *North. J. Appl. For.* 22(2):77–84.

KENEFIC, L.S., P.E. SENDAK, AND J.C. BRISSETTE. 2006. Turning data into knowledge for over 50 years: USDA Forest Service research on the Penobscot Experimental Forest. P. 26–33 in *Long-term silvicultural and ecological studies: Results for science and management*, Irland, L., A. Camp, J. Brissette, and Z. Donohew (eds.). Yale University, Global Institute for Sustainable Forestry, New Haven, CT. GISF Res. Pap. 005.

LAROUCHE, C. 2009. *La régénération du thuya après coupes partielles en peuplements mixtes.* PhD dissertation, Univ. Laval, Québec, QC, Canada. 170 p.

LAROUCHE, C., S. MORISSETTE, J.-C. RUEL, J.-M. LUSSIER, AND L.S. KENEFIC. 2007. Regeneration and growth of *Thuja occidentalis* in mixedwood stands after partial cutting. in *Proc. of stands on Carrefour de la recherche forestière*, Québec, QC, Canada. Available online at www.mrnf.gouv.qc.ca/carrefour/recherche/crf_affichage_detail_globale.asp?projet=XW2148; last accessed June 16, 2009.

MAINE DEPARTMENT OF INLAND FISHERIES AND WILDLIFE. 2007. *White-tails in the Maine Wood.* Available online at www.state.me.us/ifw/wildlife/species/deer/index.htm; last accessed June 16, 2009.

MARQUIS, D.A. 1978. Application of uneven-aged silviculture and management on public and private lands P. 25–61 in *Uneven-aged silviculture and management in the United States. Combined proceedings of two in-service workshops.* Morgantown, WV, and Redding, CA. US For. Ser. Gen. Tech. Rep. WO-24.

MINISTERE DES RESSOURCES NATURELLES. 1998. *Manuel d'aménagement forestier, document d'annexes.* Direction des programmes forestiers, RN98–3045. 122 p.

MITCHELL, S.J., AND W.J. BEESE. 2002. The retention system: Reconciling variable retention with the principles of silvicultural systems. *For. Chron.* 78(3):397–403.

MOORES, A.R., R.S. SEYMOUR, AND L.S. KENEFIC. 2007. Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands. *Can. J. For. Res.* 37(12):2715–2723.

OLIVER, C.D., AND B.C. LARSON. 1996. *Forest stand dynamics.* John Wiley & Sons, New York. 467 p.

PUETTMANN, K.J., AND C. AMMER. 2007. Trends in North American and European regeneration research under the ecosystem management paradigm. *Eur. J. For. Res.* 126:1–9.

RAYMOND, P., J.-C. RUEL, AND M. PINEAU. 2000. Effet d'une coupe d'ensemencement et du milieu de germination sur la régénération des sapinières boréales riches de seconde venue du Québec. *For. Chron.* 76(4):643–652.

ROONEY, T.P., S.L. SOLHEIM, AND D.M. WALLER. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. *For. Ecol. Manag.* 163(1):119–130.

ROSE, A.H., O.H. LINDQUIST, AND K.L. NYSTROM. 2000. *Insects of eastern larch, cedar, and juniper.* Forest Tech. Rep. 28F. Natural Resources Canada, Canadian Forest Service, Headquarters, Science Branch, Ottawa, ON. 130 p.

SAFFORD, L.O., R.M. FRANK, AND E.L. LITTLE. 1969. *Trees and shrubs of the Penobscot Experimental Forest, Penobscot Country, Maine*. US For. Serv. Res. Pap. NE-RP-128. 27 p.

SAUNDERS, M.R., AND K.J. PUETTMANN. 1999. Use of vegetational characteristics and browsing patterns to predict deer damage in eastern white pine (*Pinus strobus*) plantations. *North. J. Appl. For.* 16(2):96–102.

SCHAFFER, W.W. 1996. *Silvicultural guidelines for the eastern white cedar.* Ont. Nat. Res. Southern Region Science and Technology Transfer Unit, Tech. Rep. 006. 62 p.

SCHÜTZ, J.-P. 2002. Silvicultural tools to develop irregular and diverse forest structures. *Forestry* 75(4):329–337.

SCOTT, M.L., AND P.G. MURPHY. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *Am. Midl. Natur.* 117(1):10–16.

SENDAK, P.E., J.C. BRISSETTE, AND R.M. FRANK. 2003. Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from Penobscot Experimental Forest. *Can. J. For. Res.* 33(11):2116–2128.

Sendak, P.E., Frank, R.M., and Leak, W.B. 2006. Long-term data from Silvicultural studies: Interpreting and assessing old records for economic insights. P. 203–207 in *Long-term silvicultural and ecological studies: Results for science and management.* Yale University, New Haven, CT.

Seymour, R.S. 1995. The northeastern region. P. 31–79 in *Regional silviculture of the United States*, 3rd ed. John Wiley & Sons, New York.

Seymour, R.S., and L.S. Kenefic. 1998. Balance and sustainability in multi-aged stands: A northern conifer case study. *J. For.* 96(7):12–16.

Seymour, R.S., and M.L. Hunter, Jr. 1992. *New forestry in eastern spruce-fir forests: Principles and applications to Maine.* US Agricultural Experiment Station, Orono, ME. Pub. 716. 36 p.

Seymour, R.S., A.S. White, P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America: Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* 155(3):357–367.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. *The practice of silviculture: Applied forest ecology.* John Wiley & Sons, New York. 537 p.

Snedecor, G.W., and W.G. Cochran. 1967. *Méthodes statistiques*, 2nd ed. Association de coordination technique agricole, Paris, France. 230 p.

Wein, R.W., and J.M. Moore. 1977. Fire history and rotations in the New Brunswick Acadian Forest. *Can. J. For. Res.* 7(2):285–294.

Wein, R.W., and J.M. Moore. 1979. Fire history and recent fire rotation periods in the Nova Scotia Acadian Forest. *Can. J. For. Res.* 9(2):166–178.