United States Department of Agriculture

Penobscot Experimental Forest: 60 Years of Research and Demonstration in Maine, 1950-2010

Forest Service

Northern Research Station

General Technical Report NRS-P-123

January 2014

Abstract

The Penobscot Experimental Forest (PEF) in Maine has been the site of U.S. Department of Agriculture, Forest Service, Northern Research Station (previously Northeastern Forest Experiment Station) research on northern conifer silviculture and ecology since 1950. Purchased by forest industry and leased to the Forest Service for long-term experimentation, the PEF was donated to the University of Maine Foundation in 1994. Since that time, the University and the Forest Service have worked in collaboration to advance the PEF as a site for research, demonstration, and education. This publication reports the history of the PEF during its first 60 years (1950 to 2010) and presents highlights of research accomplishments in silviculture, ecology, ecophysiology, nutrient cycling, botany, and other areas. Issues of data management and forest management planning are addressed. Also included is a bibliography of publications originating from research on the PEF, as well as recollections of a research forester stationed there for 30 years.

More than half a century of work on the PEF has served as an important source of information for practitioners and policy makers in the Acadian Forest region of the northeastern United States and adjacent Canada, and informed the practice of silviculture nationally and internationally. Long-term consistency in treatment application and measurement; stand-level replication; and accessible, digital data, metadata, and records archives have facilitated hundreds of studies and made the PEF an invaluable and highly influential research site.

Cover Photos (all by U.S. Forest Service)

Top left: Sign at the entrance to the Penobscot Experimental Forest, 2001.

Top right: U.S. Forest Service staff constructing a footbridge on the Penobscot Experimental Forest, 1950.

Center left: Logger working on the Penobscot Experimental Forest, 1952.

Center right: U.S. Forest Service technician T. Skratt taking measurements for a tree volume study on the Penobscot Experimental Forest, 1994.

Bottom left: U.S. Forest Service research forester L. Kenefic leading a tour on the Penobscot Experimental Forest, 2011.

Bottom right: Logging operation on the Penobscot Experimental Forest, 1950s.

Published by:

USDA FOREST SERVICE
11 CAMPUS BLVD., SUITE 200
NEWTOWN SQUARE, PA 19073-3294

January 2014

For additional copies, contact:

USDA Forest Service
Publications Distribution
359 Main Road
Delaware, OH 43015-8640
Fax: 740-368-0152

Visit our homepage at: **http://www.nrs.fs.fed.us/**

U.S. Forest Service research forester R. Frank leading a tour on the Penobscot Experimental Forest, 1990s. Photo by U.S. Forest Service.

DEDICATION

Sustaining long-term research at experimental forests depends on the foresight, commitment, and dedication of many people over decades. For more than 60 years, research on forest ecology and silviculture has been conducted on the Penobscot Experimental Forest. The men and women who do this work day in, day out, deserve much of the credit for the longevity and success of this endeavor. Among those who have contributed or are continuing to contribute to this ongoing research are scientists, professionals, and technicians with the U.S. Department of Agriculture, Forest Service and the University of Maine, who work in partnership to maintain the studies and the site. Over the years, hundreds of undergraduate and graduate students from the University of Maine and elsewhere have worked side by side with others from the University and the Forest Service to carry out the research described in these pages.

We thank all those who have been involved with the Penobscot Experimental Forest since 1950 collecting, managing, and analyzing data; implementing technology transfer; maintaining the forest and infrastructure; and providing administrative support. The culmination of these efforts is a remarkable body of knowledge that has advanced our understanding of forest science and improved our management of forest ecosystems.

This volume is dedicated to all who have given their time and talent to the Penobscot Experimental Forest. Whether they spend a season—or an entire career—at the forest, their legacy is a world-class research establishment.

John C. Brissette and Laura S. Kenefic

Page intentionally left blank


View of the Penobscot Experimental Forest from a canopy crane, 1998. Photo by U.S. Forest Service.

FOREWORD

In terms of forest life, 60 years is not especially long. In terms of research, 60 years is a remarkable achievement. The Penobscot Experimental Forest is remarkable both for the duration of research that has been conducted here and for the collaboration behind that work, first with the forest industry and later with the University of Maine.

In this report, Northern Research Station scientists and collaborating scientists from a variety of institutions describe their work and how the Penobscot Experimental Forest furthered their understanding of a wide range of topics and changed how northern conifer forests are managed. Indeed, early research projects are still furthering our knowledge of forests as data collection and silvicultural treatments continue with modifications that allow us to use them to address contemporary issues in forest management.

Sixty years of data is a treasure. Experiments such as those conducted at the Penobscot Experimental Forest generate data and knowledge that have become more important with time because the level of confidence in these results improves with each passing decade.

Sharing data is as important to science as collecting data, and here too the Penobscot Experimental Forest is impressive. Today, the Penobscot database includes more than 1 million observations. These long-term data are publicly available through the Forest Service's Research Data Archive, which puts the Penobscot Experimental Forest on the forefront of forestry research and science delivery.

This report will introduce you to the Penobscot Experimental Forest and the scientists who have used this landscape to experiment and discover. In a broader sense, it tells a story about Forest Service science and the Northern Research Station. I am deeply honored to be part of both, and very proud of the people and accomplishments about which you will be reading.

Michael T. Rains
Director, Northern Research Station

Page intentionally left blank

CONTENTS

Page intentionally left blank

HISTORY OF THE PENOBSCOT EXPERIMENTAL FOREST, 1950-2010

Laura S. Kenefic and John C. Brissette

Abstract.—Though the U.S. Department of Agriculture, Forest Service has been studying the forests of the northeastern United States since the late 1800s, long-term studies were not common until experimental forests were introduced in the 20th century. These forests were established for long-term experimentation, and research questions were defined by local forest management needs. The Penobscot Experimental Forest (PEF) in east-central Maine is an example of the success and evolution of the experimental forest model. The PEF was purchased by forest industry for research by the Forest Service, and later donated to the University of Maine Foundation. Throughout its history, the PEF has been defined by successful collaboration in research. Today, the PEF is known for world-class research on northern conifer silviculture and ecology, and work continues to evolve to address research questions beyond the scope envisioned by the original proponents of the site.

INTRODUCTION

The conifer-dominated forests of northern New England (Fig. 1) and adjacent Canada have long been critical to the region's economy. The northeastern United States was a leader in softwood lumber and pulpwood production by the mid- to late-1800s (Whitney 1994, Wilson 2005), and the region's heavily utilized northern conifer forest was largely cut over by the early 20th century (Irland 1999). Widespread cutting of progressively smaller trees caused forest degradation and led to concerns about resource sustainability (Judd 1997), yet demand for wood products continued to grow.

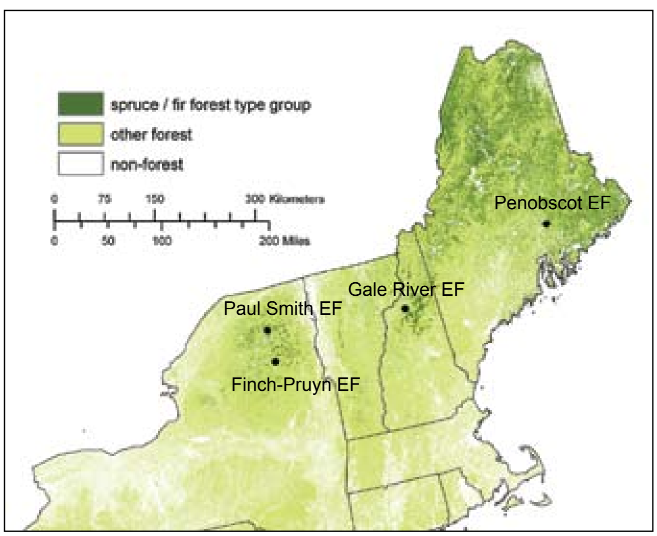


Figure 1.—Location of the northern conifer (previously called spruce-fir) forest in the northeastern United States, courtesy of B. Tyler Wilson, U.S. Forest Service, Forest Inventory and Analysis.

Though the U.S. Department of Agriculture (USDA), Forest Service had been conducting observational studies in the northern conifer (previously called spruce-fir) forest type since the 1890s (e.g., Graves 1899, Hosmer 1902, Murphy 1917, Zon 1914), manipulative research did not begin until experimental forests (EFs) were established in the 1920s. Establishment of EFs in the Northeast occurred shortly after the Forest Service formalized its research program in that region with the creation of the Northeastern Forest Experiment Station (now the Northern Research Station) in 1923 (Kenefic et al., in press). At that time, the northeastern pulp and paper industry manufactured more than half the nation's wood pulp and contributed substantially to the region's social and economic welfare (Meyer 1929, Westveld 1938).

The Forest Service's silvicultural experimentation in northern conifers began in 1926 at the Gale River EF (44°51′ N, 68°37′ W) in the White Mountains of New Hampshire. Research there was conducted under the direction of Marinus Westveld, the "Father of Spruce-Fir Silviculture." Additional experiments in northern conifer silviculture were initiated in 1934 and 1945, respectively, at the Finch-Pruyn (44°00′ N, 74°13′ W) and Paul Smith (44°26′ N, 74°14′ W) EFs in the Adirondacks of New York. Studies demonstrated the importance of establishing advance softwood regeneration prior to removing the overstory (Westveld 1930, 1931, 1938), using mechanical and chemical treatments to release overtopped softwoods (Curry and Rushmore 1955, Westveld 1933), and retaining sawtimber in managed stands (Recknagel et al. 1933). Despite these accomplishments, all three EFs were closed by the middle of the 20th century. The Gale River EF was destroyed in the New England Hurricane of 1938 (U.S. Forest Service 1939), and changes in research priorities and staffing led to closure of the Finch Pruyn and Paul Smith EFs (Berven et al. 2013).

Industrial use of the northern conifer forest continued to be heavy, particularly in Maine, where large acreages were owned by forest industry (Whitney 1994). Without Forest Service research, forest product companies would have had little scientific basis for their management (Kenefic et al., in press). Prior to the McIntire-Stennis Act of 1962, the capacity of university faculty to conduct forestry research was limited (Thompson 2004). As a consequence, the Forest Service was the sole source of information about many forest management topics, especially in the northern conifer forest.

A NEW EXPERIMENTAL FOREST

Louis Freedman, woods manager and superintendent of the Penobscot Chemical Fibre Company, suggested that forest industry purchase land for a new Forest Service experimental forest. The search for a suitable area in Maine began in earnest in the late 1940s. A number of criteria were specified for the property: 2,500 to 4,000 acres of land, all-weather road access, and location within 30 to 35 miles of a town. Though more than 20 areas were considered, one was deemed "superior in every respect."[1] The selected tract consisted of 3,800 acres owned by the Eastern Land Company in the towns of Bradley and Eddington on the east side of the Penobscot River (Fig. 2).

Repeated partial cutting had occurred on this parcel, but the forest contained large acreages of operable red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* [L.] Mill.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.), as well as hardwood and mixedwood stands dominated by red maple (*Acer rubrum* L.) and birch and aspen (*Betula* and *Populus* spp.). Two maps and unpublished reports[2] describe the forest land prior to the establishment of the experimental forest. A survey of the property in 1929 reports:

> The greater part of this area is second growth caused by an old burn and now has a growth of spruce, fir and poplar 5-8" dbh.[3] The balance of the area is old growth[4] having a stand of spruce, fir and hemlock, some pine and cedar. This area has all been cut off in [the] past five years for a mark of rather small saw logs, some as recent as last year, and there is now left standing spruce, fir and hemlock 5-8" [dbh] with a few trees of larger size. All of this land has a good growth of soft woods, spruce, fir and hemlock also poplar seedlings and saplings. A very thrifty stand.

An unpublished, undated report, "Statement Regarding a Proposed Experimental Forest, Bradley and Eddington Townships, Maine," further describes the land. Reference to a cruise by the Sewall Company in 1947 suggests that the report was written after that date, but before the experimental forest was established in 1950. The site is described as follows:

[1] Unpublished reports are on file with the U.S. Forest Service, Northern Research Station in Bradley, ME.

[2] Unpublished reports are on file with the U.S. Forest Service, Northern Research Station in Bradley, ME.

[3] Diameter at breast height.

[4] The term "old growth" refers to older trees, not old-growth forest.

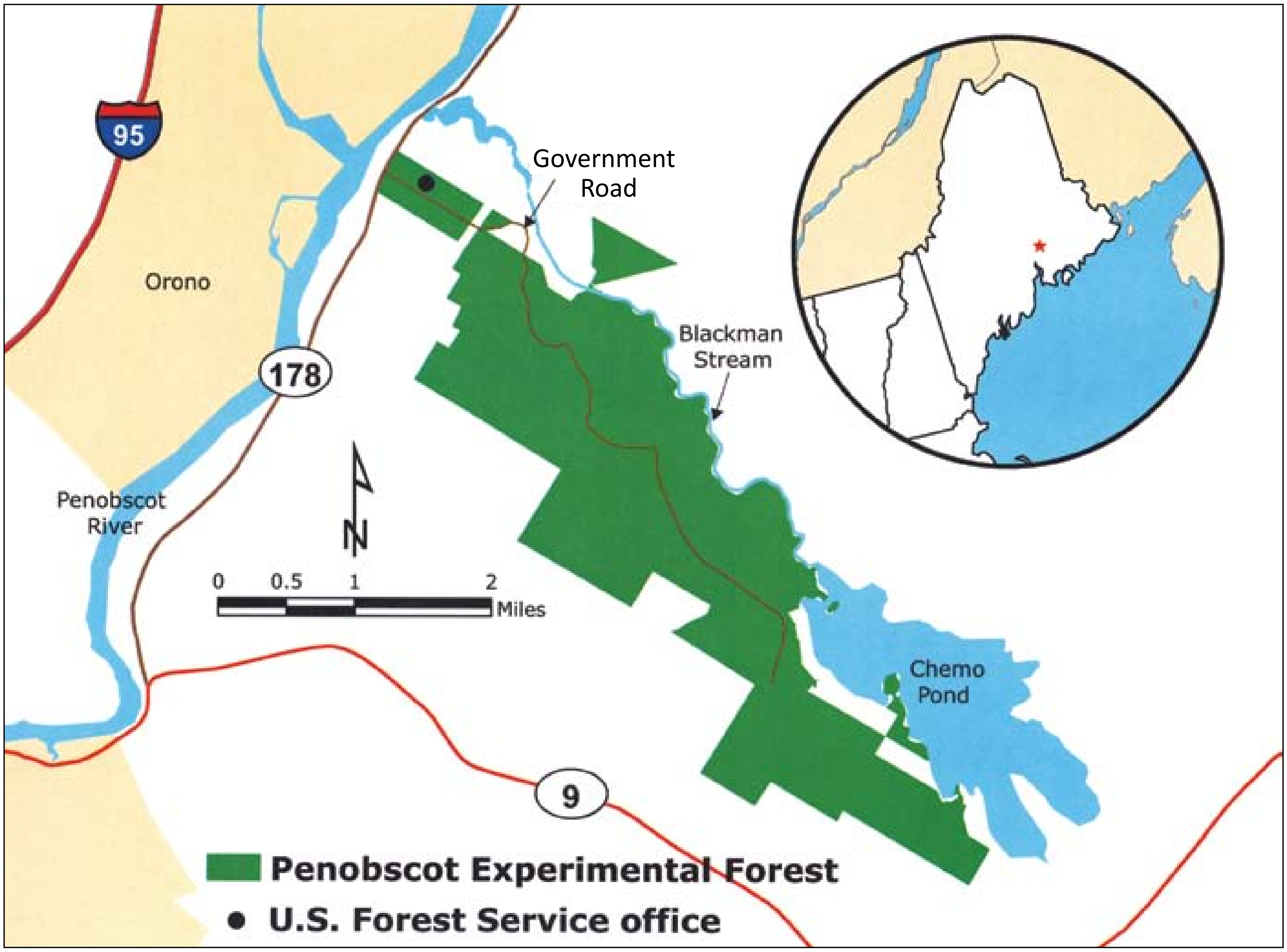


Figure 2.—Location of the PEF; map by Dale Gormanson, U.S. Forest Service, Forest Inventory and Analysis.

Practically all the area is well suited for growing spruce and fir. Heavy cutting and fires in the past have reduced the softwood types to their present distribution but the presence of spruce and fir reproduction throughout is evidence that these species are on their way back. The growth rates of spruce and hemlock are very good. Indications are that balsam fir makes very rapid growth for a short period—perhaps 40 years—then gradually goes into a decline.

The timber is all fairly young second growth, i.e. no overmature stands, in good condition, except for the fir which is showing signs of decay. One feature of the softwood stands which makes the tract particularly adaptable for research is the all-aged nature of the forest. This will permit immediate harvest cuttings on an experimental basis without the necessity for waiting until satisfactory stand conditions develop. A wide range of operating conditions is represented, from barely operable stands up to some carrying 10 or 12 cords per acre. Similarly, the non-operable portions range from young softwood stands which will be ready to cut in eight or ten years, to sprout hardwood stands where cutting will not be possible for 25 years or more.

