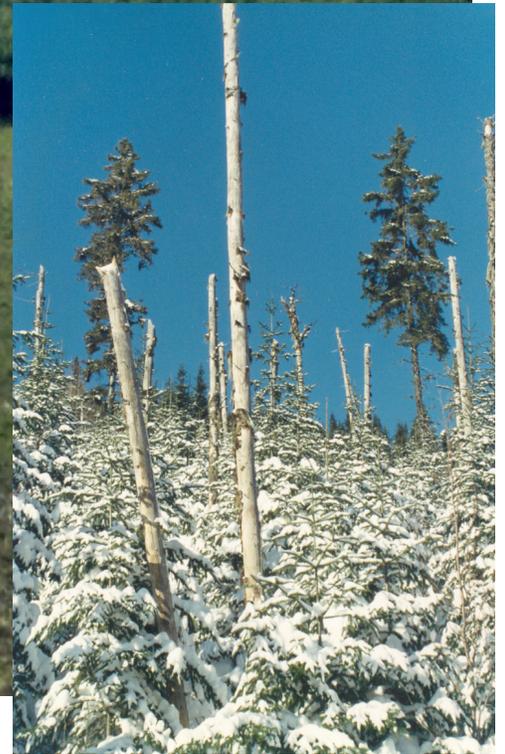


# Long-term Impacts of Timber Harvesting on Stand Structure in Northern Hardwood and Spruce-Fir Forests



**Implications for Biodiversity and Timber Production**

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MAINE   
AUDUBON

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# Long-term Impacts of Timber Harvesting on Stand Structure in Northern Hardwood and Spruce-Fir Forests:

Implications for Biodiversity and Timber Production

## ABSTRACT

### Introduction

This study compares forest stand structures that develop over time when biodiversity recommendations are incorporated into silviculture with stand structures that result from conventional, financially-motivated management systems. In addition, we explore the management implications of the results and provide some suggestions on prioritizing biodiversity recommendations and measuring progress toward biodiversity goals. The results of this study should be generally applicable across the Northern Forest - Acadian Forest region that ranges from the Tug Hill plateau in New York to Nova Scotia and from southern Quebec to central New England and in the Great Lakes region where similar forest types are found.

### Methods

The FIBER (Solomon et al. 1994) and NE TWIGS (Teck 1990) growth models were used to project the growth of stands under different silvicultural treatments. Projection periods were 70 years. Uneven-aged management in northern hardwoods was modeled by simulating partial harvests on an approximate 20-year cycle. Three runs were evaluated, including a comparatively light, uniform cut across all diameter classes for the HW BIO run, light selection harvesting for large sawtimber (HW LGSAW), and a heavy diameter-limit in the HW HIGH GRADE run. Spruce-fir management was simulated under two shelterwood regimes. The SF BIO retained 10% of the original stand to provide legacy structure, while the SF TIMBER run removed all the residual overstory after establishment of the new stand. Mortality was derived from the model outputs. Snag decay equations were developed from US Forest Service Forest Inventory and Analysis (FIA) remeasured plots in New Hampshire and Vermont.

### Results

Analysis of the FIA data suggests that almost all snags have broken up and fallen by 40 years. For uneven-aged northern hardwoods, goals for snags and stand maturity can be met by managing for large sawtimber. Goals for large snags and stand maturity cannot be met with the diameter-limit approach modeled here. The HW HIGH GRADE run produced the greatest harvest volume, while standing sawtimber volumes at the end of the HW BIO and HW LGSAW runs was more than double that of HW HIGH GRADE. For even-aged spruce-fir, the goal for snags was only met at the end of the rotation under either the biodiversity or timber approach. Likewise, after 70 years neither the SW BIO or SW

TIMBER stands reached a biologically-mature stage. Volume production was 10% higher in the SW TIMBER stand.

## **Discussion**

Biologically-mature forests that include large dead and living trees and downed wood are important components of native biodiversity. Of the approaches tested, uneven-aged management in northern hardwoods with a goal of large sawtimber production appears to be best suited to meeting stand-level goals for deadwood production and biological maturity while maximizing sawtimber growth. The same goals are unlikely to be met with a 70-year shelterwood rotation in spruce-fir. Depending on rotation, similar concerns might arise with even-aged management of northern hardwoods. These findings suggest that where even-aged management is practiced, within-stand retention alone will be inadequate to maintain conditions associated with biological maturity unless rotations are considerably longer than is typical. Thus, a landscape approach to management that integrates rotation length and/or a mix of silvicultural techniques is essential to ensure that recommended goals for biologically-mature forests will be met.

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## INTRODUCTION

Conserving the ecological integrity of the managed forest requires careful attention to both stand and landscape-level factors as well as special-value areas within the forest. Recently, regional guidelines have been developed for conservation of biological diversity and ecological processes within managed forests. While some recommendations such as maintaining snags and cavity trees have a relatively long history, others such as structural retention in even-aged harvests, are relatively new. With the growth of forest certification systems these practices are taking on greater significance as more landowners seek to include biodiversity objectives in their management while managing more intensively for timber production.

In 1999 the Maine Forest Biodiversity Project (MFBP), a collaborative process involving scientists and managers from academia, public agencies, forest industry and environmental groups, published a manual of consensus recommendations for the conservation of biodiversity on managed forest lands (Flatebo et al. 1999). A similar effort was undertaken in New Hampshire (NHFSSWT 1997). These recommendations generally take the form of a menu of options rather than a comprehensive plan for conservation. Landowners generally choose a suite of recommendations that best fit their management style and objectives. Because these recommendations are relatively new, they have only been partially evaluated over the short term in a few controlled scientific studies. There is little or no information on the long-term implications of applying these recommendations.

The primary focus of this study was to compare stand structures that develop over time by applying biodiversity recommendations with those found in more conventional, financially-motivated management systems. In addition, we explored the management implications of the results and provide some suggestions on prioritizing biodiversity recommendations and inventory and classification for biodiversity management. The results of this study should be generally applicable across the Northern Forest - Acadian Forest region that ranges from the Tug Hill plateau in New York to Nova Scotia and from southern Quebec to central New England. General concepts that emerge may apply more broadly to other regions where similar forest types or silvicultural practices are found.

## TERMS AND CONCEPTS

### Biological Diversity

There are various definitions of biodiversity, but most are similar to that used by the MFBP:

*Biodiversity refers to the variety of all forms of life – trees and other plants, invertebrate and vertebrate animals, and microorganisms – and includes the different levels on which life operates – from the level of genetic differences between individuals to the complex interactions within ecosystems (Gawler et al. 1996).*

From a practical standpoint biodiversity is impossible to measure since it is so all-encompassing and includes many elements about which we know very little. There are mathematical measures of *diversity* used in the ecological sciences. These are typically applied to a small suite of organisms that we can measure, such as vertebrates and plants, but they do not measure the entirety of biodiversity. Moreover, the term itself is frequently misinterpreted to mean “more is better.”

One benchmark frequently suggested by conservation biologists is the biological diversity of native ecosystems prior to European settlement, sometimes referred to as “native” or “natural” biodiversity. Most conservation biologists do not advocate trying to re-create the pre-settlement forest, but they do advocate for maintaining the full suite of species and forest types that occurred at that time.

Since biodiversity cannot be measured, it is common to manage for a suite of surrogates under the assumption that if managers provide the right conditions, native biodiversity can be maintained. Critical elements of biodiversity that should be maintained by forest managers are summarized in Table 1.

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**Table 1. Key elements of biodiversity to be maintained in managed forests**

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- Rare, threatened, and endangered species and their habitats
  - Well-distributed native forest communities in a range of development stages (from regeneration to old growth) sufficient to sustain healthy populations of native flora and fauna
  - Natural forest structures, such as snags and large trees
  - Ecological processes, including succession and nutrient cycling typical of natural forests
  - Sensitive habitats and rare or exemplary natural communities
- 

### **Matrix Forest and Special Value Areas**

The MFBP guidelines include over 190 recommendations that can be used by land managers to conserve native biodiversity in managed forests. In general, biodiversity guidelines can be placed in two categories: those that pertain to management of special value and/or sensitive areas, such as endangered species habitats and riparian zones, and those that pertain to the general forest matrix. Several large timberland owners in northern Maine have reported classifying roughly 20% of the forest as special value areas and the remaining 80% as matrix forest.

Matrix forest provides the vast majority of plant and wildlife habitat. Northern hardwoods, spruce-fir, white pine, and red oak are among some of the most widespread communities that make up the matrix forest. Because of suitable soils, valuable species, and significant landscape cover, matrix forest is where most commercial forestry occurs. Given the importance to biological diversity and economic interests combined with the general lack of regulatory oversight (most forestry laws focus on special value areas), there is a real need to carefully manage matrix forests.

Special value areas, which are often embedded within the matrix forest, significantly increase overall forest biodiversity. They are frequently managed for timber, but only after standard practices are modified to protect ecological values.



*Special value areas, such as this stream and wetland complex, are embedded within the Matrix Forest*

## Stand and Landscape

Biodiversity recommendations can generally be divided into stand-level and landscape-level recommendations. The stand-level recommendations, such as maintaining snags and cavity trees, are frequently applied on a variety of ownerships. Stand-level recommendations often have relatively strong scientific underpinnings and are the easiest for foresters to apply. The science of landscape ecology is less well developed, as are the available tools for implementation. An additional issue is that small woodland owners cannot implement landscape recommendations on a broad scale. However, it is possible to manage small ownerships within the context of the surrounding landscape and provide elements of biological diversity that may otherwise be missing.

## Stand Structure and Development

Because biodiversity values and ecological processes vary greatly with stand maturity, it is important to be able to classify stands in a way that reflects their ecological development. While the MFBP provided recommendations for maintaining or restoring relatively mature, mature, and late successional forest, these terms were not defined. Because stand age is only meaningful in a truly even-aged situation, a structural development class approach (e.g., Oliver and Larsen 1986) is generally preferable. The Oliver and Larsen system is based on the structural changes that occur within a stand as it matures. This system was adapted by the MFBP, but both are essentially linear models that assume an even-aged stand initiation (i.e., beginning with a clearcut or other severe disturbance) and do not reflect the variety of structures and pathways resulting from smaller natural disturbances or partial harvests that characterize many Northeastern forests. The structural classification system proposed in Table 2 builds on the work of Oliver and Larsen, the MFBP, and the Maine Council on Sustainable Forest Management (MSCFM, 1996) but is designed to classify stand structures along a maturity continuum that develops in both natural and managed forests. This system was used to evaluate the relative maturity stands in this study.



*An integrated approach to management at the stand and landscape level is essential to maintain healthy populations of animals like the American* of

More simplified approaches have been proposed that enable classification with standard inventory data. DeGraaf et al. (1992) use a system based on tree diameter and basal area. MSCFM (1996) used a similar approach, but added vertical structure as well. A combination of these two systems has been recently proposed by Maine Forest Service as part of Maine's biodiversity benchmarks (MDOC 2003).

**Table 2. Stand structural development classes for ecologically-based management**

Forest Structural Development Classification for Managed and Unmanaged Stands		Ecological Development Stage (Flatebo et al. 1999)	MCSFM (1996)	Degraaf et al. 1992; MDOC 2003
Class	Description			
Stand Initiation (0-20 years)	Early regeneration prior to canopy closure (typically <15 years) ; predominant stocking in trees < 10 ft	Stand Initiation (10 to 30 years)		Regeneration
Early Stem Exclusion (20-50 years)	Closed canopy, trees 10-40 ft and 1-6 in. DBH.	Stand Initiation-Stem Exclusion	Immature	
Young Multi-story	Young stands with partial residual overstory (<30% canopy closure) of significantly larger trees.	None	Relatively Mature if understory >20ft. tall	Sapling & Poletimber
Indeterminate	Post harvest, residual overstory (30-60% canopy closure), transitional to Young Multi-story or Understory Reinitiation, depending on stem size and residual stocking	None	None	None
Late Stem Exclusion (50-80 years)	Closed canopy, trees > 50 ft. and >6 in. DBH with competition the primary source of mortality. Little understory development. Increasing numbers of wildlife species associated with older forests likely to be found;	Stem Exclusion	Relatively Mature	
Understory Reinitiation (60-100 years)	Maturing stands that have residual mature forest components and/or gaps with younger development classes. Typical of thinned even-age stands or small-diameter selection stands.		Relatively Mature or Mature	Poletimber and Small Sawtimber
Mature >70 years for balsam fir, aspen, and birch >100 years for spruce and northern hardwoods	Canopy typically > 70 ft. with DBH of dominant trees typically >12 in. for spruce-fir, >16 in. for most hardwoods, and >20 in. for white pine and hemlock. Net growth slowing in unharvested stands; principle mortality in canopy due to pathogens, wind, and insects. Large-diameter dead wood accumulating in standing trees and on the ground. Typically one or more age classes represented in the understory or in gaps but may be virtually even-aged in the case of pine and hemlock. When long-lived species with medium to high shade tolerance are present, this stage can be maintained over time by individual-tree or group selection management.	Understory Reinitiation	Mature	
Old Growth (>150 years)	Unharvested or very limited harvest history	Old Growth (>150 years)	None	Large Sawtimber
Transitional	Mortality significantly exceeds growth leading to significant canopy loss and a new development class; typical of stands dominated by short-lived species (e.g., balsam fir, poplar, or paper birch)	Understory Reinitiation (in part)	None	

*Note: Tree heights, diameters, and ages will vary with species and site quality.*

## METHODS

The central goal of this study was to see if stand characteristics recommended for conserving native biodiversity can be developed and maintained over time using the even-aged and uneven-aged recommendations provided in the MFBP and other guidelines and to compare those results with management regimes that do not include biodiversity considerations. The even-aged recommendations were tested in the spruce-fir type, while the northern hardwood type (maple-beech-birch) was used to evaluate uneven-aged management recommendations. This project focused on the matrix forest, where a vast majority of forestry takes place.

Because a long-term operational test was not feasible due to time constraints, computer modeling was used to evaluate changes in stand structures over a 70-year period. This time period was selected because it coincides with the outer limit of expected even-aged rotations for spruce-fir, would allow the simulation of several selection harvests, and is near the limit of reasonable accuracy that can be expected for northeastern stand models. Moreover, a range of stand development stages from early or intermediate stand development through mature could be modeled, depending on the starting point of the projection. Maine Audubon contracted the L.E. Caldwell Company of Turner, Maine to model the growth and harvest. The FIBER growth model (Solomon et al. 1994), version 9.0, run on the FlexFIBER inventory and growth projection platform (Brann and Solomon 2001) was the primary model used in the study. Because FIBER is designed for pole-sized and larger stands, NE TWIGS (Teck 1990) was used where it was necessary to model the development of younger stands.

The MFBP *Guidelines for Land Management* include approximately 40 stand-level recommendations and 30 landscape-level recommendations. A suite of recommendations was selected for testing that a) could be tracked with existing stand models, b) are broadly accepted as being important for biodiversity<sup>1</sup>, and c) serve as a surrogate for other values covered by the recommendations (for example, managing for large snags should provide a steady supply of downed woody debris). The key recommendations considered by this project are shown in Table 3.

Two or three model runs were conducted in each forest type. The first run for each type was a moderately aggressive timber production run without consideration for biodiversity. The second runs apply a suite of biodiversity recommendations. The northern hardwood analysis included a third run that simulated the impacts of “high-grading” based on harvests of all the largest diameter trees. Standing and harvest volumes as well as stand structures (trees per acre by diameter class and basal area per acre of live and dead trees) were tracked over time for each of the runs. These resulting stand structure data (e.g., number of canopy layers, tree diameter, and canopy closure) were compared with the structure class descriptions (Table 2) to place the stands in one of several possible structural development classes. Because of the relatively small data set, this could be done manually; operational applications on large ownerships would require the development of an algorithm to classify the stands.

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<sup>1</sup> Opinions may vary as to the appropriate level of snags, area in retained patches, or amount of mature forest that is necessary, however there is little or no dispute that these are important elements of biodiversity management.

**Table 3. Key recommendations of the Maine Forest Biodiversity Project and related guidelines considered by this study**

Stand-Level:

- Under even-aged management, retain patches or scattered trees from the original stand, including several >12 in. DBH, into the next rotation. Uncut patches should amount to at least 5% of the harvest area with one snag or den tree >18 in. DBH as the patch nucleus. Flatebo et al. (1999) and the New Hampshire guidelines (NHFSSWT 1997) recommend leaving uncut patches amounting to 5% of the harvest area.
- Under uneven-aged management, maintain approximately 3-5% of the stocking as potential cavity trees and a source of future snags.
- Leave three cavity trees or snags per acre 14 in.-24 in. DBH and one tree >24 in. DBH or live trees in these diameters likely to lead to cavity formation<sup>1</sup>.

Landscape Level:

- Maintain the landscape matrix in relatively mature, well-stocked stands and retain or restore a significant portion of the ownership to mature, late-successional forest<sup>2</sup>.

<sup>1</sup> Flatebo et al. (1999) make this recommendation for uneven-aged stands but provide no minimum snag/cavity tree recommendation for areas under even-aged management. An earlier set of guidelines (Elliott 1988) recommends 60 snags or cavity trees per 10 acres (i.e., 6 per acre on average) >12 in. and two per 10 acres greater than 22 in. without regard to management technique. NHFSSWT (1997) recommends a total of six snags or cavity trees per acre with one > 18 in. and three > 12 in. for all stands. Maine has recently adopted a statewide goal of 4 snags plus 4 rough and rotten trees per acre ≥15 in., including one each ≥21 in (MDOC 2003).

<sup>2</sup> The Maine Forest Service biodiversity goals include at least 20% of the state in small sawtimber stands and 10% in large sawtimber stands ≥ 15 in. DBH and a basal area ≥100 ft<sup>2</sup>/ac. (MDOC 2003). DeGraaf et al. (1992) recommend a landscape with a minimum of 40% in sawtimber classes with < 10% in large sawtimber >20 in.

## Modeling Snag Density

Both FlexFIBER and NE TWIGS predict tree mortality on a periodic basis, but these dead trees are not retained by the models over time, nor do the models predict the fall rates of snags over time. Three critical parameters are necessary to estimate the density and size of snags over time: 1) the rate of mortality by diameter class; 2) the percent of trees that die due to windthrow (i.e., they never enter the snag population); and 3) the percent of snags from any particular cohort fallen as a function of time. Mortality by diameter class was predicted by FlexFIBER and NE TWIGS. Windthrow rates were estimated from FIA data for dead trees recorded on permanent plots in New Hampshire and Maine and data collected by the author in the Tug Hill region of New York.