The Penobscot Experimental Forest

The Eastern Land Company tract was selected for a new experimental forest and purchased in common and undivided ownership by nine industrial and land-holding companies: Great Northern Paper, Hollingsworth & Whitney, Oxford Paper, Eastern Corporation, S.D. Warren, Penobscot Chemical Fibre, International Paper, St. Regis Paper, and Dead River.

The land was leased to the Forest Service, which established the Penobscot EF (PEF, 44°53′ N, 68°39′ W) (Fig. 3). An American Forest Products Industries, Inc., press release at the time stated that this was "the first instance in the annals of American forestry in which a group of wood-using industries have united to purchase a large tract of timberland solely for lease to the federal government for experimental work" (Fig. 4).

Figure 3.—Sign on the PEF listing names of the landowners, circa 1950s. Photo by U.S. Forest Service.

Figure 4.—Photograph taken on September 26, 1952 of representatives of the nine companies that purchased the land for the PEF, with U.S. Forest Service staff and cooperators. In 2010, Forest Service, industry, and university retirees identified the following: Robert I. Ashman (University of Maine, 2nd from left), Louis J. Freedman (Penobscot Chemical Fibre Co., 3rd from left), Dwight B. Demeritt (Dead River Co., 6th from left), and Ed Giddings (Penobscot Chemical Fibre Co., 11th from left). Also: Robert True (S.D. Warren, 2nd from right), Gregory Baker (University of Maine, 7th from right), Art Randall (University of Maine, 9th from right), Paul Patterson (Great Northern Paper Co., 11th from right), and Henry Plummer (University of Maine, 13th from right). Photo by U.S. Forest Service.

The PEF is located south of the large industrial ownerships of northern Maine, on the southern edge of the Acadian Forest (Braun 1950, Rowe 1972). It has a much larger component of eastern hemlock than forests to the north. To increase the relevance of the study to the industrial landowners, the long-term Forest Service experiment was established in the portions of the PEF with the most spruce and fir; these sites were also more poorly drained and less productive than the portions of the forest supporting northern hardwoods (Fig. 5).

When the long-term experiment began, species composition across the study area was (in terms of basal area) 30 percent hemlock; 20 percent fir; 16 percent spruce; 12 percent northern white-cedar (*Thuja occidentalis* L.); 9 percent red maple; and 4 percent each eastern white pine (*Pinus strobus* L.), paper birch (*B. papyrifera* Marsh.), and "other." Diameter distributions (graphs of number of trees per acre by diameter class) were reverse-J shaped, with few if any trees per acre in the large sawtimber classes. These distributions reflect the presence of scattered older residuals from past cutting in otherwise aggrading stands composed of released advance and new regeneration. The forest age structure was irregularly uneven-aged.

Forest Service Research on the PEF

Station employees held different opinions about the direction that Forest Service research should take in Maine. Westveld was nearing retirement, but continued observational studies of silvics and fundamental silviculture. New silviculturist Thomas F. McLintock

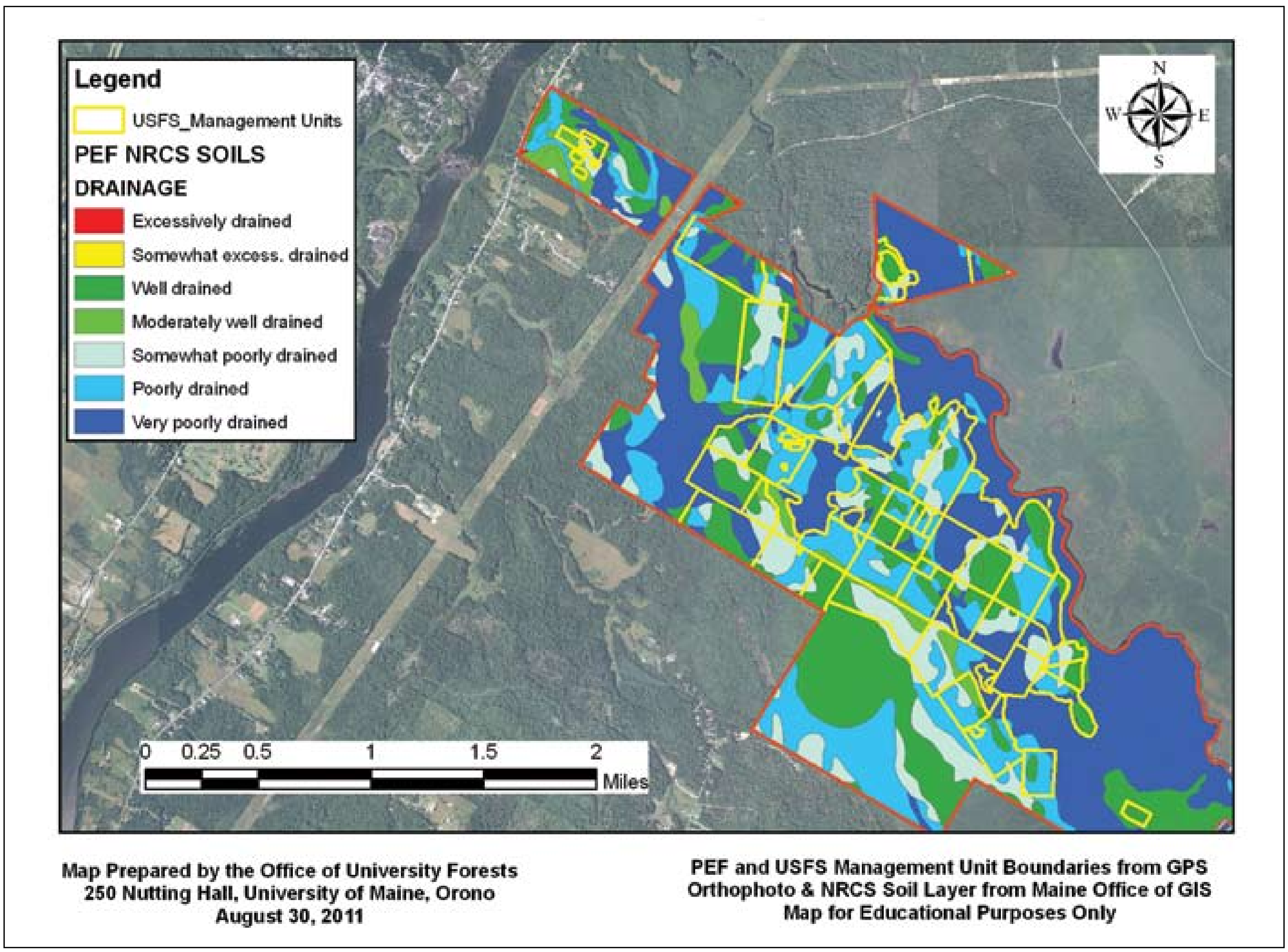


Figure 5.—Location of the U.S. Forest Service management units and soil drainage on the PEF, courtesy of Alan Kimball, University of Maine.

(Fig. 6) was focused on specific management problems, such as determining cutting cycle length and marking guidelines from growth and yield assessments. Though industrial support for forestry research was growing, the approach the Station would take in the future was not clearly defined. Ultimately, McLintock's emphasis on growth and yield was adopted and served as the basis for experiments at the PEF; this decision was a turning point for the Forest Service's research program in Maine.

Thomas F.
McLintock
1945-1956

Research
Center
Leader
(1945-1956)

Expertise:
silviculture

Arthur C.
Hart, Sr.
1948-1969

Project
Leader
(1958-1969)

Expertise:
silviculture

Grant Davis
1955-1958

Expertise:
silviculture

Franklin R.
Longwood
1956-1961

Research
Center
Leader
(1956-1961)

Expertise:
silviculture

John C.
Bjorkbom
1961-1970

Expertise:
silviculture

Francis M.
Rushmore
1962-1972

Expertise:
silviculture

Lawrence O.
Safford
1962-1970

Expertise:
soils

Robert M.
Frank, Jr.
1963-1996

Expertise:
silviculture

Carter B.
Gibbs
1971-1972

Project
Leader
(1971-1972)

Expertise:
silviculture

Figure 6.—U.S. Forest Service, Northeastern Forest Experiment Station (now Northern Research Station) scientists assigned to the PEF, 1950-present. Dates research scientists were assigned to the PEF and served as Research Center or Project Leaders are shown, as determined from memos in the PEF archives, Forest Service Organizational Directories, published biographies, and personal communication with retirees. There may be slight errors (i.e., ± 1 to 2 years), particularly regarding earlier staff. Photos by U.S. Forest Service.

Dale S. Solomon
1971-1988

Expertise: growth and yield modeling

Barton M. Blum
1971-1991

Project Leader (1972-1991)

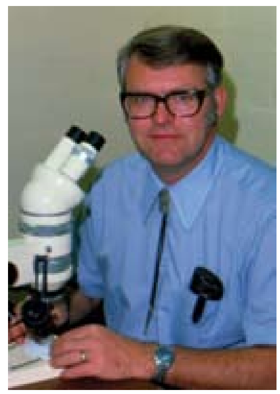
Expertise: silviculture

Miroslaw M. Czapowskyj
1973-1986

Expertise: soils

Hewlette S. Crawford, Jr.
1975-1991

Expertise: wildlife biology



Daniel T. Jennings
1976-1988

Expertise: entomology

John C. Brissette
1992-present

Project Leader (1992-present)

Expertise: silviculture

Laura S. Kenefic
1994-present

Expertise: silviculture

Figure 6 (continued).—U.S. Forest Service, Northeastern Forest Experiment Station (now Northern Research Station) scientists assigned to the PEF, 1950-present. Photos by U.S. Forest Service.

The core experiment proposed for the PEF was a "Compartment Study" of forest management options with different silvicultural treatments applied to replicated stand-level management units (MUs) (see Brissette and Kenefic, this volume). Described as "the heart of the research program," this experiment would document tree growth, mortality, logging costs, and change in forest condition through frequent inventories. This large-scale (called "pilot plant" at the time) approach to experimentation was advocated within the Forest Service, and allowed assessment of forest management alternatives at an operational scale.

In addition, though earlier studies were unreplicated, advances in statistics (i.e., Fisher 1925a,b) led to at least minimal replication (n=2) in studies established on many mid-century EFs. On the PEF, researchers also set aside a small portion of the forest (less than 50 acres) as an undisturbed area "closed to all operations and experiments, except those of an observational nature." Though not intended as such, this area would later serve as an important reference for the long-term study, against which the outcomes of management could be evaluated.

In 1946, a national assessment of forest resources divided management practices into five categories, based on what was being done relative to what was deemed the most appropriate practice for the local forest type (Harper and Rettie 1946). These categories were: "high-order," "good," "fair," "poor," and "destructive." The Northeastern Forest Experiment Station further promoted this categorization as a basis for research (U.S. Forest Service 1948). Many experimental forests in the Station established "cutting practice level" (CPL) studies which compared categories (usually the first four) of management, and served as demonstrations.

A 1952 article in "Pulp and Paper Magazine" (Anonymous 1952) described the early stages of the research on the PEF. Work was initiated by McLintock with the objective of determining what types of forest management were economically practical for the spruce-fir-hardwood region of Maine. The first step was to establish a CPL (also called management intensity demonstration, MID) area on the forest; this 40-acre area was divided into 10-acre MUs representing high-order, good, fair, and poor management, as described above. These treatments, which have since been redefined as selection cutting on 5- and 15-year cycles, fixed diameter-limit cutting, and commercial clearcutting, mirrored those on many other EFs throughout the Station. They were initially intended to serve as demonstration areas, but have since allowed comparison of similar treatments across forest types, thus expanding the scope of the local studies to a regional scale (Kenefic and Schuler 2008).

The PEF Compartment Study was also installed shortly after the PEF was established, with initial treatments applied between 1952 and 1957 to MUs averaging 25 acres in size. Though Westveld never worked on the PEF, the range of treatments there was greatly influenced by his earlier work in partial cutting (e.g., Belotelkin et al. 1942; Recknagel et al. 1933; Westveld 1938, 1953). The first draft of the study plan included variants of selection cutting, as well as common exploitative practices: diameter-limit cutting and commercial clearcutting (unregulated harvesting). This emphasis was consistent with broader trends in forestry research between 1925 and 1960, a period that has been called the "Selective Cutting Era" due to the national focus on selection and other forms of partial cutting (Seymour et al. 2006, Smith 1972). Though not initially included, variants of even-aged silvicultural systems (including shelterwood) were added to the study plan at the urging of cooperator David M. Smith, who was then a young faculty member at Yale.

Smith's suggestion proved to be an inspired one. In the 1960s, forestry nationwide shifted into what is now known as the "Production Forestry Era," during which the management paradigm was one of even-aged, high-yield, low-cost wood production (Seymour et al. 2006). Studies of planting, fertilization, thinning, strip clearcutting, and whole-tree harvesting were initiated by Forest Service scientists on the PEF, in direct response to industrial needs (Table 1, Fig. 7). Arthur C. Hart, Sr., a silviculturist who had previously worked with Westveld at the Gale River EF, took over leadership of the PEF study from McLintock; Hart and new scientist Robert M. Frank, Jr., expanded the research to include regeneration and recruitment.

Table 1.—Partial list of formal studies by U.S. Forest Service scientists on the PEF, 1950-present.

Year initiated	Study[a]	PI(s)	Study number	Status	Data available?[b]
1950	Cutting Practice Level Study (Management Intensity Demonstration)	McLintock	NE-1101-3	Active	Digital, online
1951	Small Woodland Management in the Spruce-Fir Region	McLintock, Hart	—	Closed	No
1951	Costs and Returns from Pruning Red Spruce Trees	McLintock	NE-1101-5	Closed	No
1952	Compartment Management Study (Spruce-Fir Silviculture)	McLintock	NE-1101-7	Active	Digital, local and online
1953	Effect of Seedbed Preparation on Spruce and Hemlock Reproduction	—	—	Closed	No
1954	Compartment Inventory Sampling Study	—	—	Closed	Unknown
1954	Volume Table Study	McLintock	—	Closed	Unknown
1954	Balsam Fir Mortality Study	—	—	Closed	Unknown
1954	Physical Properties of Forest Soils	McLintock	—	Closed	No
1955	White Pine Provenance Study	Schreiner, Wright	—	Inactive	Unknown
1955	Thinning Balsam Fir Thickets with Soil Sterilants	Hart	—	Closed	No
1958	Seedbed Preparation and Regeneration of Paper Birch	Bjorkbom	—	Closed	No
1958	Hybrid Spruce Plantations	Hart	NE-1101-10	Inactive	Unknown
1958	Balsam Woolly Aphid Occurrence on the PEF Compartments	Hart	NE-1101-13	Closed	Unknown
1959	Influence of Mice and Birds on Spruce-Fir Reproduction	Hart	—	Closed	No
1960	Rate of Growth of Heart Rot Fungi in Living Trees	Brandt, Shigo	—	Closed	Unknown

(Table 1 continued on next page)

Table 1 (continued).—Partial list of formal studies by U.S. Forest Service scientists on the PEF, 1950-present.

Year initiated	Study[a]	PI(s)	Study number	Status	Data available?[b]
1961	Growth Response of Released White Spruce	Hart	—	Closed	Unknown
1962	Revision: Compartment Management Study (Spruce-Fir Silviculture)	Hart	NE-1101-7	Active	Digital, local and online
1964	Amendment: Compartment Management Study (Regeneration)	Frank	NE-1101-7	Active	Digital, online
1964	Sapsucker Behavior and Feeding Habits	Rushmore	—	Closed	No
1964	Strip Clearcutting and Slash Disposal Methods	Frank	NE-1101-23	Inactive	No
1964	Production and Germination of Paper Birch Seeds	Bjorkbom	—	Closed	No
1966	Viability of Seeds in the Forest Floor After Clearcutting	Frank, Safford	—	Closed	No
1967	Nutrient Content of Red Spruce Foliage on Different Soil Series	Safford	—	Closed	No
1971	Effect of Fertilizer on Spruce Trees in a Thinned White Spruce-Balsam Fir Stands	Frank	NE-1101-41	Closed	No
1972	Height Growth Relationships Among Red Spruce, White Spruce, and Balsam Fir	Blum	NE-1101-43	Closed	Unknown
1973	Growth Response of Red Spruce, White Spruce, and Fir Along Edges of Strips	Frank	NE-1101-45	Closed	No
1973	Effects of Strip Harvesting and Slash Disposal Methods on Soils	Czapowskyj, Frank	NE-1101-46	Inactive	No
1975	Revision: Compartment Management Study (Spruce-Fir Silviculture)	Frank	NE-1101-7	Active	Digital, online
1975	Foliar Nutrient Concentrations of Young Balsam Fir Related to Soil and Slash Disposal Methods	Czapowskyj	NE1101-49	Closed	No

(Table 1 continued on next page)

Table 1 (continued).—Partial list of formal studies by U.S. Forest Service scientists on the PEF, 1950-present.