Snag fall equations based on a logistic curve equation and developed by Lester (2002) for Massachusetts forests were adapted for northern New England and applied to the mortality predicted by FlexFIBER. The general equation used was:

$$Y = \frac{l}{1 + (c * EXP(b * t))}$$

where  $Y$  is the percent of snags fallen,  
 $l$  is the limit (100% in this case),  
 $c$  is a constant (999 for this type of data),  
 $b$  is a species-specific constant derived from field data, and  
 $t$  is time in years.

Snag fall rates were developed from a sample of 1,700 dead trees on FIA remeasured plots located in Maine, New Hampshire, and Vermont. The average remeasurement period was 14 years. The Species-specific constants (*b*) were developed by fitting the general equations developed by Lester to the northern New England data. The resulting equations could then be applied to the mortality predicted by FlexFIBER and NE TWIGS.

### **Selection Silviculture in Northern Hardwoods**

The uneven-aged recommendations were evaluated for northern hardwood stands using FIBER. Eight northern hardwood plots located in Grafton County, New Hampshire were selected from the USDA Forest Inventory and Analysis (FIA) dataset to represent a well-stocked hardwood pole/small sawtimber stand. Basal area of live trees  $\geq 4.5$  inches DBH averaged 99 ft<sup>2</sup>/ac with a quadratic mean stand diameter of 9.1 in.; 83% of the stocking was in trees <15 inches DBH.

The model runs are equally applicable to the single tree or small group (i.e., up to 0.25 ac openings) selection method of silviculture. Both the HW BIO and HW LGSAW runs remove similar amounts of basal area on a 20 to 30 year cutting cycle (Table 4). HW LGSAW has an objective of large sawtimber production without specific biodiversity considerations. The initial harvest in the HW LGSAW run removed most of the basal area from the larger diameter classes (60% from trees  $\geq 12$  inches DBH) to increase revenues early in the management cycle. In contrast, the initial HW BIO (Biodiversity) harvest removed more volume from the smaller classes (75% from trees <12 inches) in an attempt to build a cohort of large trees and decadent material more quickly. For subsequent harvests the basal area removal by diameter class was similar for both runs. Under both scenarios the residual stand was within 10% of the “B-Line,” which is the suggested residual stocking for northern hardwoods under even-aged (Leak et al. 1987) and uneven-aged management (Solomon et al. 1994). The HW HIGH GRADE run was a modified diameter limit harvest: the stand was cut to the C-line by cutting all trees >16 inches DBH first and then cutting trees in the 6-15 inches DBH range until the stocking target was reached.

**Table 4. Parameters for Northern Hardwood model runs**

<b>Year</b>	<b>HW HIGH GRADE</b>	<b>HW LGSAW</b>	<b>HW BIO</b>
1	Initial basal area 99 ft <sup>2</sup> /ac. Harvest to C-line, cutting all trees >16 in. DBH first, then trees 6-15 in.	Initial basal area 99 ft <sup>2</sup> /ac. Harvest within 10% of B-line, cutting 60% of volume from trees $\geq 12$ in.	Initial basal area 99 ft <sup>2</sup> /ac. Harvest to within 10% of B-line, cutting 75% from trees <12 in.
21-71	Harvest to C-line on 20-30 year cycle, cutting all trees >16 in, then trees 6-15 in, when approximately 30 ft <sup>2</sup> /ac available for harvest.	Harvest to within 10% of B-line on 20-30 year cycle when stand reaches approximately 85 ft <sup>2</sup> /ac.	Harvest to within 10% of B-line on 20-30 year cycle when stand reaches approximately 85 ft <sup>2</sup> /ac.

The model output was summarized in tabular form as well as graphically with the Stand Visualization System (SVS; McGaughey 1997), which has been incorporated into the FlexFIBER package.

## Shelterwood Silviculture in Spruce-Fir

The spruce-fir forest type was used to test several of the key recommendations for even-aged management. Eight plots from the USDA Forest Inventory and Analysis (FIA) dataset from northern Somerset County, Maine were selected to represent a well-stocked spruce-fir sawtimber stand that would be a likely candidate for regeneration on many commercial ownerships in Maine. Initial basal area of live trees  $\geq 4.5$  inches DBH averaged 140 ft<sup>2</sup>/ac with a quadratic mean stand diameter of 9.1 in.; 75% of the basal area was in trees  $>10$  inches DBH.

A shelterwood approach to management was used for both the SW BIO and SW TIMBER runs. Specifically, the goal was to examine the long-term impact on stand structure by applying the recommended guidelines for retaining live trees and snags in the SW BIO run (Table 3). FlexFIBER was used to model the overstory trees, while NE TWIGS was used to model the regeneration until it reached approximately 5 inches DBH. FlexFIBER was preferred for the overstory because it is the most accurate model available for Northeastern spruce-fir (Schuler et al. 1993) and provides greater flexibility in selecting harvest routines than does NE TWIGS. NE TWIGS was used for the regenerating stand because FlexFIBER does not model the growth of trees less than 5 inches DBH.

The basic softwood model runs are outlined in Table 5.

**Table 5. Parameters for Spruce-Fir model runs**

Year	SW TIMBER	SW BIO
1	Initial basal area 140 ft <sup>2</sup> /ac. Harvest 40% of basal area to initiate regeneration.	Same
11	Complete overstory removal.	Retain 10% of initial overstory stocking (twice the minimum recommended by MFBP).
16	Precommercial thin regeneration to 860 trees per acre, discriminate against balsam fir.	Same, no harvest of retained overstory.
51	First commercial thinning (approximately 30% BA removal); residual BA 99 ft <sup>2</sup> /ac.	Same; no harvest in overstory; residual BA 94 ft <sup>2</sup> /ac.
71	End of projection.	Same

## RESULTS

### Fall Rates for Snags

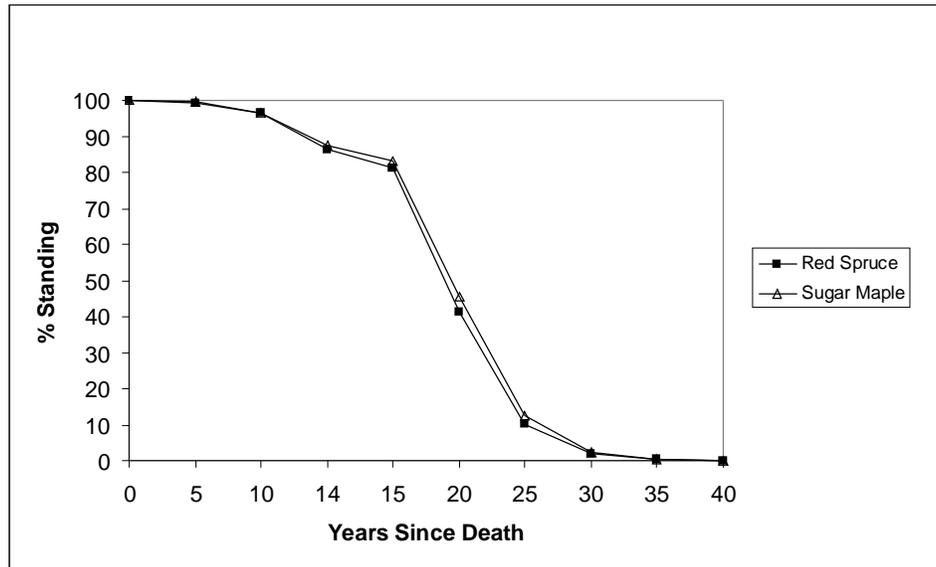
The FIA data suggest average windthrow rates amount to less than 2% of mortality. Long term data from the Harvard Forest (Foster et al., undated) indicate windthrow rates account for 5% of red oak mortality and 1.5% of red maple mortality. Data collected by the author suggest similar rates for a maturing northern hardwood stand in the Tug Hill region of New York. For the purposes of this study an initial windthrow rate of 2% was assumed for all stands. Anecdotal evidence and studies from British Columbia (e.g., Beese 2001) suggest windthrow rates for patches retained after overstory removal harvests may be much higher, but accurate data are lacking for the Northern Forest Region. Analysis of the FIA data indicated an average snag-fall coefficient (*b*) for northern hardwoods of

-0.354 and -0.363 for spruce-fir. The fate of a given cohort of snags predicted by the resulting logistic equations is shown in Figure 1. For all diameter classes  $\geq 5$  inches, data did not indicate that large snags persist longer than small snags. Lester (2002) had similar results.