Year initiated	Study[a]	PI(s)	Study number	Status	Data available?[b]
1975	Influence of Residual Basal Area Density on Growth of Spruce-Fir Stands	Solomon	NE-1101-56	Closed	No
1975	Cultural Treatments Designed to Reduce Spruce Sawlog Rotation Age	Frank	NE-1101-58	Active	Digital, online
1976	Seasonal Foods Selected by Tractable Deer in Spruce-Fir-Mixedwood Stands	Crawford	NE-1151-61	Closed	No
1977	Helicopter Propwash for Removal of Spruce Budworm	Jennings	—	Closed	No
1977	Measuring Plant Growth with Radio Link Attenuation	Crawford	NE-1151-73	Closed	No
1978	Attraction of Male Spruce Budworm to Pheromone Traps	Jennings	—	Closed	No
1978	Aspen and Red Maple Sprouting After Cutting	Blum	NE-1151-77	Closed	No
1978	Even-Aged and Shelterwood Regeneration of Residual Strips in Spruce-Fir Strip Harvests	Frank	NE-1151-83	Inactive	No
1979	Survival and Development of Advance Regeneration After Shelterwood Harvest	Blum	NE-1151-87	Inactive	Unknown
1979	Spruce Budworm Monitoring	Blum	NE-1151-89	Closed	Unknown
1981	Variation in Bud Flushing Among White Spruce Provenances	Blum	NE-1151-92	Closed	No
1981	Early-Larval Dispersal of the Spruce Budworm	Jennings	NE-1151-94	Closed	No
1984	Comparison of Whole-Tree and Conventional Logging Damage to Spruce and Fir Regeneration	Frank	NE-1151-100	Inactive	Unknown
1994	Irregular Shelterwood (New Forestry)	Frank	—	Active	Digital, local
1995	Age Structure of the Selection Compartments	Kenefic, Seymour	—	Inactive	Digital, local

(Table 1 continued on next page)

Table 1 (continued).—Partial list of formal studies by U.S. Forest Service scientists on the PEF, 1950-present.

Year initiated	Study[a]	PI(s)	Study number	Status	Data available?[b]
1995	Leaf Area – Growth Efficiency Relationships in Multi-Cohort Stands	Kenefic	—	Inactive	Digital, local
1995	Role of Fungi in Biotransformation and Nutrient Cycling in the Forest Ecosystem	Shortle, Jellison, Smith	NE-4505-95-2	Active	No
2001	Quantifying Carbon in Northern Forests (Emphasis on Soils)	Hoover	FS-NE-4152-177	Inactive	Digital, local
2001	Timber Marking Costs in Northern Conifer Stands	Sendak	—	Inactive	Digital, local
2005	Substrate Availability and Regeneration Microsites of Tolerant Conifers	Kenefic, Weaver	—	Closed	Digital, local
2006	Relationships Between Understory Vegetation and Soil, Site, and Silviculture	Kenefic, Bryce	—	Inactive	Digital, local
2008	Revision: Compartment Management Study (Northern Conifer Silviculture)	Brissette, Kenefic	NRS-07-08-01	Active	Digital, online
2008	Rehabilitation of Cutover Mixedwood Stands	Kenefic	NRS-07-08-01 Appendix	Active	Digital, local
2009	Effects of Silvicultural Treatment on the Dynamics of Eastern White Pine in Mixed Stands	Brissette, Seymour	—	Inactive	Digital, local
2010	Seedling Herbivory	Kenefic, Weiskittel, Berven	—	Inactive	Digital, local
2010	How Well Do the Permanent Sample Plots Represent Stand Conditions?	Brissette, Weiskittel, Kenefic	—	Active	Digital, local

— Indicates unknown (PI or study number) or unassigned (study number).

[a] This list includes studies conducted wholly or partly on the PEF and for which U.S. Forest Service scientists served as principal investigators. Active studies are ongoing with regularly scheduled treatments and inventories. Inactive studies are not being treated and/or inventoried at this time, but boundaries and/or plots are maintained for future remeasurement. Closed studies cannot be relocated or remeasured. This list is not complete; it includes only those studies for which documentation is on file.

[b] Data may be available for download (online) or in a locally stored digital format with limited accessibility (e.g., text, spreadsheet, or pdf). Availability of data from inactive or closed studies may be unknown due to the volume of records held by the Forest Service at the PEF; such data may be in paper or scanned (pdf) format or lost. Data that are not available are confirmed to be lost, with the exception of NE-4505-95-2, for which data are being processed at this time. Summaries of the data or results of analyses from most of the studies listed here have been published (see Kenefic and Brissette, "Publications," this volume).

a. 1968

a. present

b. 1976

b. present

c. 1984

c. present

Figure 7.—Examples of production forestry research on the PEF: (a) eastern white pine provenance plantation (1968 and present), (b) precommercial thinning (1976 and present, after commercial thinning), and (c) biomass operation with whole tree harvesting (1984 and present). Photos by U.S. Forest Service.

It was toward the end of this period, in the late 1970s and early 1980s, that a severe spruce budworm (*Choristoneura fumiferana* [Clemens]) infestation spread through southeastern Canada and northern New England. During the budworm years, Forest Service staffing in Maine and related research activity on the PEF increased. Though less severe than in forests farther north, the spruce budworm infestation on the PEF generated an abundance of literature related to budworm impacts and control (e.g., Blum 1985; Collins and Jennings 1987; Houseweart et al. 1980, 1982; Jennings and Crawford 1983; Jennings and Houseweart 1983, 1986, 1989; Jennings et al. 1984; Kendall et al. 1982). In addition, heavy cutting throughout the region before and during the budworm era created large areas of naturally regenerated, softwood-dominated stands. Industrial landowners had questions about the best ways to manage these densely stocked stands, and whether early stand treatments were warranted. Some of the earliest studies on precommercial thinning in the region were conducted on the PEF, and would ultimately provide important information about the effectiveness of various operational methodologies and spacings (Brissette et al. 1999; Weiskittel et al. 2009, 2011).

Over the years, numerous studies have been conducted on the PEF, and close to 300 technical and scientific publications written (see Kenefic and Brissette, this volume). In addition to an abundance of research on forest ecology and silviculture, studies done by or in cooperation with Forest Service scientists have covered a range of topics, such as measurement techniques (Brissette et al. 2003, Kidd 1952, Lindemuth 2007), tree growth (Blum and Solomon 1980, Solomon and Frank 1983, Solomon and Seegrist 1983), leaf area relationships (DeRose and Seymour 2003, 2010; Gilmore and Seymour 1996; Kenefic and Seymour 1999; Maguire et al. 1998), root structure (Tian 2002), soils and site quality (Czapowskyj et al. 1977, McLintock 1959), wood properties and decay (Garber et al. 2005, Smith et al. 2007), genetics (Hawley et al. 2005), understory plants (Dibble et al. 1999, Olson et al. 2011, Safford et al. 1969), songbirds (Horton and Holberton 2009, Johnston and Holberton 2009), insects (Collins and Jennings 1987, Su and Woods 2001), spiders (Jennings and Houseweart 1989, Jennings and Sferra 2002), and wildlife (Abbott and Hart 1961, Crawford 1982, Crawford and Frank 1988, Grisez 1954). There has always been great potential for additional research, using the conditions represented within the long-term study to answer questions about ecology and management. In addition, many of the Forest Service's data from the long-term silvicultural studies on the PEF are available online, facilitating collaborative research (Brissette et al. 2012a, 2012b).

The University of Maine and the PEF

In the 1990s, forest product companies in the Northeast underwent profound changes involving consolidation, downsizing, and turnover in mill and forest ownership. Early mills had acquired large amounts of land and held it against wood shortages, but returns on investment were low. As long as timberland was cheap, the mills retained their forest property, but with land values rising and demand for pulpwood declining, many began to sell their property in the 1990s (Acheson 2000, Hagan et al. 2005). Frequent turnover of ownership within the forest industry, desire to increase university cooperation, and concerns about the Forest Service's long-term commitment to the PEF (Frank and Kenefic, this volume) motivated the industrial owners to donate the property to the University of Maine Foundation in 1994.

As a result of mergers and acquisitions of the original companies, the forest owners at the time of the donation were Boise Cascade, Champion International, Great Northern Paper, J.M. Huber, International Paper, J.D. Irving, James River Timber, Prentiss and Carlisle, Scott Paper, Seven Islands, and J.W. Sewall (Fig. 8). The Forest Service has continued its research under a memorandum of understanding since that time. In addition, University of Maine faculty and graduate students have expanded the research on the forest to include an additional 300 acres of forest

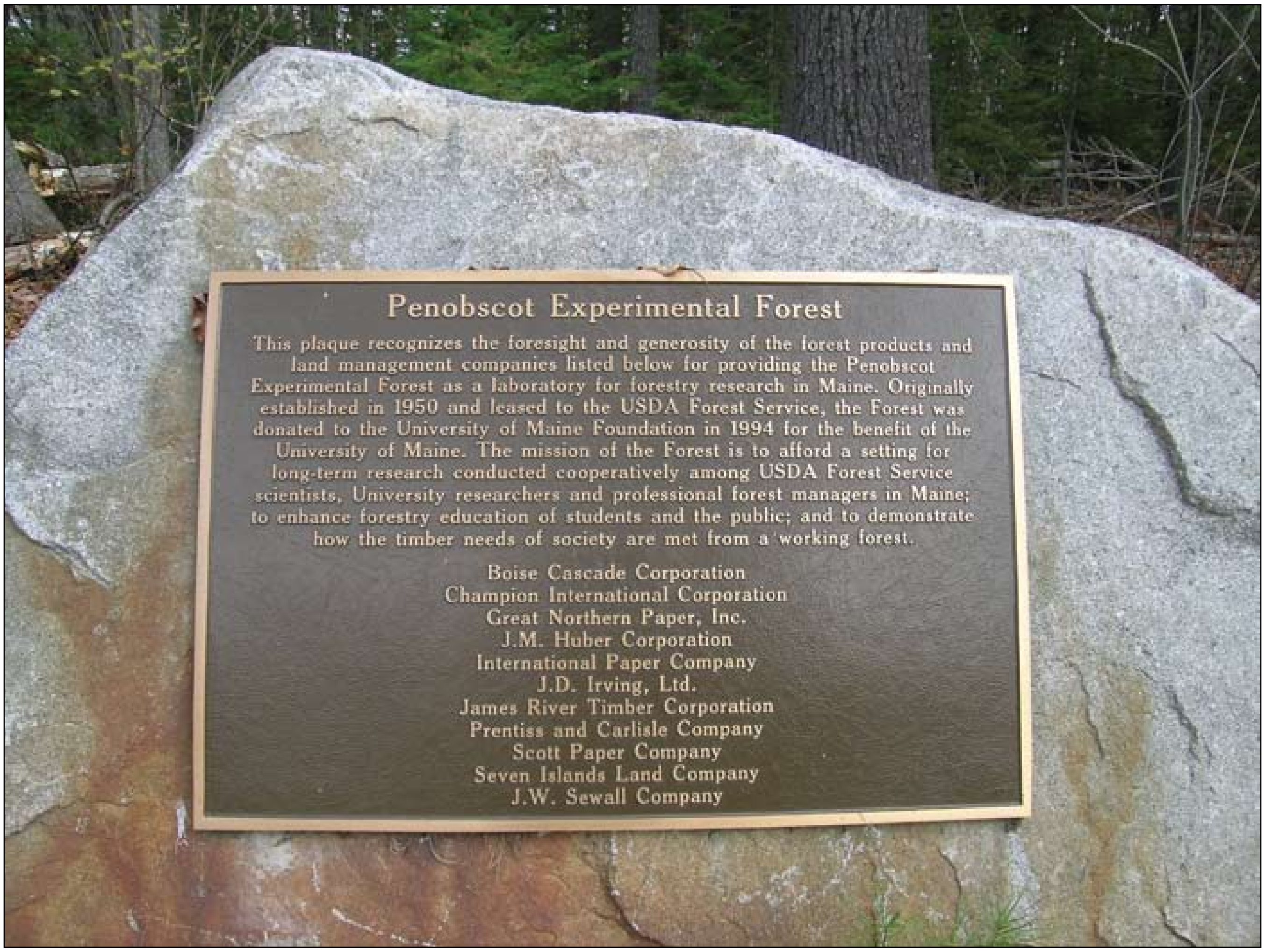


Figure 8.—Sign on the PEF listing names of the landowners, circa 1990s. Photo by U.S. Forest Service.

management experiments (see Nelson and Wagner, this volume; Saunders et al., this volume; Seymour et al., this volume), as well as 1,000 acres of wetlands and reserves and 1,500 acres of "working forest" managed by the University Forests Office for income generation, education, and research (see Kimball, this volume). The PEF is also open to many types of recreation.

CONCLUSIONS

One of the articles published at the time of the PEF's establishment concluded that "[t]here is every reason to think it [the PEF] should return rewards… It is a project established on a large enough scale, and to extend over a long enough period of time, to permit true scientific investigation" (Anonymous 1952). This prediction has proven to be true; the cutting practice level (MID) and large-scale Compartment Study have been continued by the Forest Service until the present day, making the PEF one of the oldest replicated, continuously operated and inventoried forest research sites in North America. The PEF studies provide invaluable information on the long-term consequences of various forest management alternatives. We give dozens of tours each year to landowners, researchers, forestry students, and land managers. Though visitors are usually from the Northeast and eastern Canada, we have had guests from throughout North America and as far away as Australia and Siberia. Perhaps most important, we continue to maintain and expand the research envisioned by our predecessors and in so doing, pay tribute to those Maine forestry pioneers.

ACKNOWLEDGMENTS

We thank Robert M. Frank, Jr., and Lawrence O. Safford (USDA Forest Service, retired) for their assistance with the historical aspects of this paper. Robert Seymour and Justin Waskiewicz (University of Maine, School of Forest Resources) provided helpful reviews of an earlier version of this manuscript. Amy Doole of the National Forest Service Library provided invaluable assistance with research.

LITERATURE CITED

Abbott, H.G.; Hart, A.C. 1961. **Mice and voles prefer spruce seed.** Stn. Pap. 153. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 12 p.

Acheson, J. 2000. **Clearcutting Maine: implications for the theory of common property resources.** Human Ecology. 28: 145-169.

Anonymous. 1952. **Maine Experimental Forest.** Pulp and Paper Magazine 53(6): 76, 80.

Belotelkin, K.T.; Reineke, R.H.; Westveld, M. 1942. **Spruce-fir selective logging costs.** Journal of Forestry. 40(4): 326-336.

Berven, K.; Kenefic, L.; Weiskittel, A.; Twery, M.; Wilson, J. 2013. **The lost research of early northeastern spruce-fir experimental forests: a tale of lost opportunities.** In: Irland, L.; Camp, A.; Carroll, C.J.W., eds. Long-term silvicultural and ecological studies. GISF Research Paper 13. New Haven, CT: Yale University, Global Institute of Sustainable Forestry: 103-115. Vol. 2.

Blum, B.M. 1985. **Appropriate silviculture.** In: Spruce-fir management and spruce budworm: Society of American Foresters, Region VI, Technical Conference; 1984 April 24-26; Burlington, VT. Gen. Tech. Rep. NE-99. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 185-191.

Blum, B.M.; Solomon, D.S. 1980. **Growth trends in pruned red spruce trees.** Res. Note NE-294. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 6 p.

Braun, E.L. 1950. **Deciduous forests of eastern North America.** Philadelphia, PA: Blakiston Co. 596 p.

Brissette, J.C.; Ducey, M.J.; Gove, J.H. 2003. **A field test of point relascope sampling of down coarse woody material in managed stands in the Acadian Forest.** Journal of the Torrey Botanical Society. 130(2): 79-88.

Brissette, J.C.; Frank, R.M., Jr.; Stone, T.L.; Skratt, T.A. 1999. **Precommercial thinning in a northern conifer stand: 18-year results.** The Forestry Chronicle. 75(6): 967-972.

Brissette, J.C.; Kenefic, L.S.; Russell, M.B. 2012a. **Precommercial thinning x fertilization study data from the Penobscot Experimental Forest.** Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0009.

Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012b. **Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest.** Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008.

Collins, J.A.; Jennings, D.T. 1987. **Nesting height preferences of eumenid wasps (Hymenoptera: Eumenidae) that prey on spruce budworm (Lepidoptera: Tortricidae).** Annals of the Entomological Society of America. 80: 435-438.

Crawford, H.S. 1982. **Seasonal food selection and digestibility by tame white-tailed deer in central Maine.** Journal of Wildlife Management. 46(4): 974-982.

Crawford, H.S.; Frank, R.M. 1988. **Rating spruce-fir silviculture for wildlife and forestry.** Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Information Management Group. 23 p.

Curry, J.R.; Rushmore, F.M. 1955. **Experiments in killing northern hardwoods with sodium arsenite and ammonium sulfamate.** Journal of Forestry. 53(8): 575-580.

Czapowskyj, M.M.; Rourke, R.V.; Frank, R.M. 1977. **Strip clearcutting did not degrade the site in a spruce-fir forest in central Maine.** Res. Pap. NE-367. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

DeRose, R.J.; Seymour, R.S. 2003. **Relationships between leaf area, structure and relative density in even-aged spruce-fir stands in Maine.** In: Cooperative Forestry Research Unit: 2003 annual report. Misc. Rep. 2684. Orono, ME: Maine Agriculture and Forest Experiment Station: 28-30.

DeRose, R.J.; Seymour, R.S. 2010. **Patterns of leaf area index during stand development in even-aged balsam fir - red spruce stands.** Canadian Journal of Forest Research. 40: 629-637.