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**Figure 1. Snag fall curves for Maine and New Hampshire**

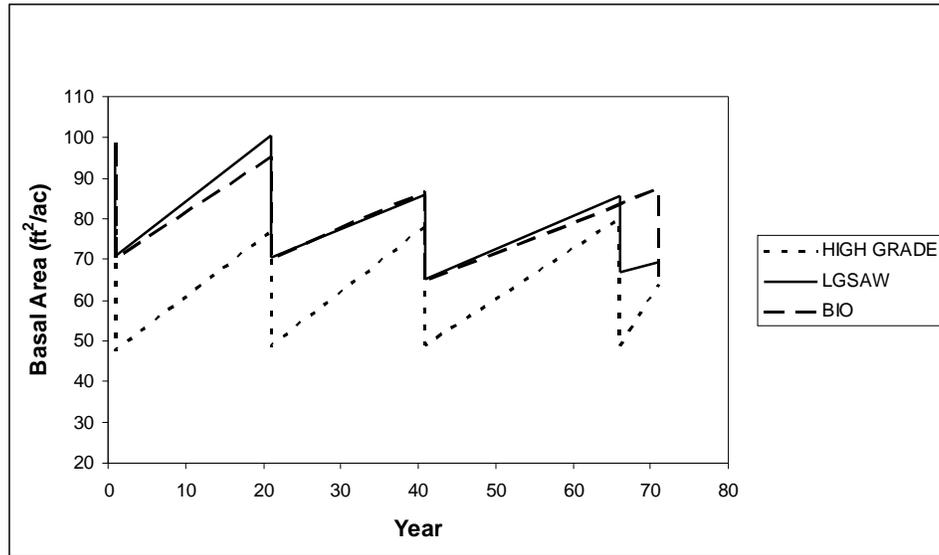
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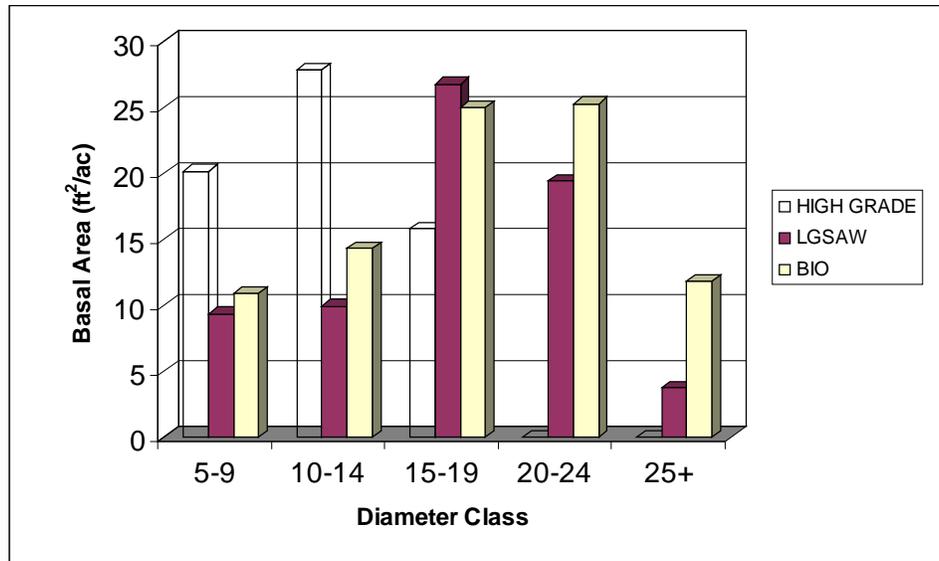
### Selection Silviculture in Northern Hardwoods

**Live Trees.** Initial stand conditions, post-harvest stand conditions (Year 1) and the results after three additional selection harvests are shown in Figures 2, 3, and 4. The HW BIO and HW LGS AW had similar basal area trends (Figure 2). Although the HW HIGH GRADE had a lower basal area throughout the projection, annual basal area growth remained relatively constant throughout the projection, while basal area growth declined over time in the other two runs as some of the trees approached maximum diameter (Figure 2). The HW BIO basal area of live trees  $\geq 20$  inches DBH exceeded that of the HW LGS AW run by approximately 40% at Year 71, while the HW HIGH GRADE run had no trees over 20 inches (Figure 3). For all trees  $\geq 5$  inches DBH, almost 50% of the HW BIO basal area is in trees  $\geq 20$  inches DBH. Although the initial period between harvests was 20 years, slower growth near the end of the projection required that the interval be lengthened to 25 years for the HW LGS AW run and 30 years for the HW BIO run in order to meet the pre-harvest basal area goal of 85  $\text{ft}^2/\text{ac}$ . The lower stocking of the HW HIGH GRADE run is evident in Figure 4.

**Figure 2. Live tree basal area over 70 years of selection management in Northern Hardwoods**



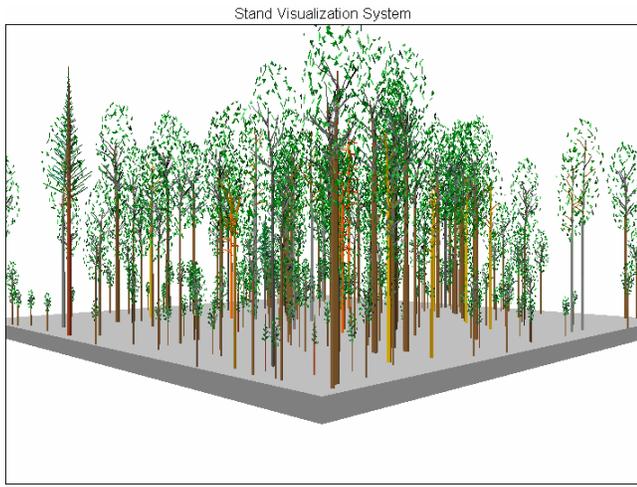
**Figure 3 Northern Hardwood live tree diameter distribution at year 71**



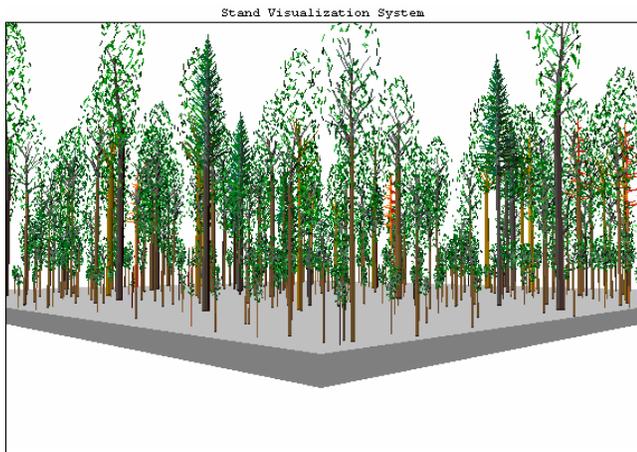
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**Figure 4. SVS images of simulated selection management in Northern Hardwoods**

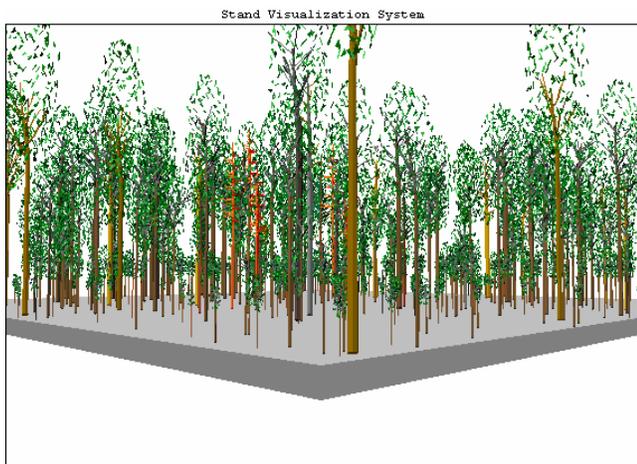
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HW HIGH GRADE Year 71