Dibble, A.C.; Brissette, J.C.; Hunter, M.L., Jr. 1999. **Putting community data to work: Some understory plants indicate red spruce regeneration habitat.** Forest Ecology and Management. 114(2-3): 275-291.

Fisher, R.A.1925a. **Statistical methods, experimental design and scientific inference.** Oxford, UK: Oxford University Press.

Fisher, R.A.1925b. **Statistical methods for research workers.** Edinburgh, Scotland: Oliver and Boyd Ltd.

Garber, S.M.; Brown, J.P.; Wilson, D.S.; Maguire, D.A.; Heath, L.S. 2005. **Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine.** Canadian Journal of Forest Research. 35: 787-796.

Gilmore, D.W.; Seymour, R.S. 1996. **Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA.** Forest Ecology and Management. 84(1-3): 209-218.

Graves, H.S. 1899. **Practical forestry in the Adirondacks.** Bull. 26. Washington, DC: U.S. Department of Agriculture, Division of Forestry. 85 p.

Grisez, T.J. 1954. **Results of a mouse census in a spruce-fir-hemlock forest in Maine.** Forest Res. Note No. 28. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Hagan, J.M.; Irland, L.C.; Whitman, A.A. 2005. **Changing timberland ownership in the northern forest and implications for biodiversity.** Report MCCS-FCP-2005-1. Brunswick, ME: Manomet Center for Conservation Sciences. 25 p.

Harper, V.L.; Rettie, J.C. 1946. **The management status of forest lands in the United States. Report 3 from a reappraisal of the forest situation.** Washington, DC: U.S. Department of Agriculture, Forest Service. 22 p.

Hawley, G.J.; Schaberg, P.G.; DeHayes, D.H.; Brissette, J.C. 2005. **Silviculture alters the genetic structure of an eastern hemlock forest in Maine, USA.** Canadian Journal of Forest Research. 35: 143-150.

Horton, B.M.; Holberton, R.L. 2009. **Corticosterone manipulations alter morph-specific nestling provisioning behavior in male white-throated sparrows, *Zonotrichia albicollis*.** Hormones and Behavior. 56: 510-518.

Hosmer, R.S. 1902. **A study of Maine spruce.** In: Fourth report of the Forest Commissioner of the State of Maine. Augusta, ME: 65-108.

Houseweart, M.W.; Jennings, D.T.; Berkett, L.P.; Brann, T.B. 1980. **Parasitic mites (Acari: Erythraeidae) on spruce budworm moths (Lepidoptera: Tortricidae).** The Canadian Entomologist. 112(2): 193-197.

Houseweart, M.W.; Southard, S.G.; Jennings, D.T. 1982. **Availability and acceptability of spruce budworm eggs to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae).** The Canadian Entomologist. 114: 657-666.

Irland, L.C. 1999. **The Northeast's changing forest.** Petersham, MA: Harvard Forest and Harvard University Press. 401 p.

Jennings, D.T.; Crawford, H.S. 1983. **Pine siskin preys on egg masses of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae).** The Canadian Entomologist. 115: 439-440.

Jennings, D.T.; Frank, R.M.; Houseweart, M.W. 1984. **Attraction of male spruce budworm moths, *Choristoneura fumiferana* (Clemens), to pheromone-baited traps in small-tree thinnings.** Journal of Chemical Ecology. 10(1): 125-133.

Jennings, D.T.; Houseweart, M.W. 1983. **Sticky-board trap for measuring dispersal of spruce budworm larvae.** Res. Pap. NE-526. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Jennings, D.T.; Houseweart, M.W. 1986. **Helicopter propwash dislodges few spruce budworms.** Res. Note NE-333. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Jennings, D.T.; Houseweart, M.W. 1989. **Sex-biased predation by web-spinning spiders (Araneae) on spruce budworm moths.** Journal of Arachnology. 17(2): 179-194.

Jennings, D.T.; Sferra, N.J. 2002. **An arthropod predator-prey-kleptoparasite association.** Northeastern Naturalist. 9(3): 325-330.

Johnston, J.C.; Holberton, R.L. 2009. **Forest management and temporal effects on food abundance for a ground-foraging bird (*Catharus guttatus*).** Forest Ecology and Management. 258(7): 1516-1527.

Judd, R.W. 1997. **Common lands, common people: The origins of conservation in northern New England.** Cambridge, MA: Harvard University Press. 335 p.

Kendall, D.M.; Jennings, D.T.; Houseweart, M.W. 1982. **A large-capacity pheromone trap for spruce budworm moths (Lepidoptera: Tortricidae).** The Canadian Entomologist. 114: 461-463.

Kenefic, L.S.; Brissette, J.C.; Judd, R. [In press]. **Northern conifer research: multiple species and multiple values.** In: Crawford, R.; Hayes, D.; Stout, S., eds. Research for the long-term: the interplay of societal need and research on USDA Forest Service Experimental Forests and Ranges. Springer.

Kenefic, L.S.; Schuler, T.M. 2008. **Regional synthesis of long-term findings from U.S. Forest Service management intensity demonstrations.** In: Poster Abstracts of the Central Hardwood Forest Conference; 2008 April 8-9; Lafayette, IN. FNR-402-W. Purdue Extension Publication. West Lafayette, IN: Purdue University: 9.

Kenefic, L.S.; Seymour, R.S. 1999. **Leaf area prediction models for *Tsuga canadensis* in Maine.** Canadian Journal of Forest Research. 29: 1574-1582.

Kidd, W.J., Jr. 1952. **A small-tree diameter gauge.** Journal of Forestry. 50: 220.

Lindemuth, R.M. 2007. **A field trial comparison of sampling methods for estimating basal area and volume in partially harvested stands in Maine.** Orono, ME: University of Maine. 100 p. M.S. thesis.

Maguire, D.A.; Brissette, J.C.; Gu, L. 1998. **Canopy structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine.** Canadian Journal of Forest Research. 28: 1233-1240.

McLintock, T.F. 1959. **Soil moisture patterns in a northern coniferous forest.** Stn. Pap. 128. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 5 p.

Meyer, W.H. 1929. **Yields of second-growth spruce and fir in the Northeast.** Tech. Bull. No. 142. Washington, DC: U.S. Department of Agriculture, Forest Service. 52 p.

Murphy, L.S. 1917. **The red spruce: its growth and management.** Bull. No. 544. Washington, DC: U.S. Department of Agriculture, Forest Service. 100 p.

Olson, E.K.; Kenefic, L.S.; Dibble, A.C.; Brissette, J.C. 2011. **Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: influence of site, silviculture and land use history.** Journal of the Torrey Botanical Society. 138(4): 453-464.

Recknagel, A.B.; Churchill, H.L.; Heimberger, C.; Westveld, M. 1933. **Experimental cutting of spruce and fir in the Adirondacks.** Journal of Forestry. 31(6): 680-688.

Rowe, J.S. 1972. **Forest regions of Canada.** Publ. 1300. Ottawa, ON: Canadian Forestry Service, Department of the Environment. 172 p.

Safford, L.O.; Frank, R.M.; Little, E.L., Jr. 1969. **Trees and shrubs of the Penobscot Experimental Forest, Penobscot County, Maine.** NE 128. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 27 p.

Seymour, R.S.; Guldin, J.; Marshall, D.; Palik, B. 2006. **Large-scale, long-term silvicultural experiments in the United States: historical overview and contemporary examples.** Allgemeine Forst-und Jagdzeitung. 177(6/7): 104-112.

Smith, D.M. 1972. **The continuing evolution of silvicultural practice.** Journal of Forestry. 70(2): 89-92.

Smith, K.T.; Shortle, W.C.; Jellison, J.; Connolly, J.; Schilling, J. 2007. **Concentrations of Ca and Mg in early stages of sapwood decay in red spruce, eastern hemlock, red maple, and paper birch.** Canadian Journal of Forest Research. 37: 957-965.

Solomon, D.S.; Frank, R.M. 1983. **Growth response of managed uneven-aged northern conifer stands.** Res. Pap. NE-517. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 17 p.

Solomon, D.S.; Seegrist, D.W. 1983. **Growth and yield analysis of thinned uneven-aged spruce and fir stands in Maine.** In: Proceedings: planning, performance, and evaluation of growth and yield studies; 1979 September; Oxford, England. IUFRO Subject Group S4.01, Commonwealth Forestry Institute Occasional Paper 20. Oxford, UK: University of Oxford Press: 149-156.

Su, J.C.; Woods, S.A. 2001. **Importance of sampling along a vertical gradient to compare insect fauna in managed forests.** Environmental Entomology. 30(2): 400-408.

Thompson, D.H. 2004. **Senator John C. Stennis: champion of forestry.** Forest History Today. (Spring/Fall): 27-34.

Tian, S. 2002. **Effect of precommercial thinning on root development and root and butt decay incidence of red spruce and balsam fir.** Orono, ME: University of Maine. 265 p. Ph.D. dissertation.

U.S. Forest Service. 1939. **Annual report for 1938.** New Haven, CT: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 34 p.

U.S. Forest Service. 1948. **Annual report for 1948.** Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 98 p.

Weiskittel, A.R.; Kenefic, L.S.; Li, R.; Brissette, J.C. 2011. **Long-term influence of precommercial thinning treatments on stand-level attributes in a northern conifer stand of central Maine.** Northern Journal of Applied Forestry. 28(2): 92-96.

Weiskittel, A.; Kenefic, L.S.; Seymour, R.S.; Phillips, L.M. 2009. **Long-term effects of precommercial thinning on stem form, volume, and branch characteristics of red spruce and balsam fir crop trees.** Silva Fennica. 43(3): 397-409.

Westveld, M. 1930. **Suggestions of management of spruce stands in the Northeast.** Cir. 134. Washington, DC: U.S. Department of Agriculture. 24 p.

Westveld, M. 1931. **Reproduction on the pulpwood lands in the Northeast.** Tech. Bull. 223. Washington, DC: U.S. Department of Agriculture, Forest Service, Washington Office. 52 p.

Westveld, M. 1933. **Experimental cutting area in the Adirondacks.** Journal of Forestry. 31(5): 599.

Westveld, M. 1938. **Silvicultural treatment of spruce stands in northeastern United States.** Journal of Forestry. 36(10): 944-950.

Westveld, M. 1953. **Ecology and silviculture of the spruce-fir forests of eastern North America.** Journal of Forestry. 51(6): 422-430.

Whitney, G.G. 1994. **From coastal wilderness to fruited plain.** New York: Cambridge University Press. 451 p.

Wilson, J. 2005. **Nineteenth century lumber surveys for Bangor, Maine: implications for pre-European settlement forest characteristics in northern and eastern Maine.** Journal of Forestry. 103(5): 218-223.

Zon, R. 1914. **Balsam fir.** Bull. 55. Washington, DC: U.S. Department of Agriculture, Forest Service. 68 p.

PENOBSCOT EXPERIMENTAL FOREST: RESOURCES, ADMINISTRATION, AND MISSION

Alan J. Kimball

Abstract.—The Penobscot Experimental Forest (PEF) was established more than 60 years ago as a result of private forest landowners' interest in supporting forest research in Maine. In 1950, nine pulp and paper and land-holding companies pooled resources and purchased almost 4,000 acres of land in east-central Maine. The property was named the Penobscot Experimental Forest and was leased to the U.S. Department of Agriculture, Forest Service for 99 years to provide a location for long-term forest management research in a mixed northern conifer forest.

The PEF is large enough to encompass a variety of stand, site, and soil conditions. From the very beginning, its proximity to the University of Maine has fostered a close working relationship among U.S. Forest Service and university researchers. In 1994, the landowners donated the PEF to the University of Maine Foundation. The deed and subsequent memorandum of understanding outlined the mission of the PEF, its management, and its governance as a joint venture by the U.S. Forest Service, the University of Maine, and the University of Maine Foundation. Today the PEF supports a broadened research mission; provides scholarships for students at the University's School of Forest Resources; and exemplifies the benefits of a lasting, shared commitment to long-term silvicultural and ecosystem research, education, and outreach.

PROPERTY HISTORY

The 3,855-acre Penobscot Experimental Forest (PEF) is centrally located in Maine, east of the Penobscot River in the towns of Bradley and Eddington (Fig. 1). Since 1950, the PEF has been the site of internationally recognized long-term forest ecosystem and silvicultural research on Northern Forest types. The University of Maine Foundation has owned the PEF since 1994. Today the PEF has a broadened research mission and provides scholarship support for students at the University's School of Forest Resources.

The PEF arose from private forest landowners' need for and willingness to support forest research in Maine. In the mid-1940s, nine pulp and paper and land-holding companies discussed establishing a long-term research area for the spruce-fir (*Picea-Abies*) forest type so important to Maine.

The history of the PEF before 1950 is not well documented. It is known that by 1859 there were 14 single-board mills, 3 mills with gangs of saws, 4 clapboard mills, 4 lath machines, and 3 shingle mills in Bradley village alone (Town of Bradley 2012). Only a small portion of the PEF was cleared for agriculture or grazing, though most of the area was cut lightly in the 20 to 40 years before 1950 for pine (*Pinus*), hemlock (*Tsuga*), and spruce sawlogs. Earlier cutting may have been heavier. The presence of charcoal and old burned stumps in some areas indicates that fires occurred following the cutting of pine stands. In 1950, stands on the PEF were 60 to 100 years old with a few older trees scattered throughout the area (U.S. Forest Service 2006).

In 1950, the nine companies pooled resources and purchased close to 4,000 acres of land in east-central Maine, 10 miles north of the city of Bangor and

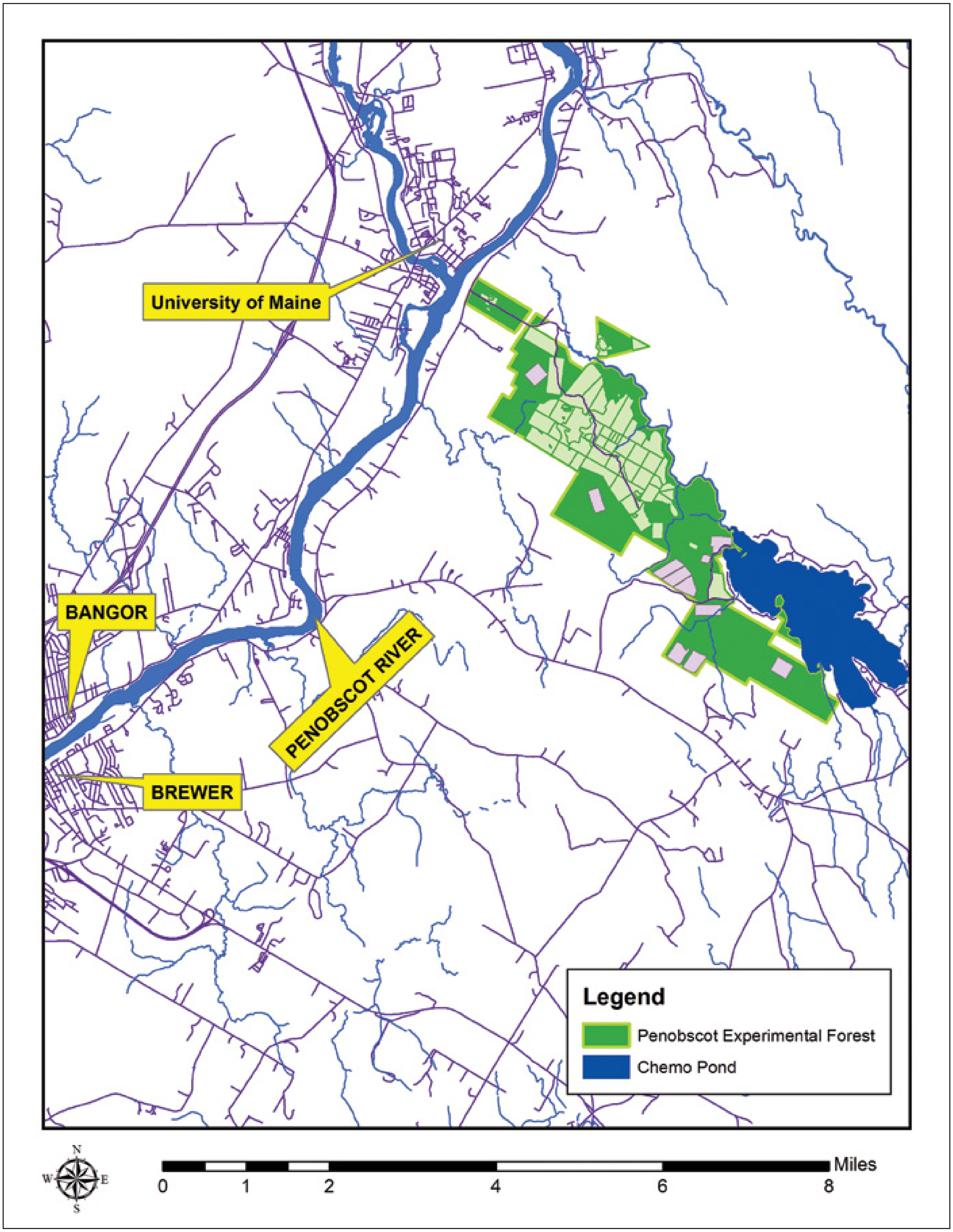


Figure 1.—Location of the Penobscot Experimental Forest.

15 miles from the University of Maine campus. The property was named the Penobscot Experimental Forest and was leased to the U.S. Department of Agriculture (USDA), Forest Service, Northeastern Forest Experiment Station (now the Northern Research Station) for 99 years to provide a location for long-term forest management research in a mixed northern conifer forest.

In 1984, the then-12 private firms that owned the PEF in common, undivided ownership each deeded their respective interest in the 225 acres surrounding the historic Leonard's Mills dam to the Maine Forest and Logging Museum, Inc. This transaction reduced the PEF to its present size. All 12 deeds reserved rights of way over and across Government Road and also across what is now known as the IP Road.

In 1994, the landowners donated the PEF to the University of Maine Foundation. The deed and subsequent memorandum of understanding (MOU) between the Northeastern Forest Experiment Station and the University of Maine contained specific language outlining the mission of the PEF and its governance. According to the MOU, "The primary mission of the PEF is to provide a location where long-term research, developmental activities, and demonstrations on forested ecosystems may be carried out… . Closely related to the primary mission is the role that the PEF plays in the education of students, professionals, and the general public."

Under the MOU between the University of Maine and the Northeastern Forest Experiment Station, the U.S. Forest Service will maintain control of its 1,257 acres of long-term research sites for the balance of the original 99-year lease; any new research on the PEF is subject to approval by the Research Operations Team, a committee comprising University and U.S. Forest Service scientists.

AREA DESCRIPTION

The PEF is located on the east side of the Penobscot River northeast of Bangor, Maine and presently contains 3,855 acres[1] in the towns of Bradley and Eddington. The PEF is accessible by the Chemo Pond Road from Maine Route 9 when traveling east from Brewer, or from Maine Route 178 to the main entrance in Bradley. From the main entrance the Government Road, a gravel road, traverses the PEF for 5 miles to the Chemo Pond Road; a gravel road continues southerly across the remaining PEF property for another 1.5 miles. Along the Government Road there are multiple side roads that provide gated access to various parts of the PEF.

The PEF is in the heart of the region known as the lower Penobscot Valley. The cities of Bangor and Brewer are less than 15 miles from the PEF (Fig. 1) and represent one of the largest and fastest growing population centers in Maine. The towns around this urban center report increased residential home and second home construction. A recent report by the U.S. Forest Service suggests that this portion of Maine "is among the 15 watersheds in the Nation projected to experience the greatest increases in housing density on private forests by 2030" (Stein et al. 2005: 7). If expectations about population and home construction prove true, the forest land surrounding the PEF will be subjected to substantial development pressure. Consideration of these trends will have to be part of the management and research planning process. Increased growth holds a variety of implications for recreational use, wildlife habitat, invasive species, and the economics of the timber industry in the immediate area and entire region.

[1] Most acreages quoted in this document are based on geographic information systems analysis using a combination of photo interpretation and global positioning system technology. These are not survey acres and this document does not intend to represent them as such.

Forest Soils

The soil survey published by the USDA Natural Resources Conservation Service for Penobscot County (Soil Survey Staff 1963) includes a general soil map that shows the vicinity of the PEF as being covered by three distinct soil associations. These three associations are arranged from northwest to southeast and from the shores of the Penobscot River to the shores of Chemo Pond. The association that lies along the Penobscot River is the Suffield-Buxton-Biddeford association, described as silty, well-drained to very poorly drained soils on rolling and depressional topography that developed in the fine-textured lacustrine or marine materials deposited when the glaciers sunk Maine's coastline. Soils of marine origin are found along the Penobscot River to Passadumkeag, and up the Passadumkeag River nearly to Saponac Lake. Farther from the river, the Plaisted-Thorndike-Howland association occurs and is characterized by moderately well to well-drained, stony and ledgy, deep to shallow, granitic and slaty soils that developed in the glacial tills of the upland. The Monarda-Burnham-Dixmont association surrounding Chemo Pond is composed of wet, dominantly very stony soils that also developed in the glacial tills of the uplands. This coarse overview is useful for placing the soils into a landscape context. Figure 2 depicts the soils of the PEF categorized by drainage class.

Water Resources

About 6.5 miles of the PEF property boundary fall along Blackman Stream and Chemo Pond (Fig. 2). The pond, the stream, their tributaries, and several hundred acres of associated wetlands (both forested and nonforested) contribute to the beauty, diversity, and habitat value of the PEF. The many wetlands adjacent to and flowing into Blackman Stream and Chemo Pond from the PEF afford locally and regionally important habitat for a host of game and nongame species. Wood ducks, otters, mink, turtles, and frogs are abundant in these wetlands. Moose, beavers, great blue herons, black ducks, loons, and eagles are often seen by those enjoying the winding, flat water as they paddle upstream on Blackman Stream from Leonard's Mills to Chemo Pond.

Chemo Pond is a large, predominantly shallow (maximum depth 24 feet), warm-water pond. Anglers enjoy fast action for white perch, yellow perch, chain pickerel, and small-mouthed bass in both winter and summer. Chemo Pond has slightly below-average water quality. The surrounding peatlands and wetlands contribute phosphorus responsible for the tea-like color of the water. The Pond has a number of seasonal and year-round homes that ring the shore on all but the PEF frontage. These homes are reached from Route 9 easterly via the private Chemo Pond Road; northerly via Bruckoff, Scott Point, and Getchell Roads; or westerly via Yawaca Road. There is a commercial campground and boat launch, Dean's Landing, located where the Chemo Pond Road meets the pond shore. The stream and pond are thus important recreational resources for people living along them as well as for visitors from the entire region.

Blackman Stream and Chemo Pond are currently priority waters in the forefront of a major collaborative effort to improve passage for sea-run fish to their original habitats in several major watersheds in New England. One of the goals of this effort is to reestablish the impressive spawning runs of alewives in Blackman Stream that have been impossible since the construction of the first timber crib dams at Veazie and Great Works in the 1830s (Watts 2003). Currently the Penobscot River Restoration Trust is working to enhance energy production at the dams in Stillwater, West Enfield, and Medway so that the Veazie and Great Works dams can be breached or removed to allow passage for Atlantic salmon, alewives, herring, sturgeon, and eels (Penobscot River Restoration Trust 2013). In addition, they plan to establish a bypass for fish around the Howland dam. Based on the apparent success of those efforts, the U.S. Department of the Interior, Fish and Wildlife Service and the Atlantic Salmon Federation approached the Maine Forest and Logging Museum and built an aesthetically complementary fishway around the historic Leonard's Mills dam in Bradley. Protecting the shorelines, water quality, wetlands, and associated viewsheds of Blackman Stream and Chemo Pond all need to be considered when planning management and research activities within the PEF.

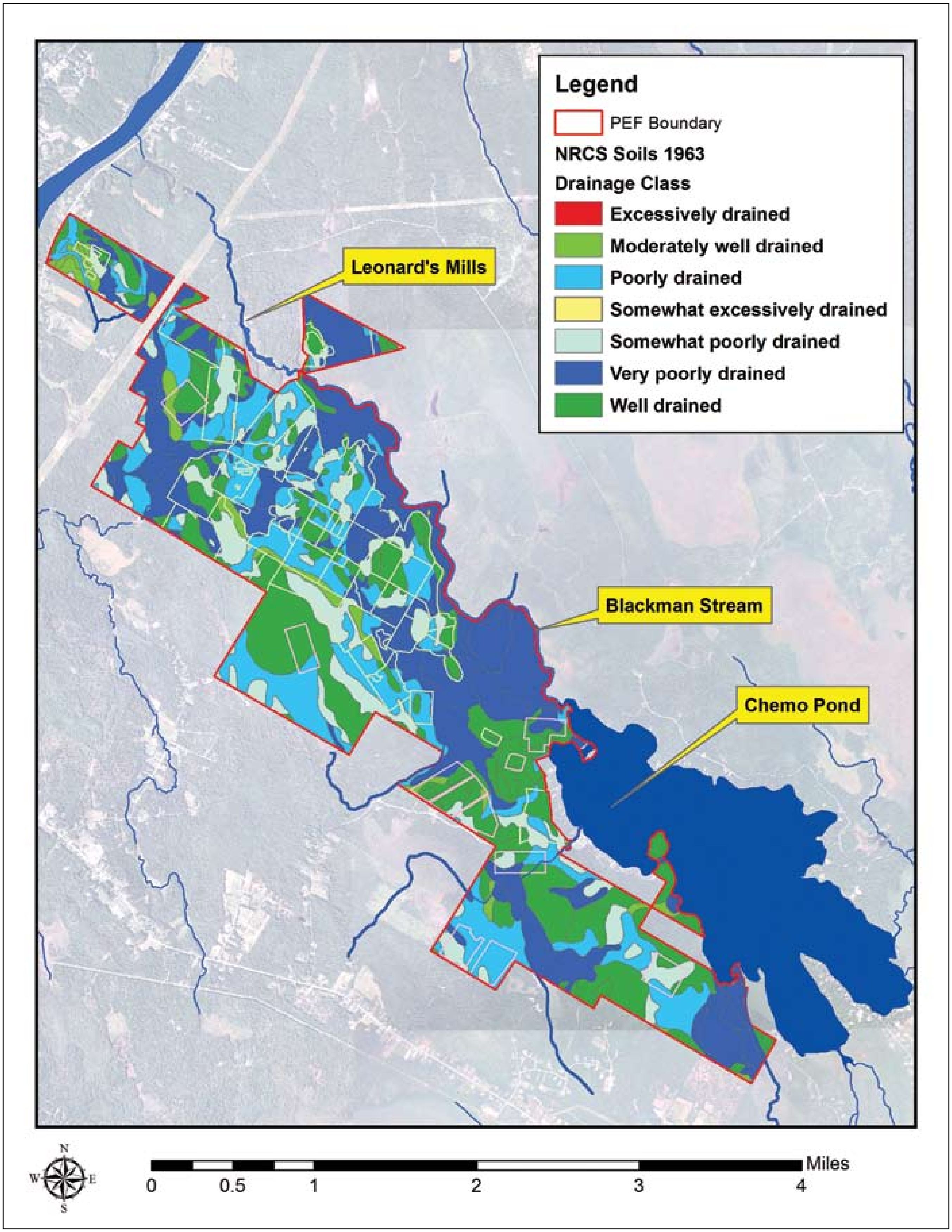


Figure 2.—Soils of the Penobscot Experimental Forest by drainage class.

Special Management Zones and Conservation Areas

State Shoreland Zoning (SLZ) regulations govern management on a sizable portion of the PEF. Maine's minimum mandatory shoreland zoning requirements currently call for SLZ partial-harvest or no-harvest buffer distances of 75 to 250 feet around water bodies, riparian corridors, and significant wetlands, depending on the size and character of the feature. These buffers directly influence the management options on more than 225 acres of the PEF. Additional special habitat areas occur on the PEF and receive specific protections.

An eagle nest on the south side of Chemo Pond receives special protection at the State and Federal levels. Management of the forest around the nest is conducted under guidelines from the Maine Department of Inland Fish and Wildlife. Harvesting is prohibited within 330 feet of the nest and this buffer area overlaps with the shoreland zoning buffer as well. The PEF staff takes extra care to identify nest sites to ensure that management activities do not negatively affect them.

ADMINISTRATION AND MANAGEMENT

The administration of the PEF is governed by the 1994 deed from Penobscot Experimental Forest, Inc. to the University of Maine Foundation and was further clarified in the MOU that was signed in 1995 between the Northeastern Forest Experiment Station and the University of Maine's College of Natural Sciences, Forestry and Agriculture (NFA). The deed specifies the provision of an annual Penobscot Experimental Forest Scholarship, which covers in-state undergraduate tuition to the University of Maine for 1 year for a student majoring in forest resources. It also specifies that this scholarship be fully funded each year before any other expenditures are made for research or management on the PEF. The MOU was to remain in effect for 50 years (the balance of the U.S. Forest Service's 99-year lease), with periodic reviews every 5 years.

In compliance with the 1995 MOU, a Research Operations Team (ROT) was formed consisting of one representative from NFA appointed by the dean, one representative from the Maine Agricultural and Forest Experiment Station appointed by the director, and two representatives from the U.S. Forest Service appointed by the director of the Northeastern Forest Experiment Station. Any new research on the PEF is subject to approval by the ROT. The ROT administers the research funds derived from harvests on the PEF and as funds permit, issues requests for proposals and awards those research funds on a competitive basis.

Chairing of the ROT alternates annually between University and U.S. Forest Service personnel. The ROT works with the forest manager of the University of Maine (who is also the forest manager for the University of Maine Foundation) to set policies for the PEF. The University's forest manager and the chair of the PEF ROT are responsible for the day-to-day operations, management, and maintenance of the PEF. The University's forest manager is responsible for non-research management activities on the PEF, e.g., property boundary line and road maintenance, oversight of harvesting activities, and interaction with recreational users and municipal and state authorities.

In 2007, a new MOU was signed between the U.S. Forest Service, Northern Research Station and the University of Maine's School of Forest Resources. This MOU made only minor revisions (mostly recognizing the new names for the respective agencies) and was in effect for 5 years. Work is underway on the next MOU, which will add the University of Maine Foundation as signatory and reflect the evolution of the administration of the PEF.

Areas of Management and Research Responsibility

The original MOU gave the U.S. Forest Service full administrative control over all PEF areas containing ongoing research or demonstrations installed prior to the date of the agreement (see Figure 3). The U.S. Forest Service's long-term research area is located

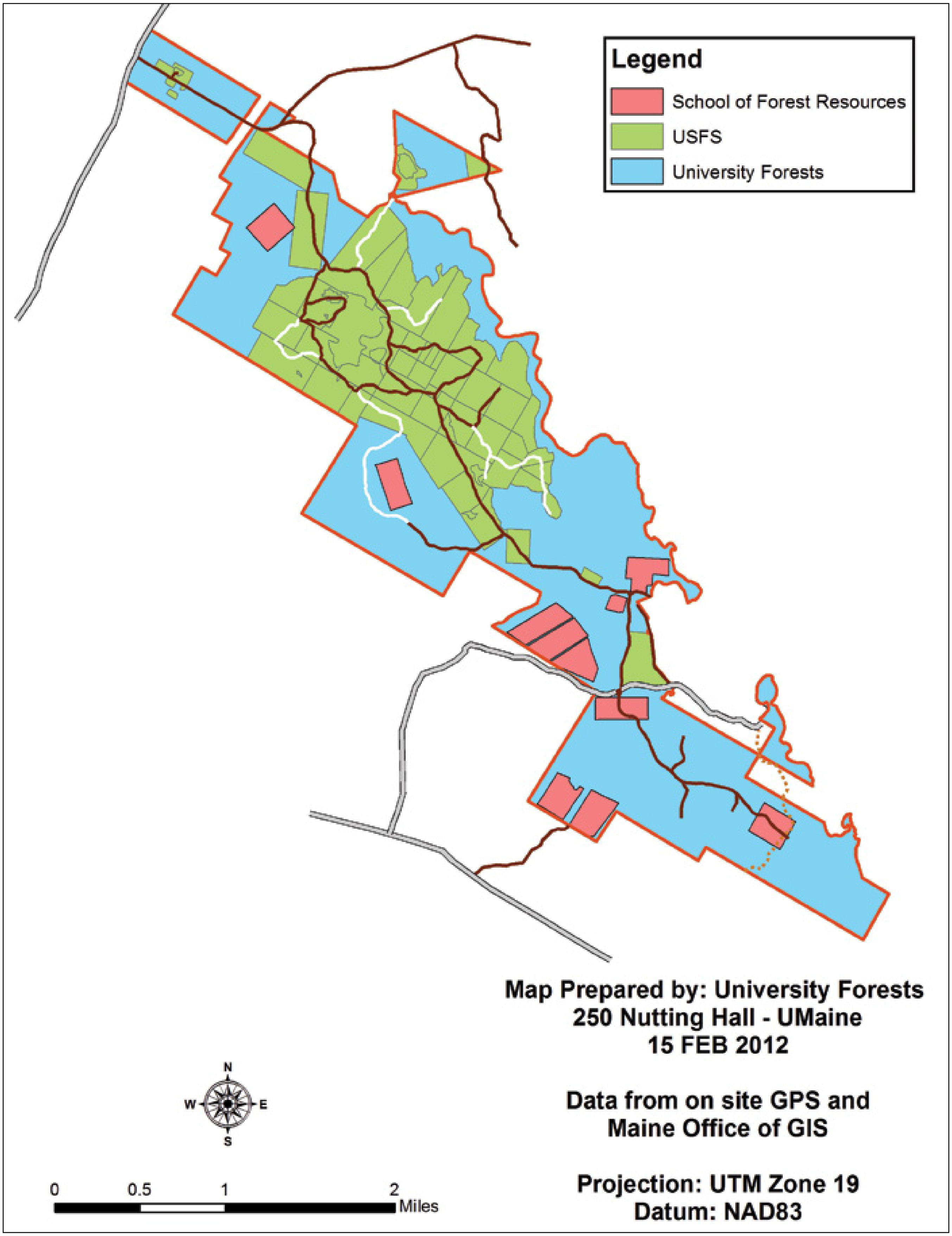


Figure 3.—Research and management responsibility at the Penobscot Experimental Forest.

approximately in the middle of the PEF and covers 1,257 acres (Table 1). This area has been host to a number of cooperative studies with University researchers including work on forest growth and development, wildlife habitat, forest insects, and studies of commercial thinning (the last in cooperation with the School's landowner-funded Cooperative Forestry Research Unit).