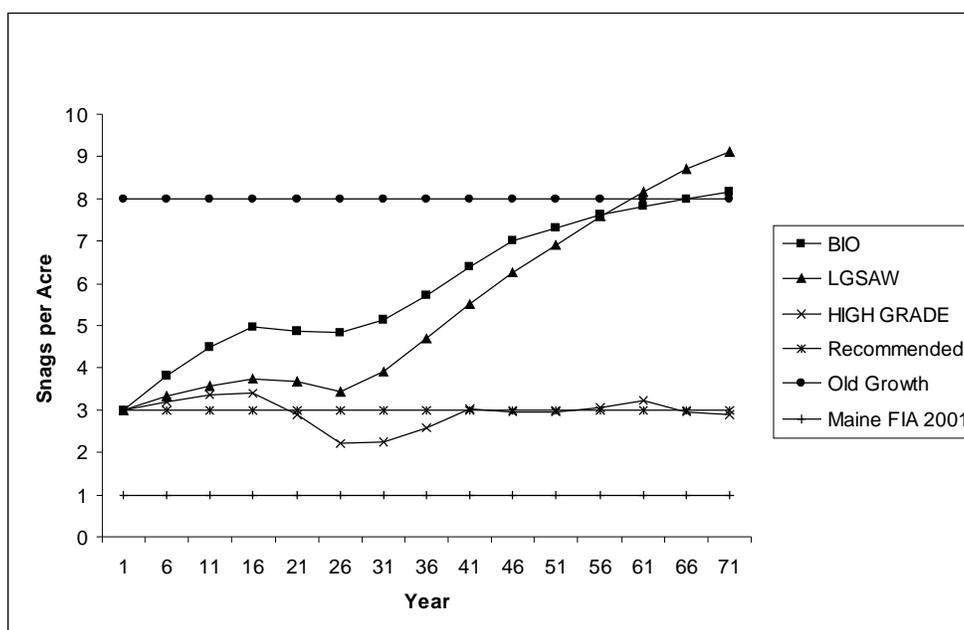
HW TIMBER – Year 71



HW BIO – Year 71

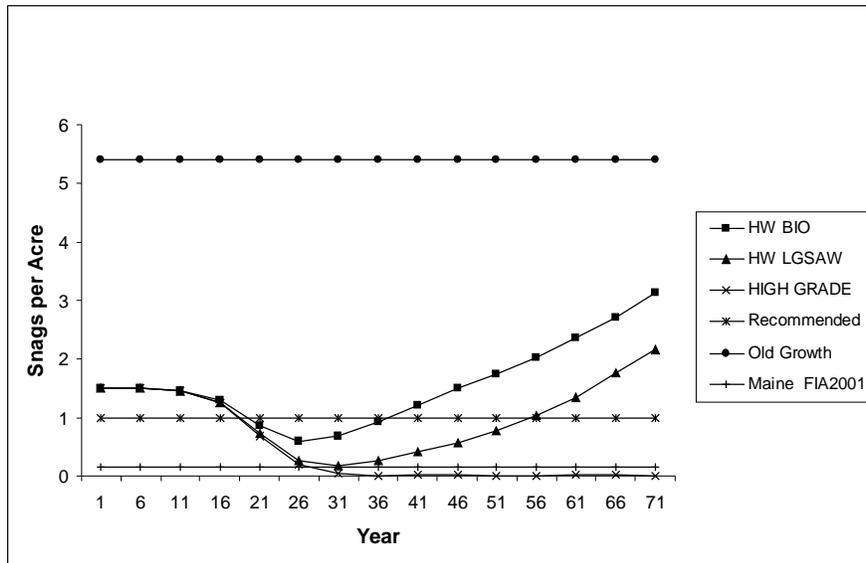
**Snags.** For snags  $\geq 15$  inches DBH, heavier cutting of large diameter trees in the first harvest of the HW LGSAW run leads to fewer large snags than the HW BIO run for the first 50 years, but for both treatments the number of snags remains above generally recommended levels (Figure 5). The HW HIGH GRADE snag density remains approximately at the recommended level for all snags over 15 inches DBH. While the HW LGSAW had more snags  $\geq 15$  inches DBH than HW BIO at the end of the simulation run, HW BIO had slightly higher snag basal area in these classes. For snags  $\geq 20$  inches the differences are more acute, with the HIGH GRADE treatment failing to meet recommended levels by eventually eliminating all snags in this diameter class (Figure 6). All treatments fall well below the average number of snags  $\geq 20$  inches DBH found by McGee et al. (1999) in old growth northern hardwoods.

**Figure 5. Northern Hardwood snags  $\geq 15$  inches DBH<sup>1</sup>**



<sup>1</sup>The Recommended levels are rough averages based on Maine and New Hampshire guidelines (Flatebo et al. 1999, NHFSWTTS 1997, and MDOC 2003) standardized to 5-inches DBH classes.

**Figure 6. Northern Hardwood snags  $\geq 20$  inches DBH<sup>1</sup>**



<sup>1</sup>The Recommended levels are rough averages based on Maine and New Hampshire guidelines (Flatebo et al. 1999, NHFSWITS 1997, and MDOC 2003) standardized to 5-inches DBH classes.

**Structural Development Classes.** Although the HW BIO run has a greater number of large trees, overall the HW LGSAW and HW BIO runs exhibited little long-term difference in structural development classes (Table 6). The HW HIGH GRADE column shows the likely outcome if the largest trees are repeatedly harvested in the stand on a diameter-limit basis, a common practice on all types of ownerships. In actual practice, the HW HIGH GRADE scenario is more prevalent than the HW TIMBER scenario modeled here, which has 30% of its basal area in trees > 20 inches DBH at year 66.

**Table 6. Structural development classes and stand size class (in parentheses) resulting from uneven-aged hardwood management**

Year	HW HIGH GRADE	HW LGSAW	HW BIO
1-	Understory reinitiation (Poletimber)	Understory reinitiation (Poletimber)	Understory reinitiation (Poletimber)
21	Understory reinitiation (Small Sawtimber)	Understory reinitiation (Small Sawtimber)	Understory reinitiation (Small Sawtimber)
41	Understory reinitiation (Small Sawtimber)	Mature (Large Sawtimber)	Mature (Large Sawtimber)
66	Understory reinitiation (Small Sawtimber)	Mature (Large Sawtimber)	Mature (Large Sawtimber)
71	Understory reinitiation (Small Sawtimber)	Mature (Large Sawtimber)	Mature (Large Sawtimber)

Stand size classes are those used by the US Forest Service and Maine Forest Service:  
 Poletimber: Softwood stands 5.0-8.9 in. DBH; hardwood stands 5.0-10.9 in. DBH  
 Small Sawtimber: Softwood stands 9.0-14.9 in. DBH; hardwood stands 11.0-14.9 in. DBH  
 Large Sawtimber: Trees  $\geq 15.0$  in. DBH comprise at least 50% of basal area

Although both HW BIO and HW LGSAW reach a mature stage, they fall short of the structural characteristics of old growth northern hardwoods in the Northern Forest region in terms of live trees (Table 7) and large snags (Figure 6). No trees >20 inches DBH develop in the diameter-limit harvesting regime of the HW HIGH GRADE run (Table 7).

**Table 7. Density of live trees  $\geq 20$  in DBH compared with old growth Northern Hardwoods<sup>1</sup>**

<b>Stand Type</b>	<b>Live Trees per acre <math>\geq 20</math> inches DBH</b>
HW HIGH GRADE	0.0
HW LGSAW	8.8
HW BIO	10.8
Old Growth Minimum	12.4
Old Growth Maximum	21.6

<sup>1</sup>Old growth data based on four studies from New Hampshire and New York reported by McGee et al. (1999).

**Hardwood Volume Growth and Harvest.** The HW HIGH GRADE run produces the greatest cubic foot and board foot harvests, (Table 8) but HW LGSAW had the greatest volume of standing timber and board foot growth (Table 9).

**Table 8. Simulated harvest volumes for selection silviculture in Northern Hardwoods**

<b>Year</b>	<b>Total Volume (ft<sup>3</sup>/ac)</b>			<b>Sawtimber (bf/ac)</b>		
	<b>HW HIGH GRADE</b>	<b>HW LGSAW</b>	<b>HW BIO</b>	<b>HW HIGH GRADE</b>	<b>HW LGSAW</b>	<b>HW BIO</b>
	1	1542	915	815	3731	2938
21	899	929	799	3007	3172	2539
41	975	711	722	4077	2687	2811
61	1045	0	0	3994	0	0
66		647	0	0	2743	0
71	0	0	712	0	0	2745
<b>Total</b>	<b>4461</b>	<b>3202</b>	<b>3048</b>	<b>14809</b>	<b>11540</b>	<b>9368</b>

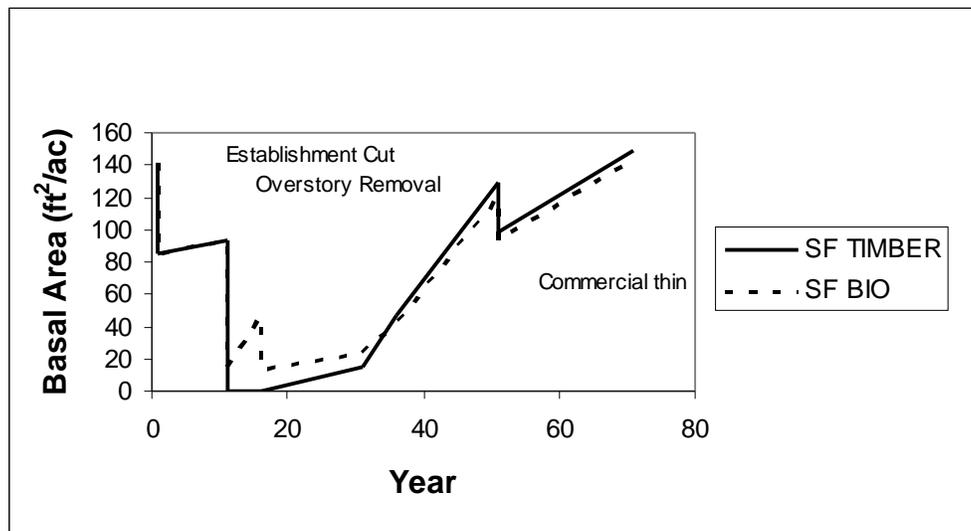
**Table 9. Northern Hardwood stocking and growth**

	<b>HW HIGH GRADE</b>	<b>HW LGSAW</b>	<b>HW BIO</b>
Standing Volume Year 71 (ft <sup>3</sup> /ac)	1889	2318	2223
Standing Volume Year 71 (bf/ac)	4283	9450	9355
Mean Sawtimber Growth (bf/ac/yr)	189	216	183

## Shelterwood Silviculture in Spruce-Fir

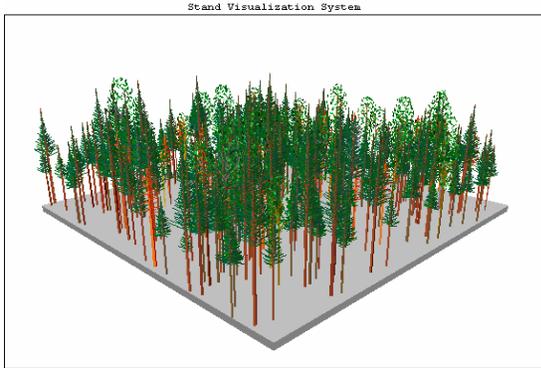
**Live Trees.** Results for selected points in the 70-year shelterwood regime are shown in Figure 7, Figure 8, and Figure 9. Retaining twice the basal area recommended by biodiversity guidelines at the time of overstory removal in the SF BIO run (10% of the original stand, or 14 ft<sup>2</sup>/ac) appears to have minimal impact on the structure of residual stand (e.g., see Figure 8, Year 16)<sup>2</sup>. Differential growth rates between species and individuals as well as mortality of the retained overstory component in the SF BIO stand results in nearly identical stand structures after 70 years. Overall basal area is similar, as is the basal area in trees greater than or equal to 15 in. DBH. The two treatments differ only in that the SF BIO run has about 5 ft<sup>2</sup>/ac in trees (1-2 trees/ac.) greater than 25 in. DBH, whereas the SF TIMBER treatment has none.