Two University-sponsored programs—the Acadian Forest Ecosystem Research Program (AFERP) and the Land-Use Effects on Amphibian Populations Program (LEAP)—were initiated as long-term research on the PEF separate from the U.S. Forest Service studies. These two programs occupied 302 acres across the PEF (Table 1). Part of the AFERP study area was later used for the University's Silvicultural Intensity and Species Composition (SIComp) Study. As of October 2009 the two LEAP arrays on the PEF were discontinued and now AFERP constitutes the largest area of University research outside of the U.S. Forest Service's long-term research area (Fig. 3).

Deducting PEF land used in the U.S. Forest Service studies, AFERP, and SIComp (Table 1 and Fig. 3) leaves the working forest portion, which is managed by the University Forests office in accordance with the 2009 forest management plan (Morrill and Kimball 2009). Faculty, staff, and students at the School of Forest Resources, as well as U.S. Forest Service personnel and practicing professionals from across New England, worked together to develop this plan. A current forest inventory and forest simulation software were used to create multiple management scenarios, the results of which were evaluated both spatially and temporally. Sustainable harvest estimates, derived from growth modeling with the Landscape Management System software, were integrated into a comprehensive harvest planning schedule.

Compartments A, B, and C (1,260 acres; Table 1) are managed under this plan. Most of Compartment D, which borders Blackman Stream to the north and includes a large percentage of forested and unforested wetland along the riparian zone, is designated as a reserve area (629 acres).

The original MOU states, "All forestry operations will be planned and executed in such a way that research needs are given priority" and further defines the role of the PEF to include educating students, professionals, and the public. The management objectives for the working forest portion of the PEF are designed to:

1. Yield a sustainable supply of timber and associated income to satisfy scholarship, research, and management goals. In addition, management actions will achieve the reasonable regulation of acreage and volumes harvested over the long term. The forest will be managed for a diversity of structural conditions using a variety of silvicultural systems.

Table 1.—Acres of Penobscot Experimental Forest features and research

From PEF 2009 management plan	U.S. Forest Service research area	University of Maine research area	Non-forested wetland	Roads and landings	Non-wetland reserves	SLZ 75-foot buffer	No current access	Forest land under University of Maine management	Grand total acres
Compartment A	NA	26	70	5.86	0	27	87	244	460
Compartment B	NA	105	0	15.53	0	4	0	495	620
Compartment C	NA	148	111	11.47	29	69	0	521	889
Compartment D	NA	23	426	1.94	180	NA	NA	0	631
Total acres	1,257	302	607	34.8	209	100	87	1,260	3,857

2. Continue support of current research projects and provide opportunities for new projects in the future. As outlined in the MOU, obligations of annual contributions to research and scholarship funds will be fulfilled. Venues and support for field demonstrations and tours open to students, forestry professionals, and the public will be provided.
3. Support biodiversity by providing a diversity of plant species, developmental stages, and structures across all management compartments. Diverse and unique habitat types, significant to a broad spectrum of plant and animal species, will be maintained and enhanced where appropriate. Unique habitats and imperiled species will be protected.
4. Maintain water quality and soil integrity through attention to appropriate silvicultural and operational principles to include meeting or exceeding all applicable state water quality Best Management Practices.
5. Protect historical and cultural resources.
6. Provide a spectrum of safe recreational experiences for a variety of users insofar as that is possible without compromising the first five objectives. The PEF is first and foremost a research forest; recreation is therefore a second-tier objective. Nonetheless, given the projections of rapid development in the lower Penobscot watershed, the recreational pressure on the area's three largest public forests—the Bangor City Forest, the University's Dwight B. Demeritt Forest, and the PEF—can only be expected to increase.

THINKING BACK AND LOOKING FORWARD

The PEF's last 60 years stand as an example of what can be accomplished through cooperation and a lasting, shared commitment to long-term silvicultural and ecosystem research. The U.S. Forest Service, University of Maine, and University of Maine Foundation are committed to continuing the PEF's long-standing leadership in supporting a diversity of research in the Acadian Forest Region. As we celebrate the accomplishments of the first 60 years, it is with renewed resolve to ensure that the PEF remains a focal point of applied forest research, education, and outreach vital to Maine and the entire Acadian Forest Region for decades to come.

ACKNOWLEDGMENTS

Reviews of an earlier version of this manuscript were provided by John Kabrick and Laura Kenefic of the U.S. Department of Agriculture, Forest Service, Northern Research Station.

LITERATURE CITED

Morrill, R.; Kimball, A. 2009. **Penobscot Experimental Forest forest management plan.** Available at https://forest.umaine.edu/files/2010/08/PEF_Mgt_Plan_2009_FinalVersion_mar2010.pdf. (Accessed December 2012).

Penobscot River Restoration Trust. 2013. Homepage. Available at http://www.penobscotriver.org/. (Accessed February 2013).

Soil Survey Staff. 1963. **Soil Survey of Penobscot County, Maine.** Washington, DC: U.S. Department of Agriculture, Soil Conservation Service in cooperation with the University of Maine Agricultural Experiment Station.

Stein, S.M.; McRoberts, R.E.; Alig, R.J.; Nelson, M.D.; Theobald, D.M.; Eley, M.; Dechter, M.; Carr, M. 2005. **Forests on the edge: housing development on America's private forests.** Gen. Tech. Rep. PNW-GTR-636. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 16 p.

Town of Bradley. 2012. **History of Bradley.** Available at http://www.townofbradley.net/history.html. (Accessed December 2012).

U.S. Forest Service. 2006. **Penobscot Experimental Forest.** Available at http://www.fs.fed.us/ne/durham/4155/penobsco.htm. (Accessed August 2009).

Watts, D.H. 2003. **A documentary history of the alewife (*Alosa pseudoharengus*) in its native habitat in Maine and New England.** Available at www.friendsofmerrymeeting.org. (Accessed April 2012).

CENTERPIECE OF RESEARCH ON THE PENOBSCOT EXPERIMENTAL FOREST: THE U.S. FOREST SERVICE LONG-TERM SILVICULTURAL STUDY

John C. Brissette and Laura S. Kenefic

Abstract.—Established between 1952 and 1957, the U.S. Department of Agriculture, Forest Service experiment comparing several silvicultural treatments is not only the centerpiece of research on the Penobscot Experimental Forest in Maine, it is also one of the longest-running, replicated studies of how management techniques influence forest dynamics in North America. Ten treatments representing even- and uneven-aged silvicultural systems and exploitative cutting are replicated twice on operational-scale experimental units averaging 21 acres in size. Treatments are applied uniformly to experimental units in accordance with prescriptions designed to direct both stand structure and composition. In some treatments harvests are scheduled at intervals (e.g., 5, 10, or 20 years); in others, harvests are triggered by stand conditions. Each experimental unit, or compartment (most recently termed management unit), has an average of 18 permanent sample plots (PSPs) for measuring attributes of trees ≥0.5 inches in diameter at breast height. Tree regeneration and other vegetation are measured on multiple subplots within each PSP. Measurements are taken before and after harvests and, in many treatments, at intervals between harvests. Over the past 60 years, this long-term experiment and associated short-term studies have generated fundamental knowledge about forest ecosystems and silvicultural guidelines for the northern conifer forest type, and, in a more general sense, have contributed to our understanding of mixed-species forest science and management.

INTRODUCTION

Between 1952 and 1957 the U.S. Department of Agriculture, Forest Service established a long-term silvicultural experiment on the Penobscot Experimental Forest (PEF) in Maine. It is currently titled Silvicultural Effects on Composition, Structure, and Growth of Northern Conifers in the Acadian Forest Region: Revision of the Compartment Management Study on the Penobscot Experimental Forest. This experiment was one of a series of similar studies on experimental forests across the United States. These experiments were called "compartment management studies" because they were designed around large, essentially operational-scale, experimental units (≈20-40 acres) (metric conversions are in Appendix I) known as compartments. Very few of those studies were continued as planned, but research has proceeded on the PEF with periodic harvests and regular re-measurement of treatment effects on tree and stand growth and other response variables.

A series of study plans has guided the long-term silvicultural experiment on the PEF. The most recent plan, by J.C. Brissette and L.S. Kenefic, was approved January 2008 and was an update and revision of one submitted by R.M. Frank, Jr. and approved in May 1975. Frank's study plan superseded the original plan of January 1953 by T.F. McLintock and subsequent revision by A.C. Hart in June 1962. Each of the revisions updated the long-term study to adjust to changing research priorities, build on what had been learned thus far, and ensure the relevance of the experiment for future scientists and managers. Results from the first 40 years of this study were summarized by Sendak et al. (2003). This paper focuses on the experiment as it is being carried out under the current study plan. Details about changes that have occurred over the years in treatment structure and response variables can be found in metadata associated with the measured data (Brissette et al. 2012).

Much has changed in the 60 years since this study was first conceived. Social and political ramifications of forest management have brought debate about appropriate silviculture into the public arena. Logging systems have advanced from hand felling and horse skidding to cut-to-length processors and forwarders. However, many of the fundamental issues that prompted installation of the study remain the same. Spruce budworm (*Choristoneura fumiferana*) is still a threat and discussions continue about the role of silviculture in reducing impacts during outbreaks. Diameter-limit harvesting is still practiced and its long-term effects debated. For social, economic, and biologic reasons, natural regeneration remains the predominant method of establishing new trees and stands in the northeastern United States, but many questions about ensuring adequate regeneration of desired species are yet unanswered. Because of the silvics of the major species in the northern conifer forest of which the PEF is representative—red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* [L.] Mill), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* [L.] Carr), paper birch (*Betula papyrifera* Marsh), and red maple (*Acer rubrum* L.)—both even- and uneven-aged silvicultural systems can be used and no one system has achieved universal acceptance. Questions remain about the entire array of silvicultural options available to natural resource managers.

The long-term study on the PEF has experimental design limitations that cannot be corrected, the most serious being only two replicates of the treatments (see Frank and Kenefic, this volume) and separation of the control from the rest of the experiment (Kenefic et al. 2005b). However, the study is unique because of its longevity, integrity of the original treatment structure, timeliness of treatment application, and the quality of the long-term database (Brissette et al. 2006; Kenefic et al. 2006; Russell et al., this volume). We feel that these qualities more than make up for the shortcoming in experimental design.

The primary objective of the study is to quantify tree and stand response to silvicultural treatment. Response variables are regeneration; species composition; and tree and stand growth, productivity, and quality. These data provide information about the interaction of natural and human disturbances and their effects on stand dynamics. To meet this objective, the hypotheses address some of the important unanswered questions about managing mixed northern conifer stands in the region. For example: Do responses vary between…

… managed and unmanaged stands?

… stands managed with clear silvicultural objectives and stands exploited for current timber production with no concern for future composition, structure, or condition?

… stands managed for one or two cohorts and stands managed for multiple cohorts?

… stands that once regenerated are left to develop naturally and stands that receive tending treatments such as cleaning or thinning?

Because of the range of response variables measured, this experiment not only answers questions about *whether* treatments differ but also addresses *how* treatments differ and *what* about them differs.

Defining hypotheses to test is an important part of study planning. But in a long-term experiment such as this one, the most enlightening outcomes cannot be planned for; that is, an important aspect of this experiment is studying the unpredicted and unexpected. Although the unexpected cannot be articulated in a hypothesis statement, it can be stated that this study addresses questions about the uncertainty inherent in any silvicultural treatment because of the long-term nature of stand development and the unpredictability of sporadic natural disturbance events and the likely prolonged effects of climate change. In addition to understanding the various pathways of stand development initiated by particular silvicultural manipulations, managers need to know the likelihood of achieving their desired objectives along those pathways. Such knowledge is best attained through long-term monitoring, where understanding increases incrementally with every measurement cycle.

A secondary objective of this study is to provide a variety of forest structures at one location to be used as the framework for short-term experiments in ecology and silviculture (see Appendix II for some examples). The long-term experiment can best be described as empirical; the short-term studies are often process-oriented and thus can address *why* treatments differ.

Ultimately, results from this long-term experiment and associated short-term studies generate fundamental knowledge about forest ecosystems and science-based management guidelines for northern conifers and associated species in the Acadian Forest Region of Atlantic Canada and adjacent Maine. In a broader sense, results from this study influence forest science and management of shade-tolerant conifers globally.

To fully understand the design and significance of the experiment, it is important to put it into context regarding its location, the range of silvicultural alternatives represented in the treatment structure, and the silvics of the species under study.

Acadian Forest

The Acadian Forest contains a mixture of northern conifers and hardwoods dominated by spruces (*Picea* spp.) and balsam fir. Species composition is highly variable and influenced by both latitude and site, with a greater proportion of conifers on low-lying and more northerly areas. Halliday (1937) first described the Acadian Forest Region in a classification of Canada's forests. The Acadian Forest spans the provinces of New Brunswick, Nova Scotia, and Prince Edward Island, and in the United States, Maine and higher elevations of the Appalachian Mountains. The adjacent and closely related Great Lakes-St. Lawrence Forest Region extends west through southern Quebec and Ontario (Rowe 1972). The Boreal Forest Region lies north of the Acadian and Great Lakes-St. Lawrence regions. Maine juts into eastern Canada, with New Brunswick to the east and north, and Quebec to the north and west. The Laurentian Mixed Forest Province, Warm Continental Division (McNab and Avers 1994) north of Portland, Maine, has been identified with the Acadian Forest (Braun 1950).

The PEF is located in the southern extent of the Acadian Forest Region, in the towns of Bradley and Eddington in east-central Maine (44°54' N, 68°38' W) (Fig. 1). The dominant conifers are shade-tolerant and regenerate well under canopy cover. Advance regeneration is prolific (Brissette 1996), and without it regenerated stands are converted to a hardwood composition (Hart 1963). Balsam fir and spruce species are the principal commercial softwoods. Though the amount and early growth rates of fir regeneration surpass those of spruce, fir longevity and maximum diameter are approximately half those of the spruce species. Fir is also the preferred host of the spruce budworm (see below). Furthermore, the ability of fir to extend its root system on better sites gives it

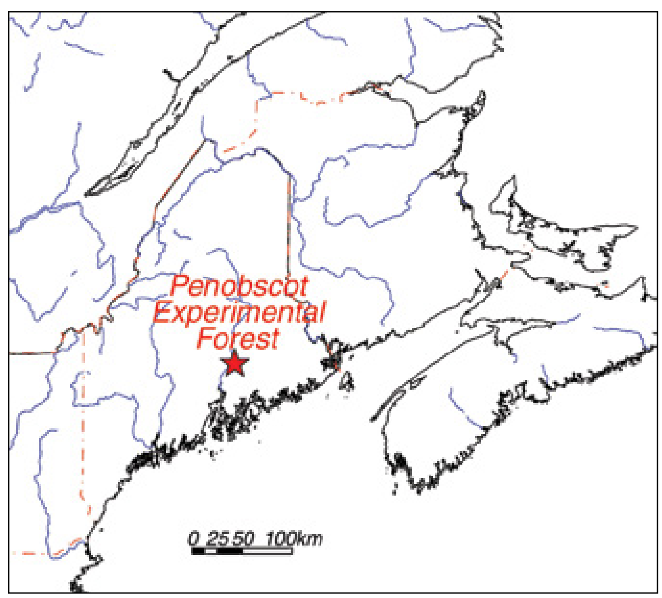


Figure 1.—Location of the Penobscot Experimental Forest in the northern conifer forest region.

an additional advantage over spruce, which has a more shallow rooting system (Blum et al. 1983, Tian and Ostrofsky 2007). Management of spruce-fir stands should utilize a short (<70-year) rotation, and/or favor spruce over fir during intermediate treatments (Hart 1963, Westveld 1946).

Natural stand-replacing disturbances are rare in the Acadian Forest Region. Partial disturbances resulting from windthrow and isolated pockets of insects and disease are common. The spruce budworm, an insect with cyclic outbreaks that causes mortality and growth suppression in balsam fir and spruce species, has a significant impact on forest structure and composition (MacLean 1984). Budworm mortality is positively related to the proportion of fir and poor-vigor trees (Baskerville 1975a, McLintock and Westveld 1946), drainage and hybrid index (Osawa 1989), and tree age (MacLean 1980, 1984). The relationship between stand structure and budworm susceptibility is less certain, and both even-aged structures (Baskerville 1975b) and uneven-aged structures (Crawford 1984, Crawford and Jennings 1989, Westveld 1946) have been recommended. When an outbreak is at full strength, however, it may not matter because many ecological and stand relationships noted with spruce budworm at other times simply disappear (Osawa 1989).

Though the budworm promotes the release of advance regeneration and thus naturally rejuvenates mature spruce-fir stands (Baskerville 1960), outbreaks threaten short-term production capacity (MacLean 1984). Protection through spraying, although effective with regard to maintaining production, may reduce the outbreak interval by maintaining higher populations of host species (Baskerville 1975b).