**Figure 7. Live tree basal area over 70 years of shelterwood management in Spruce-Fir**

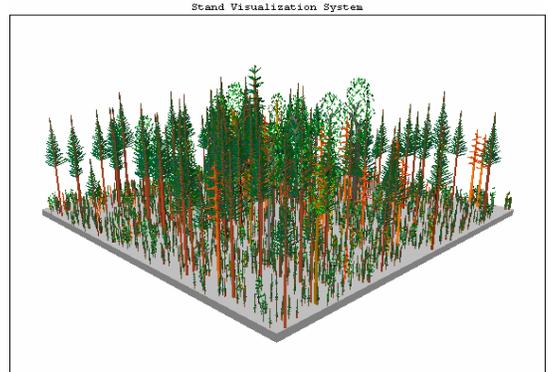


<sup>2</sup> The SVS program randomly locates trees. In practice, it is likely that the retention trees in the SF BIO run would have been grouped in an “island” to promote windfirmness and minimize the impacts to understory plants.

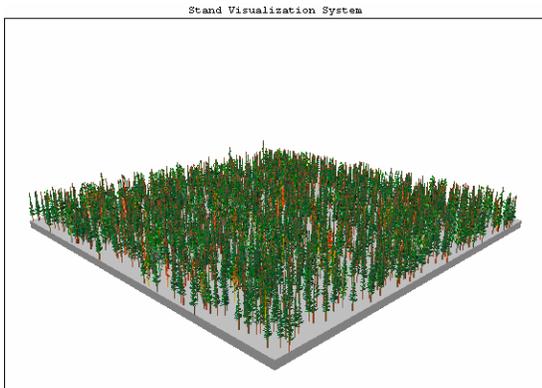
**Figure 8. Results of simulated shelterwood management in Spruce-Fir**



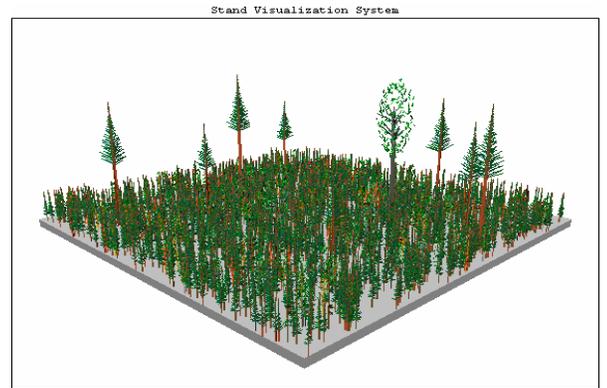
Year 1 - Initial Conditions – both treatments prior to regeneration cut



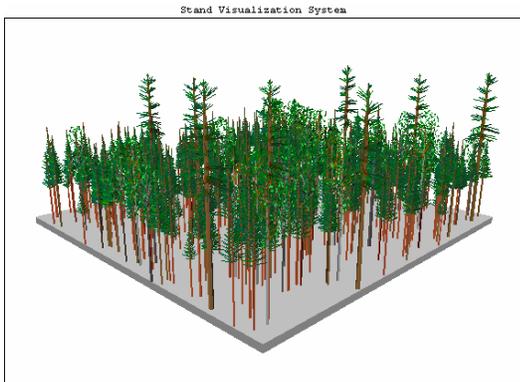
Year 11 – Prior to Overstory Removal



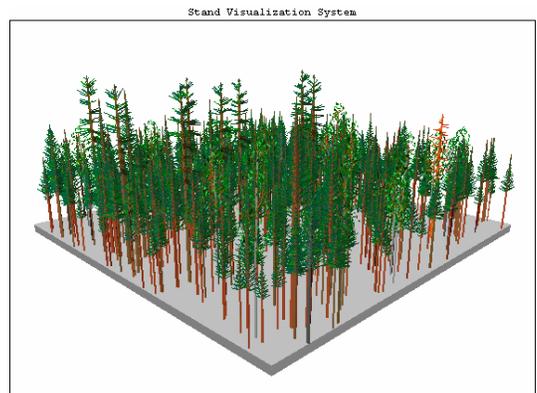
SF TIMBER – Year 16: 5 years after Overstory Removal



SF BIO – Year 16: 10% Overstory Retention

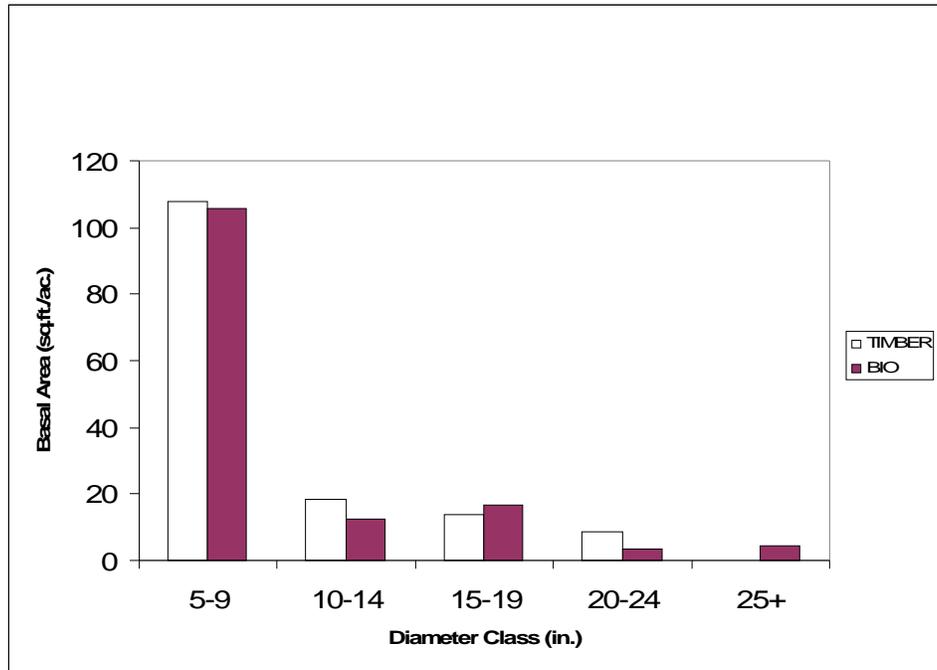


SF TIMBER Year 71: Prior to Regeneration Cut



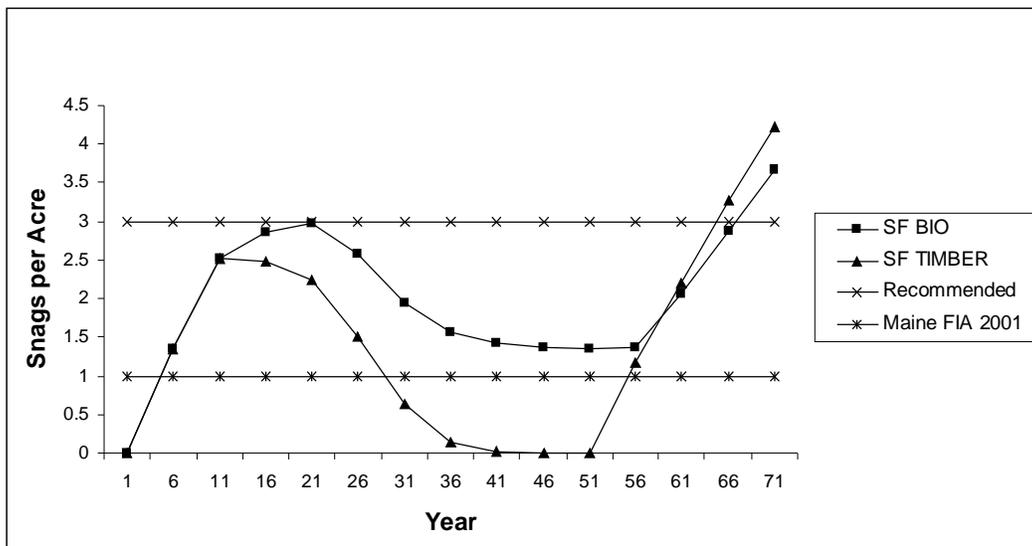
SF BIO Year 71: Prior to Regeneration Cut

**Figure 9. Spruce-Fir live tree diameter distribution at year 71**



**Snags.** For most of the 70-year shelterwood run both treatments fall short of the recommended stocking of snags greater than or equal to 15 inches DBH (Figure 10). Because the initial stand had no snags > 15 inches DBH, the stocking of snags was solely dependent on mortality during the treatment period. Had the initial stocking met the recommended level, both might have exceeded the minimum for the first 20-30 years. Only near the end of the 70-year rotation were the snag recommendations met. Assuming these snags are carried over after the initial harvest into the next rotation, the stocking goals for large snags in a maturing forest condition may be present for 10-15 years.

**Figure 10. Spruce-Fir snags ≥15 inches DBH**



**Structural Development Classes.** The model results suggest slight structural class differences between the SF TIMBER and SF BIO runs that persist approximately 40 years after overstory removal (Table 10), but no difference in stand size class. After that time (year 50 in the simulation runs) the new stand dominates the site to such an extent that the two-story SF BIO stand has in effect become a single-story stand with a few supercanopy trees (or a small patch of mature trees within a young stand). On a seventy year shelterwood rotation, the maximum age commonly discussed for spruce-fir production on most large ownerships, neither the SF TIMBER nor SF BIO approach will lead to a mature stand condition and the stand remains in the poletimber class.

**Table 10. Structural development classes and stand size classes (in parentheses) in the Spruce-Fir shelterwood system**

Year	Management Phase	SF TIMBER	SF BIO
1	Initial Stand	Understory Reinitiation (Small Sawtimber)	Understory Reinitiation (Small Sawtimber)
2-10	Post shelterwood establishment cut	Mature/Regeneration (Small Sawtimber)	Mature/Regeneration (Small Sawtimber)
11- 20	Post overstory removal & precommercial thinning	Stand Initiation (Seedling/Sapling)	Stand Initiation/Residual (Seedling/Sapling)
20-40	Young Stand development	Early Stem Exclusion (Seedling/Sapling)	Young Multi-Story (Seedling/Sapling)
41-50	Young stand development	Early Stem Exclusion (Poletimber)	Early Stem Exclusion (Poletimber)
51-70	Commercial thin to end of rotation	Late Stem Exclusion (Poletimber)	Late Stem Exclusion (Poletimber)

*Stand size classes are those used by the US Forest Service and Maine Forest Service:*

*Seedling/Sapling: Stands 1.0-4.9 in. DBH.*

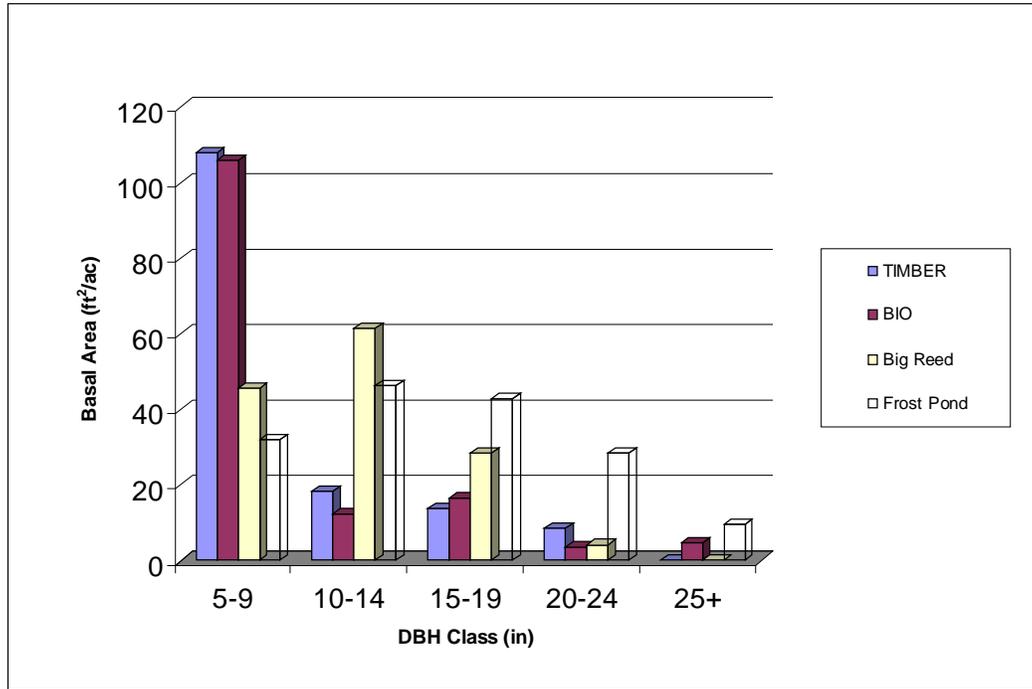
*Poletimber: Softwood stands 5.0-8.9 in. DBH; hardwood stands 5.0-10.9 in. DBH*

*Small Sawtimber: Softwood stands 9.0-14.9 in. DBH; hardwood stands 11.0-14.9 in. DBH*

*Large Sawtimber: Trees  $\geq 15.0$  in. DBH comprise at least 50% of basal area.*

Figure 11 compares the stand structures resulting after 70 years of shelterwood management with old growth spruce-fir stands at Big Reed Preserve and near Frost Pond in the Baxter State Park Scientific Management Area in Maine. The HW TIMBER and HW BIO have the majority of basal area in trees less than 10 in. DBH, while in the old growth stands the vast majority of basal area is in trees 10 inches DBH and over.

**Figure 11. Comparison of Spruce-Fir shelterwood stands at year 70 with old growth stands**



**Spruce-Fir Harvest Volume.** The SF TIMBER scenario yields about 10% more harvest volume than SF BIO over an 80-year period. This difference is directly attributable to the overstory removal harvest, when 10% of the overstory basal area is retained in the SF BIO approach.

**Table 11. Predicted harvest volumes for the Spruce-Fir model runs (ft<sup>3</sup>/ac)<sup>1</sup>**

Year	Treatment	SF TIMBER	SF BIO
1	Initial stand	1340	1340
11	Overstory removal	2468	2054
51	First commercial thinning	701	750
71	Regeneration cut	1200	1200
81	Overstory removal	2394	2078
Total:		8103	7422
Original stand:		3808	3394
New Stand:		4295	4028

<sup>1</sup>The actual FlexFIBER runs ended at year 71. Year 71 and Year 81 harvests based on Year 71 volume and expected 10 year growth.

## DISCUSSION

### Selection Silviculture

***Snags, Cavity Trees, and Downed Woody Debris.*** The study results suggest that selection management in northern hardwoods can provide abundant large snags and cavity trees under both a biodiversity management approach and an approach with an emphasis on large sawtimber. Although this study did not evaluate downed woody debris, the constant decay and breakup of snags should provide an adequate supply of large-diameter logs and other woody debris on the forest floor if the objectives for standing deadwood are met. A high grading approach based on diameter limit harvests or repeated heavy harvests will likely lead to a lack of large snags, cavity trees, and deadwood. However, where lack of markets for low-value timber focuses harvesting on quality sawlogs, adequate levels of decadent material may accumulate.

***Structural Development Classes.*** Hagan and Whitman (2003b) have expressed concern that late-successional stands (essentially equivalent to “mature” stands as defined in Table 2) and their unique biota (notably mosses, lichens, and liverworts) are at imminent risk of loss in Maine. This study suggests that single tree or group selection with a goal of large sawtimber production is well suited to developing and maintaining mature/late successional forest conditions where species composition and site conditions permit. Diameter limit harvesting will eliminate late-successional characteristics and maintain stands in younger, non-maturing development classes. Neither selection management nor all but the heaviest of “partial cuts” will provide habitat for species such as chestnut sided warblers and mourning warblers that require the youngest stand development stages.

***Timber Growth and Harvest.*** While the HW HIGH GRADE had the highest volume harvest, HW LGSAW had the highest standing volume and board foot growth. While this study did not model changes in timber quality, Jacobsen (2001) found that the net present value of management that favored growth of large-diameter, quality stems exceeded that of high grading. A shift in species composition to lower-value species (e.g. a shift from dominance by sugar maple to dominance by beech or red maple) is also often a side-effect of diameter limit or high-grade harvesting.

The stand structures for the HW HIGH GRADE have a much lower basal area in large-diameter trees and lower overall basal area than recommended by Leak et al. (1987) for quality sawtimber production in uneven-aged northern hardwoods. In contrast, the HW BIO and HW LGSAW were overstocked in the large diameter classes at the end of the projection relative to the recommendations of Leak et al. The high stocking of large trees likely resulted in lower basal area growth for these runs because trees were approaching their maximum diameters. The growth and yield results from this study suggest the uneven-aged management residual structure objectives proposed by Leak et al. are probably about optimum for quality sawtimber production. With careful attention to large snags, cavity trees and other attributes of late-successional



*Photo by J. Hagan  
found on sugar maple over 90 years old, is an indicator of ecologically mature forest.*

stands, the Leak et al. structure objectives should also allow managers to meet structural targets for mature-forest biodiversity.

## Shelterwood Silviculture

**Snags, Cavity Trees, and Downed Woody Debris.** The shelterwood system in spruce-fir is generally inadequate to maintain levels of decadent material recommended by stand-level biodiversity guidelines. Over a 70-year rotation structural goals for snags may only be met for a 10-20 year window that spans the end of one rotation and the regeneration phase of the next. This supports the recommendations of Woodley and Forbes (1997) that forests can best be managed for cavity nesters by using selection management techniques. Although patch retention will provide more dead wood for longer periods than will even-aged management without patch retention, even leaving 10% of the original stand (twice the minimum recommended by the MFBP) is inadequate to meet the goals for large ( $\geq 15$  inches DBH) cavity trees and snags if they are not present at the time of the initial shelterwood entry. Rotations of 60 years or less are likely to be of limited value for deadwood production in spruce-fir. The problems created by shelterwood management in spruce-fir may also be manifest when the technique is applied in northern hardwoods.