The Acadian Forest has a long history of use by human beings. Virgin, or unharvested, forest is restricted to a few remote areas likely atypical of the region as a whole. Repeated diameter-limit cutting began in the 1800s and has continued until the present day (Cary 1896; Kenefic and Nyland 2005; Seymour 1992, 1995; Westveld 1928). Preferential harvesting of large trees and desired species has resulted in a forest that is currently only 9 percent large sawtimber with a softwood to hardwood ratio of 0.7:1 while the underlying forest habitat suggests that ratio should be 1.6:1 (McWilliams et al. 2005). Harvesting in response to the spruce budworm outbreak of the 1970s and 1980s contributed to these imbalances.

Silvicultural Systems

A review of silvicultural concepts and terminology will set the stage for understanding and interpreting the long-term experiment on the PEF. Silviculture is the art and science of controlling the establishment, growth, composition, health, and quality of forest stands to meet specific objectives on a sustainable basis. Silvicultural systems are planned series of treatments for tending, harvesting, and regenerating stands (Helms 1998).

Even-aged Silviculture

Even-aged silviculture is applied to create and maintain stands with a single age class of trees. The even-aged regeneration methods include clearcut, seed tree, and shelterwood, and differ in terms of the source of regeneration and amount of cover provided during stand initiation.

Clearcutting allows regeneration to be established from seed or sprouts after the overstory is removed. It is not effective for natural regeneration of shade-tolerant species, which will likely be outcompeted by fast-growing shade intolerants in an open stand. Additionally, research on the PEF has shown that northern conifer seed in the forest floor remains viable for only 1 year and is thus not a reliable source of regeneration following clearcutting (Frank and Safford 1970). The seed tree method, which leaves scattered residual trees for the sole purpose of providing seed for the new cohort, is also not effective for the shade-tolerant conifers because the intolerant hardwoods outcompete them and the shallow-rooted residuals lack windfirmness (Frank and Bjorkbom 1973, Seymour 1995). The seed tree method has been applied with some success for eastern white pine (Wendel and Smith 1990), a companion species in many northern conifer stands, but does not provide overhead protection from the white pine weevil (*Pissodes strobi*).

The most effective even-aged regeneration method in northern conifers is shelterwood (Brissette and Swift 2006, Seymour 1995). In this method, the overstory is removed in two or more stages over the course of several years, providing seed and shade for the new cohort. This method can be used to regenerate dense stands of shade-tolerant trees, though the choice of seed trees, length of the overstory removal period, and intensity of the harvests determine the degree of shade and thus species composition of the new stand.

Additionally, shelterwood may be used to create two-aged stands if reserves, or trees from the older cohort, are retained after the regeneration harvest for reasons not related to regeneration. This shelterwood method may be implemented to increase growth and value during the next rotation, enhance vertical structure, improve aesthetics, and provide large trees for snags or downed logs (Nyland 2002).

Thinning is an intermediate treatment applied to immature even-aged stands to reduce stand density in order to improve overall growth of the stand or of individual trees, or capture mortality. These treatments may be precommercial, done as an investment before the trees are merchantable, or commercial. The timing, intensity, and type of thinning all vary depending on management objectives. The types of commercial thinning commonly applied (dominant, crown, and low thinning [Smith et al. 1997]) vary in terms of the crown classes from which trees are cut. Thinning of dominants (previously "selection" thinning) is used to remove poor form or otherwise undesirable dominants and should be applied only once to avoid high-grading (the removal of the most commercially valuable trees, often leaving a residual stand composed of trees of poor condition or undesirable species composition [Helms 1998]). Crown thinning is used to release desired crop trees in codominant and dominant canopy positions. Low thinning, which is generally lighter and more frequent, is applied to capture mortality in the intermediate and overtopped crown classes. Research on stand response to various combinations of timing, intensity, and types of commercial thinning has only recently begun in the northern conifer type (Wagner et al. 2002), although research on the PEF has established the positive effects of precommercial thinning (PCT) on species composition, growth, and mortality (Brissette et al. 1999; Weiskittel et al. 2009, 2011).

Uneven-aged Silviculture

Uneven-aged silviculture is used to create and maintain stands with three or more age classes of trees and is accomplished via selection cutting. The selection system has traditionally been applied to create a specific diameter distribution that is believed necessary for balancing growth and removals, and is manifest in long-term consistency and sustainability of structure and production (Meyer 1952, O'Hara 1996). Structural goals are defined in numerous ways, though primarily using empirical structures from previous experiments (e.g., Arbogast 1957) or mathematical derivations (Meyer 1952, Nyland 2002, Smith et al. 1997).

The mathematical structures, such as q, have the advantage of being easy to use, but their relevance to biological processes is debated (Davis 1966, Oliver and Larson 1996). The approach historically applied on the PEF is the BDq method (Fiedler 1995, Guldin 1991, Marquis 1978), in which a target residual basal area (BA), maximum diameter (D), and q-factor are determined based on financial or biological maturity, residual stocking goals, and desired distribution of growing stock among saplings, poles, and sawtimber (Kenefic and Brissette 2001). Using multiple q-factors to define a single structure has been suggested (Hansen and Nyland 1987, Leak and Filip 1975). The higher the q, the more growing stock in the smaller size class, and vice versa. The higher the basal area goal, the more trees in each size class, without any change in the proportional distribution of trees.

The often-cited advantages of uneven-aged silviculture include comparatively little soil disturbance, high vertical structural diversity, high canopy cover, and continuous production of high-value sawlogs (Nyland 2002, Smith et al. 1997, Troup 1928). The last objective is best met through the application of structural goals that allocate a high proportion of growing space to the sawtimber classes. This approach is supported by research on the PEF that found that upper canopy trees generally produce more stemwood per unit leaf area than those lower in the canopy (Seymour and Kenefic 2002). However, too much overstory will suppress the development of poletimber and may impede regeneration and growth of small trees. The amount of overstory that can be carried without suppressing smaller trees to the point of structural instability has yet to be determined for northern conifers, though species' competitive advantage is clearly related to amount and quality of overstory light (Moores et al. 2007). Data from the PEF demonstrate that even trees released from suppression do not grow as well as those that have been free growing; that is, older trees in the uneven-aged stands grow less stemwood per amount of foliage than younger trees do (Seymour and Kenefic 2002). Unfortunately, preliminary assessment of sapling ingrowth dynamics in the uneven-aged PEF stands revealed slow growth and high mortality, generating additional questions about long-term sustainability (Kenefic and Brissette 2005).

Although it is critical not to have too many trees in the sawtimber classes of uneven-aged northern conifer stands, it is also important not to create imbalances in other portions of the stand structure. The recommended diameter distribution should be followed for two reasons: to provide sufficient trees in each size class to replace those from larger classes as they grow in size or are cut, and to moderate growth of smaller trees (Arbogast 1957, Solomon and Frank 1983). Though timely regeneration of desired species is necessary to sustain uneven-aged stands, quality and distribution of growing stock should not be overlooked. In particular, it is necessary to tend immature trees in order to accumulate high-quality growing stock (Hart 1963). Thus, a deficit in the mid-size classes, for example, both endangers sustainability of production as the sawtimber-sized trees are removed, and results in poor control over growth in the sapling classes.

Short-term sacrifices in quality and growth may be necessary for attainment of structural goals, particularly during periods of conversion to an uneven-aged condition or rehabilitation of unmanaged or mismanaged stands (Nyland 2002). This approach is due in part to the need to sustain old trees in order to maintain an uneven-size structure during conversion (Nyland 2003). It has been suggested that such losses could be minimized in extreme cases by reducing the residual stocking goal (i.e., BA), and correspondingly lengthening the cutting cycle (Nyland 1987, 2002). This type of action would be short-term only and has the disadvantages of a delayed next entry and some loss of control over mortality and quality due to the longer cutting cycle.

The regeneration method utilized in uneven-aged silviculture is the selection method. Selection cuttings are applied on a fixed cutting cycle to remove mature timber, tend the immature classes, and establish new regeneration (Nyland 1987). The distribution of removals is across all size classes and may be single-tree or in groups. Furthermore, though age and size are assumed to be equivalent, and thus size structures are utilized instead of age structures, research on the PEF has demonstrated that this relationship is poor in multi-aged stands of shade-tolerant species (Blum 1973, Kenefic and Seymour 1999b, Seymour and Kenefic 1998). However, the extreme difficulty of determining tree age from phenological characteristics of a tree requires use of the traditional diameter distribution but justifies exploratory age analysis and adjustment of growth expectations and structural goals based on the results of such.

Within the confines of the allowable cut per size class as determined by the structural goal defined above, removals are distributed to improve growth, quality, and species composition (Frank and Blum

1978, Leak et al. 1969). In traditional application, it is important that desires to make short-term gains in these factors do not jeopardize longer-term attempts to create a balanced structure. In applying such a treatment, species composition goals and marking guides are important, and all trees for harvest should be marked under the supervision of an experienced selection marker. The use of designated skid trails and directional felling are desirable because of the potential for residual stand damage associated with repeated partial harvests (Baker and Bishop 1986).

Much remains unknown about the short- and long-term dynamics of growth in managed uneven-aged northern conifer stands. Many questions of interest to researchers and practitioners, such as whether there is a production advantage to utilizing uneven- instead of even-aged silviculture, cannot be answered until both systems have been applied in a single experiment for the equivalent of a full rotation (approximately 80-100 years in northern conifers). The PEF and the Acadia Research Forest in New Brunswick are the only locations with long-term experiments in the selection system in the Acadian Forest, and among few such sites in the world.

Exploitative Cutting

Exploitative cutting occurs when trees are removed without regard for residual stand condition. This type of harvesting occurs when short-term volume and value removals are given priority over long-term sustainability of composition and structure (Kenefic and Nyland 2005, Nyland et al. 1993). The intensity of the harvest varies, and ranges from diameter-limit cutting, in which valuable trees above specific size thresholds are removed, to commercial clearcutting, in which all merchantable trees are removed from a stand without tending or attention to regeneration (thus, as described here, commercial clearcutting is different from clearcutting as a silvicultural treatment). Both are examples of high grading, removing the most valuable trees from the stand. Though commonly practiced, removal-driven harvesting is rarely experimentally applied. The PEF is the site of the oldest known replicated experiment in diameter-limit and commercial clearcutting of northern conifers, and research on the PEF has documented the degrading effects of these practices on residual stand condition (Kenefic and Nyland 2005, 2006; Kenefic et al. 2005a).

It has been theorized that stands subjected to repeated diameter-limit cuts will develop a structural imbalance that will ultimately suppress the establishment of regeneration and prevent periodic harvests (Roach 1974). Modeling work in northern hardwoods has suggested a number of negative impacts, including reduced stand value, structural imbalance, and species and quality degradation (Nyland 2005, Nyland et al. 1993). However, along with the experiment on the Fernow Experimental Forest in West Virginia (Schuler et al. 2005) and studies installed in the Central Hardwood Region (Fajvan 2006), the studies on the PEF are among the few sources of information about the results of experimentally controlled exploitative cutting. Though results from the PEF demonstrate shifts in species composition, degraded stand value, loss of sawtimber production, and increases in the proportion of unmerchantable trees, it is not yet known whether the repeated partial entries can be sustained. Modeling suggests, however, that the PEF fixed diameter-limit cut stands will not sustain another harvest of equal volume for many years (Kenefic et al. 2005a).

Researchers in the Central Hardwoods have suggested an alternative to fixed diameter-limit cutting called modified (flexible) diameter-limit cutting. This alternative is similar to guiding diameter-limit cutting, which was developed for loblolly-shortleaf pine in the southern United States (Guldin 1987, Reynolds et al. 1984), although the allowable cut in modified diameter-limit cutting may not be restricted to growth as it is in guiding diameter-limit cutting. Because removals are based on pre-determined size thresholds, modified diameter-limit cutting does not create or maintain a specific residual condition. However, it is regarded by some as a compromise that allows landowners to accumulate the benefits of selection cutting without the necessity of tending the unmerchantable classes (Miller and Smith 1993). As applied on the PEF, this treatment differs from fixed diameter-limit cutting in that trees below the diameter limits may be harvested if they are expected to die, and trees above the diameter limits may be left for wind protection or seed production. Preliminary analysis of data from the PEF suggests that stands treated with modified diameter-limit cutting are more similar to selection stands than to fixed-diameter-limit cut stands, and that these differences become more apparent over time (Kenefic et al. 2004).

Stand Development

Stand development is the competitive process of tree initiation, growth, senescence, and death (Smith et al. 1997). It is important for managers to be familiar with expected stand development patterns when they are applying silvicultural treatments and assessing stand response. These patterns, described by Oliver (1981) and Oliver and Larson (1996), provide an ecological basis for understanding and communicating stand growth. In even-aged stands resulting from stand-replacing disturbances, stands move sequentially through four stages: stand initiation, stem exclusion, understory reinitiation, and (in unmanaged stands) old growth. When this terminology is used to describe stand development, even people unfamiliar with the forest type may understand the processes and structures in the stands. Definitions (from Oliver 1981 and Oliver and Larson 1996) are as follows:

- Stand initiation: Begins when a disturbance removes the existing stand and makes growing space available for a new cohort, and continues as long as trees are establishing.
- Stem exclusion: Begins when sufficient leaf area develops to prevent new cohorts from establishing, and continues as long as new cohorts are excluded. At this stage the processes of differentiation into crown classes (dominant, codominant, intermediate, and overtopped) and self thinning occur, and intermediate treatments and/or regeneration cuttings are applied.
- Understory reinitiation: Begins when gaps in the canopy (from crown abrasion or tree mortality) allow new cohorts to establish. An old-growth stand will result, unless a disturbance, such as harvesting, occurs. This is the stage when regeneration cuttings are often applied.
- Old growth: Begins when all trees from the initial cohort have died, and normally is not reached in stands managed for commodity production.

In uneven-aged stands the stem exclusion and understory reinitiation stages will likely occur in different places within the same stand at the same time. Additionally, in both even- and uneven-aged mixed-species stands, stratification occurs due to differences among species in height growth patterns, shade tolerance, and longevity, resulting in increased structural complexity.

With this background on the Acadian Forest, silviculture, and stand development to provide context, we now consider the details of the long-term silvicultural experiment on the PEF.

METHODS

Treatment Overview

The PEF long-term silvicultural experiment involves 10 treatments (Table 1), each replicated twice in a completely random experimental design (Fig. 2). The compartments (now called management units in the PEF study) average 21 acres in size and the experiment covers 418 acres of the approximately 3,900-acre PEF. Considering that most of the compartment management studies established in the 1950s on experimental forests were either abandoned or scaled back, the long-term experiment on the PEF stands out for having remained true to its original intent. Harvest activities and sample plot remeasurements have stayed close to schedule throughout the life of the experiment (Fig. 3). In the early 2000s, the measurement interval between harvests was increased from 5 years to 10 to accommodate measurement of several additional response variables.

Table 1.—Treatments and compartments to which they are applied on the Penobscot Experimental Forest

System	Treatment		Management Unit
	Code	Description	
Even-aged silviculture	SW2	Uniform shelterwood, 2-stage overstory removal	21, 30
	SW3	Uniform shelterwood, 3-stage overstory removal; without precommercial thinning	23b, 29b
	SW3 PCT	Uniform shelterwood, 3-stage overstory removal; with precommercial thinning	23a, 29a
Uneven-aged silviculture	S05	Single tree and group selection, 5-year cutting cycle	9, 16
	S10	Single tree and group selection, 10-year cutting cycle	12, 20
	S20	Single tree and group selection, 20-year cutting cycle	17, 27
Exploitative cutting	CC	Commercial clearcutting	8, 22
	FDL	Fixed diameter-limit cutting	4, 15
	MDL	Modified diameter-limit cutting	24, 28
Reference	REF	Unmanaged reference	32a, 32b

Treatment Descriptions

Prior to treatment initiation, the study area was dominated by a second-growth forest of irregular age and size structure (Fig. 4a,b). Though land-use history before 1950 is not well documented, descriptions on maps indicate that it was “mixed softwood second growth” with pole-size spruce and fir, hemlock up to sawtimber size, scattered hardwoods, and good spruce and fir regeneration in 1929, and “operable spruce-fir-hemlock” in 1949[1]. These conditions most likely resulted from a long history of periodic partial cutting and subsequent natural stand development (Kenefic et al. 2006, Sendak et al. 2003).

The first study plan (McLintock 1953) presented the silvicultural treatments as a range of management options from “poor” to “high-order” and specified tentative residual stand structural and compositional goals as a basis for experimentation. Subsequent revisions of this plan by Hart (1962) and Frank (1975) clarified the silvicultural terminology and specifics of the treatments. The status of the treatments and current prescriptions, per the most recent study plan revision (Brissette and Kenefic 2008), are outlined in the following descriptions.

Even-Aged Silvicultural Treatments

Shelterwood System, Two-Stage Overstory Removal (SW2): This treatment is replicated in management units 21 (27 acres) and 30 (18 acres) (Fig. 2). In both management units the final overstory removal was completed in 1967 (Fig. 3), leaving well-established advance regeneration and an average of 77 trees per acre in the 5-inch and larger diameter at breast height (d.b.h.) classes. The stands have two-storied structures with the larger residuals in the upper stratum. The new cohort reached the stem exclusion stage of stand development by the 1990s. Although the new cohort would benefit from removing

[1] Unpublished documents on file at the Penobscot Experimental Forest and available from the authors.