Much remains to be learned about the benefits of retained patches. Concentrating snags and cavity trees in retained patches (say 1-2 acres out of 20) may provide an adequate density of snags for animals with large territories (e.g. barred owls), but they may avoid the patch until the stand matures due to the patch's isolated nature. The benefits of patch retention are probably greater for small organisms with low mobility, such as understory plants and flightless insects. Recent studies in the northeast have shown that many understory plants decline or disappear after clearcutting (Whitman and Hagan 2000, Roberts 2002, Roberts and Zhu 2002), and even the strongest proponents of structural retention policies admit that the benefits of patch retention are not well known (e.g., Lindenmayer and Franklin 2002).



*This study found that on commercial rotations of 70 years or less, patch retention is inadequate to meet recommended numbers of large snags.*

**Structural Development Classes.** With a 70-year even-aged rotation structural development is truncated at the late stem exclusion stage and the stand never reaches the U.S. Forest Service small sawtimber size class, even if structure retention recommendations are followed at the time of overstory removal. This suggests that spruce-fir managed on rotations of 70 years or less will not contribute to the DeGraaf et al. (1992) goals for 40% of the landscape in sawtimber size classes and similar landscape goals for mature stands (e.g., MCSFM 1996, Flatebo et al. 1999, MDOC 2003). Although trees retained by applying biodiversity recommendations will provide some structural diversity in the early stages of stand development, after 50 years stands that have small percentages of retained patches from the previous rotation will be generally similar to purely even-aged stands. Thus, while many authors have highlighted the importance of retaining biological legacies (e.g. NHFSSWT 1997, Flatebo et al. 1999, Hagan and Whitman 2003a), retention of patches and other structural legacies should not be seen

as a “biodiversity cure-all” for even-aged silviculture. Although this study did not model shelterwood management in northern hardwoods, similar conclusions would apply. Only through extended rotations – probably in excess of 80 years for spruce-fir and 100 years for northern hardwoods – will even-aged management result in mature stand conditions.

Most vertebrates that prefer older forests can probably be accommodated in even-aged stands at or beyond the late stem exclusion stage as long as there is sufficient suitable habitat to support self-sustaining populations. This suggests that a 70-year shelterwood rotation can provide a 30-year habitat window for most older-forest vertebrates that bridges the end of one rotation and the beginning of the next. This window would be reduced to 20 years for the clearcutting system.

Extended rotations, selection management, plus careful retention of long-lived cavity trees will likely be required to sustain those 30 species that prefer medium to large (>12 in.) cavities. Other organisms, such as some old-forest macrolichens, appear to be limited to old (>90 years), high-basal area stands (J. M. Hagan pers. com.).



*The production of large cavity trees, needed by animals like this barred owl, will benefit a wide range of organisms that depend on dead or decaying wood.*

**Timber Growth and Harvest.** The results suggest that 10% long-term patch retention will result in 10% loss of harvest volume. The financial impacts of this retention can be minimized by leaving trees with low monetary value that may have long-term benefits for wildlife and mature-forest epiphytes. Examples might include eastern hemlock, defective white pine, or hardwoods with decay pockets that will provide potential cavity sites.

## MANAGEMENT RECOMMENDATIONS

The results of this study suggest that managing for stand structures characteristic of older forests will require an approach that integrates stand and landscape-level considerations. An active approach to managing structure increases in importance as the area in even-aged management increases and as rotations decrease. Some specific recommendations, building on the results of this study and previous management guides (e.g., DeGraaf et al. 1992, MCSFM 1996, NHFSSWTS 1997, Woodley and Forbes 1997, Flatebo et al. 1999, Lindemayer and Franklin 2002) follow.

### Stand Level

- ✓ Selection management for large sawtimber is the best method to maintain a constant, well-distributed supply of large-diameter live trees, snags, cavity trees, and downed woody material.
- ✓ In even-aged management, long rotations will probably be necessary to create old-forest stand conditions.

- ✓ Managers with a focus on financial returns will need to make an effort at each entry to maintain adequate levels of snags and/or potential cavity trees.
- ✓ Adequate levels of decadent material can also be maintained in spruce-fir and mixedwood stands where conditions permit selection management for large sawtimber.
- ✓ Because hardwoods grow to larger sizes and have more cavities than spruce and fir, maintaining a component of decadent hardwood in spruce-fir stands is important.
- ✓ A snag inventory should be a standard element of forest inventories and pre-harvest cruises. Because snags occur less frequently than live cavity trees, obtaining an adequate inventory of snags may be a problem at the stand level. Most vertebrate wildlife populations are sustained at the multi-stand or landscape level, however, so property-wide averages on small ownerships or landscape-level averages on large ownerships will provide reasonably accurate, low-cost information on an important element of forest ecosystem integrity.
- ✓ Stands should be classified by structural maturity (Table 2) or size class (see footnote, Table 10) to assist in biodiversity evaluation. The stand-size class approach is simple to apply, but should be augmented by describing vertical structure (i.e., one story, two stories, more than two stories) as recommended by MFSFM (1996) and recently adopted by the Maine Forest Service for statewide biodiversity benchmarks (MDOC 2003). A late-successional stand index that is being developed by the Manomet Center (Hagan pers comm.) promises to be a valuable tool for assessing stand maturity.

## Landscape Level

Maine Forest Service data (MFS 2002) suggest that approximately 60% of large industrial and investor forests are being managed with even-aged methods. This study found that for rotations of 70 years or less, goals for forest maturity recommended by most authors will not be met. Depending on rotations and the size, distribution, and total area of mature, structurally-complex stands, this could be harmful to wildlife and plants that are characteristic of older forests. In central and southern New England, where low harvest rates and partial harvesting are prevalent, the decline of young forest habitat is the primary concern of many wildlife biologists.

Disturbance history and stand maturity has a strong influence on the abundance of plants and lichens. This suggests that some form of partial harvesting that maintains canopy dominance at the patch or stand level will help maintain healthy populations of mature-forest plants.



*As demands on the forest increase, landscape planning is essential to ensure that there is adequate mature-forest*

These constraints suggest the following integrated approach to landscape planning and management.

- ✓ Identify the sites on all ecosite types where continuous canopy management (i.e., stands managed by various forms of partial harvesting) will be practiced. This would include single tree and group selection or variable harvest retention with high-residual basal area (e.g., Lindemayer and Franklin 2002). Candidates for continuous-canopy management include sensitive areas such

- as riparian corridors, forests adjacent to vernal pools, sites that support rare or disturbance-sensitive plants, and gap-replacing matrix forest communities throughout the landscape.
- ✓ Areas managed with even-aged silvicultural methods (clearcut, shelterwood, and variable harvest retention with low residual basal area) can be identified after the constraints for selection silviculture have been met.
  - ✓ The MFBP goal of maintaining the landscape matrix in “relatively-mature, well stocked stands” (Table 3) or sawtimber (e.g., DeGraaf et al 1992, MDOC 2003) can be met by a combination of even-aged and uneven-aged management. Stands under even-aged management that are at or beyond the late stem exclusion stage or small sawtimber stages would contribute to this goal as well as all selection stands with sawtimber.
  - ✓ The MFBP goal to “maintain or restore a significant portion of the ownership in mature, late-successional forest” was not precisely defined. Mature stands (e.g., >100 years for even-aged stands, or dominant overstory trees exceeding 100 years in selection stands) of long-lived species should contribute to this goal. Goals recommended by a panel of advisory scientists to the Maine Department of Conservation (2003) include a minimum 10% of the landscape in the “large sawtimber” (roughly analogous to “mature” or “late-successional”) condition.
  - ✓ A simple spreadsheet model with inputs including forest type, expected rotation or tree age, silvicultural technique, and reserve areas can be used to quickly evaluate the expected percent of the landscape in various stand development or size classes.

### **Limitations of modeling**

The forest growth models used in this study are the best available for this region, yet they are only able to project approximations of what might actually occur. They are best used for evaluating relative responses to alternative treatments under average conditions rather than predicting the precise condition or output of any particular stand. Despite their limitations, they are the best tools currently available for predicting future forest conditions under alternative management scenarios.

### **Next Steps**

The recommendations in this report are not designed to be a comprehensive approach to biodiversity but rather are limited to a general approach to manage for mature-forest structure. As is always the case, scientific research often reveals what little we know. In particular, further study is needed to better understand the dynamics of deadwood production and decay in northeastern forests, the benefits of structural retention in even-aged harvests, and threshold limits to maintain populations of sensitive species. Nonetheless, there is much we do know that should be implemented now. While forests are generally maturing in New Hampshire and Vermont, the extent of truly mature forest (e.g. Table 2) is not known. On average over 1,400 acres of forest are harvested every day in Maine, and old forests are rapidly disappearing. Management must directly address mature, late-successional forest characteristics at both the stand and landscape scales to ensure that the full suite of native plants and animals will persist into the future.

## ACKNOWLEDGEMENTS

- Todd Caldwell of L.E. Caldwell Co. of Turner Maine ran the growth models for this study and generously donated time to the project beyond the contract amount.
- Anna Lester (University of Massachusetts and U.S. Forest Service) generously shared her unpublished analytical techniques for analysis of snag fall rates.
- Fraser Papers provided access to forest management data and an extensive tour of their management operations that helped shape the modeling scenarios. They also provided assistance from their wildlife biologist Steve Young, who helped in the process of selecting key stand parameters to be reviewed.
- Andy Whitman (Manomet Center), Jensen Bissel (Baxter State Park Scientific Management Area), and David Publicover (Appalachian Mountain Club) reviewed and provided helpful comments on the manuscript.
- This project would have been impossible without the financial support of the Merck Family Fund and the members and friends of Maine Audubon.

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