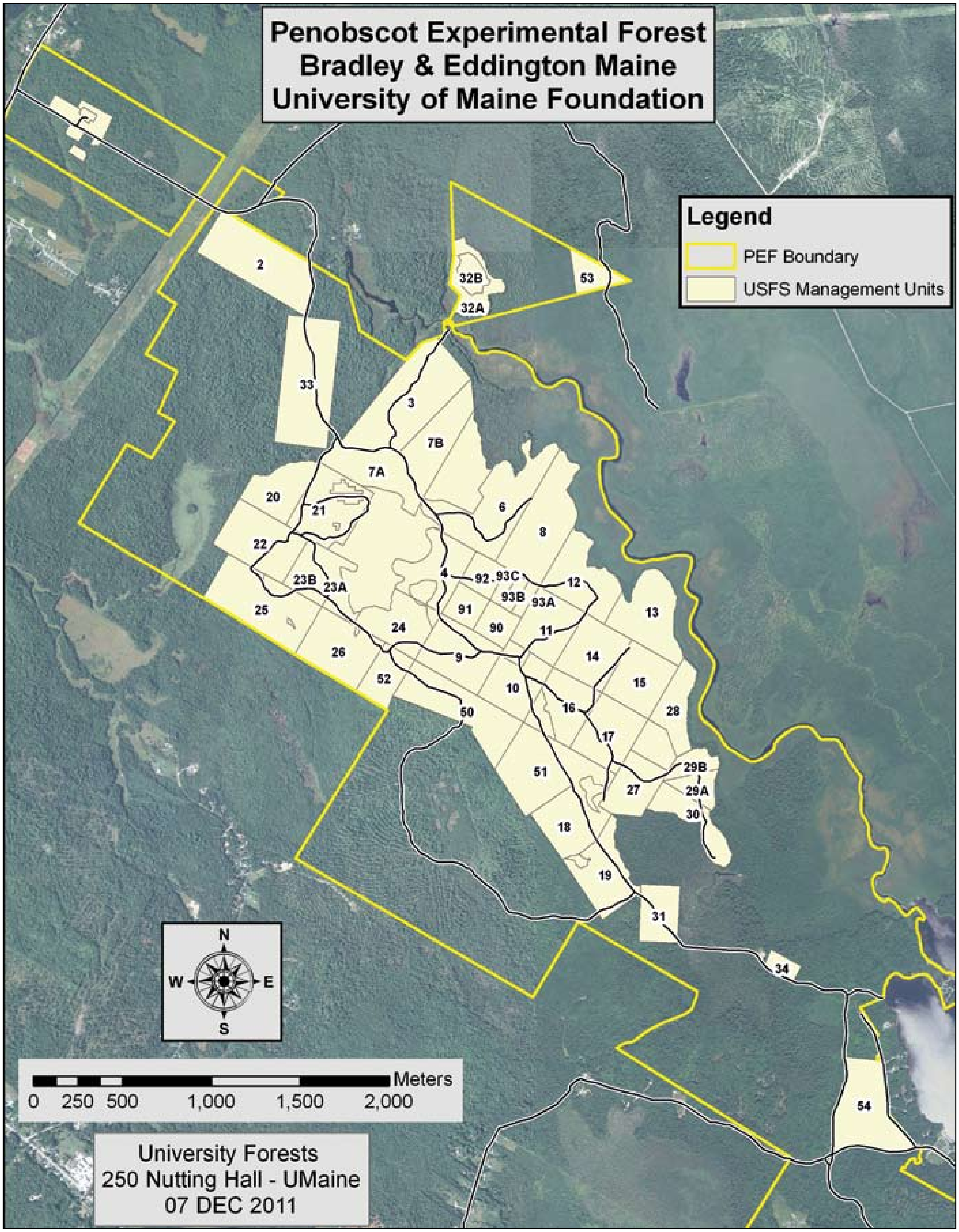


Figure 2.—Locations of all U.S. Forest Service management units on the Penobscot Experimental Forest, including those in the long-term silvicultural experiment. Map courtesy of Alan Kimball, University of Maine.

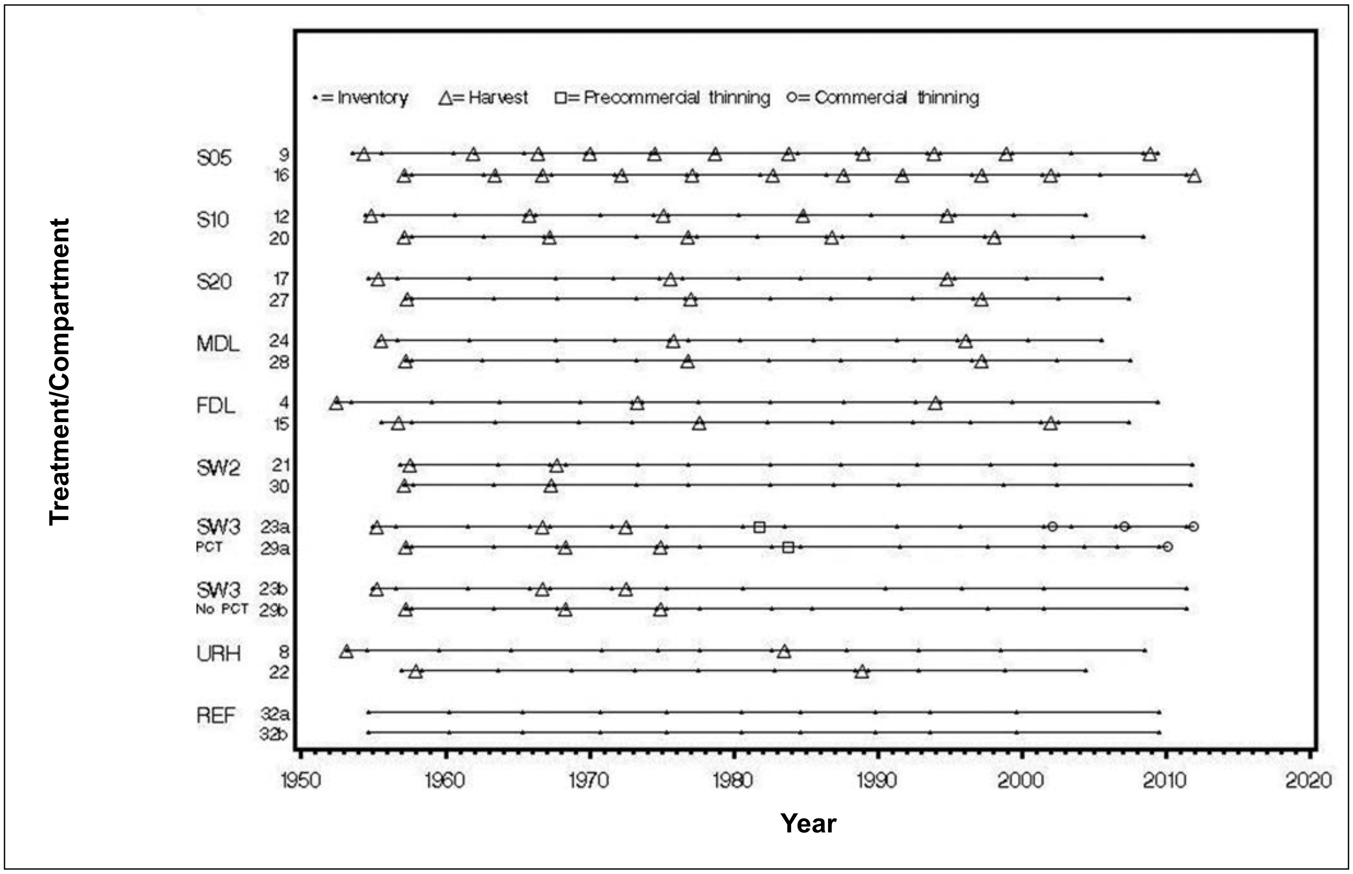


Figure 3.—Timeline of treatments and inventories in the long-term silvicultural experiment on the Penobscot Experimental Forest through 2011.

Figure 4a,b.—Forest composition and structure prior to initiation of the long-term silvicultural experiment on the Penobscot Experimental Forest in the 1950s. Photos by U.S. Forest Service.

the overtopping residuals, there has not previously been enough merchantable volume to support a commercial thinning. The next planned intervention in this treatment will be a thinning. The authors and cooperators are working on a thinning prescription that will be applied in the next year or so; overstory BA will be reduced by no more than 40 percent.

Shelterwood System, Three-Stage Overstory Removal (SW3 and SW3 pct): The final overstory removal in MU23 was in 1971, and in MU29 in 1974 (Fig. 3). Unlike SW2, all residual trees >2.5 inches in d.b.h. were cut during or immediately after the final overstory removal. About 10 years after the overstories were removed, these management units were split into approximately equal areas. Half of each management unit received PCT and half was left to develop without PCT.

Shelterwood System, Three-Stage Overstory Removal without PCT (SW3): The replicates for this treatment are MU23b (12 acres) and MU29b (8 acres) (Fig. 2). Both stands are in the stem exclusion stage of development, and self thinning is occurring. A thinning will be applied in this treatment when there are sufficient merchantable-sized trees in the new cohort to support a commercial harvest.

The likely thinning prescription will focus on maximizing stand-level volume production (see Seymour 1999) while also releasing high-quality eastern white pine and spruce crop trees from competition. The thinning method used will be a combination of crown and low thinning to capture mortality and release crop trees. Crown class, species, live crown ratio, and stem form and quality will be used to identify trees for either removal or retention.

Shelterwood System, Three-Stage Overstory Removal with PCT (SW3 pct): This treatment is replicated in management units 23a (12 acres) and 29a (9 acres) (Fig. 2). Manual PCT to a residual spacing of approximately 6 feet by 9 feet was applied in MU23a in 1983 and in MU29a in 1984 (Fig. 3). The PCT lengthened the period of stand initiation and allowed new seedlings to become established. It enhanced diameter growth on the residual trees enough that these stands were further subdivided and commercially thinned. Both were included in the University of Maine's Commercial Thinning Research Network (Seymour et al., this volume). MU23a and MU29a were commercially thinned in 2001 and 2010, respectively (Fig. 3).

Uneven-Aged Silvicultural Treatments

Selection System, 5-Year Cutting Cycle (S05): Replicates of this treatment are MU9 (27 acres) and MU16 (16 acres) (Fig. 2). The eleventh selection cutting was in 2009 in MU9, and in 2011 in MU16 (Fig. 3). Stands are vertically and horizontally diverse, with areas in both stem exclusion and understory reinitiation. The stands are highly stratified, and trees within each stratum are differentiated into crown classes.

The 2008 study plan revised the BD*q* structural goal to reflect species-specific growth rates and longevities. The previous version of the study plan did not account for species differences and had only one target diameter distribution (q=1.96 on 1-inch d.b.h. classes) and maximum diameter (MaxD, 19 inches d.b.h.) for the treatment. When all species are combined, the q for this treatment now averages 1.6 (decreasing from 1.8 in the saplings to 1.4 in the large sawtimber) and stand-level MaxD (excluding eastern white pine emergents) is 22 inches d.b.h. Species composition goals were also modified to better reflect the species assemblage occupying the site (the target BA was lowered for spruce and increased for hemlock). Efforts are being made to sustain spruce and reduce structural bimodality (too few trees in poletimber classes and too many in sawtimber) through increased recruitment and reduction of sawtimber excesses. An excess of seedlings and saplings has reduced the need to establish regeneration, and PCT is conducted to release spruce saplings from within-stratum competition.

Species composition goals, expressed as a proportion of BA ≥4.5 inches d.b.h. are as follows:

- eastern hemlock, 30 percent
- spruce species, 40 percent
- hardwoods, 15 percent
- balsam fir, eastern white pine, and northern white-cedar (*Thuja occidentalis* L.), 5 percent each

Marking guidelines by order of priority are:

- remove cull trees, except northern white-cedar unless it exceeds the stand-level composition goal and/or is negatively impacting the growth of a merchantable tree
- remove high-risk trees (i.e., trees expected to die before the next entry)
- remove unacceptable growing stock (UGS; trees without potential for volume or value increase)
- remove trees from d.b.h. classes and species that are in excess relative to the goals
- release or thin potential crop trees in the sapling, pole, and small sawtimber classes
- remove trees beyond species MaxD

Trees are not cut from size classes that are deficient relative to the diameter distribution unless they fall into the cull, high-risk, or UGS classifications. Trees with active cavities are not cut, nor are trees that will damage a snag with active cavities when felled. One to two trees greater than MaxD may be retained per management unit, if of exceptional size and quality for their species.

Target residual BA is 105 ft^2/acre ≥4.5 inches d.b.h., and the difference between actual and target stand BA in the 4.5-inch d.b.h. and larger classes equals the allowable cut. If allowable cut is less than 5 ft^2/acre (i.e., 1 ft^2/acre × cutting cycle length in years), then harvest is delayed until the next scheduled entry.

For structural control, the following species groups and maximum diameters are recognized:

- eastern hemlock and spruce species, 22 inches d.b.h.
- balsam fir, 10 inches d.b.h.
- northern white-cedar, 12 inches d.b.h.
- hardwoods, 18 inches d.b.h.
- eastern white pine, 24 inches d.b.h.

Selection System, 10-Year Cutting Cycle (S10): This treatment is replicated in management units 12 (31 acres) and 20 (21 acres) (Fig. 2). The fifth selection cutting was applied in 1994 in MU12, and in 1998 in MU20 (Fig. 3). Stands are vertically and horizontally diverse, with areas in both stem exclusion and understory reinitiation. The stands are highly stratified, and trees within each stratum are differentiated into crown classes.

Like the 5-year selection, this treatment had a single *q*-factor (1.96) and MaxD (18 inches d.b.h.) prior to the 2008 study plan revision. When all species are combined, the *q* for this treatment now averages 1.6 (decreasing from 1.8 in the saplings to 1.4 in the large sawtimber) and stand-level MaxD (excluding eastern white pine emergents) is 20 inches d.b.h. Species composition goals and marking guidelines are the same as for the 5-year selection, and PCT is conducted to release selected spruce saplings.

Target residual BA is 90 ft^2/acre ≥4.5 inches d.b.h., and the difference between actual and target stand BA in the 4.5-inch d.b.h. and larger classes equals the allowable cut. If allowable cut is less than 10 ft^2/acre (i.e., 1 ft^2/acre × cutting cycle), then harvest will be delayed until the next scheduled entry.

For structural control, the following species groups and maximum diameters are recognized:

- eastern hemlock and spruce species, 20 inches d.b.h.
- balsam fir, 8 inches d.b.h.

- northern white-cedar, 12 inches d.b.h.
- hardwoods, 16 inches d.b.h.
- eastern white pine, 24 inches d.b.h.

Selection System, 20-Year Cutting Cycle (S20): The replicate management units for this treatment are MU17 (26 acres) and MU27 (20 acres) (Fig. 2). The third selection treatment was applied in 1994 in MU17, and in 1996 in MU27 (Fig. 3). Stands are vertically and horizontally diverse, with areas in both stem exclusion and understory reinitiation. The stands are highly stratified, and trees within each stratum are differentiated into crown classes.

Like S05 and S10, this treatment had a single *q*-factor (1.96) and MaxD (16 inches d.b.h.) prior to the 2008 study plan revision. When all species are combined, the *q* for this treatment now averages 1.6 (decreasing from 1.8 in the saplings to 1.4 in the large sawtimber) and stand-level MaxD (excluding eastern white pine emergents) is 18 inches d.b.h. Species composition goals, use of PCT, and marking guidelines are the same as those for the 5- and 10-year selection treatments.

Target residual BA is 70 ft^2/acre ≥4.5 inches d.b.h., and the difference between actual and target stand BA in the 4.5-inch d.b.h. and larger classes equals the allowable cut. As in the other selection treatments, if allowable cut is less than 20 ft^2/acre (i.e., 1 ft^2/acre × length of cutting cycle), then harvest will be delayed until the next scheduled entry.

For structural control, the following species groups and maximum diameters are recognized:

- eastern hemlock and spruce species, 18 inches d.b.h.
- balsam fir, 6 inches d.b.h.
- northern white-cedar, 10 inches d.b.h.
- hardwoods, 14 inches d.b.h.
- eastern white pine, 22 inches d.b.h.

Exploitative Cutting

Commercial Clearcut (CC): Replicates of this treatment are management units 8 (43 acres) and 22 (34 acres) (Fig. 2). These management units were initially cut in 1953 (MU8) and 1957 (MU22); the second harvests were in 1982 and 1988 (Fig. 3). All merchantable trees were removed; lower merchantability standards resulted in heavier cuts in the second entries. The stands are in the stand initiation and stem exclusion phases of development. Portions of the management units in this treatment are being used to study a range of stand rehabilitation techniques (Kenefic et al. 2010).

Fixed Diameter-Limit Cutting (FDL): This treatment is replicated in management units 4 (25 acres) and 15 (26 acres) (Fig. 2). The third diameter-limit cut was applied in MU4 in 1992 and in MU15 in 2001 (Fig. 3). Though some areas are in stem exclusion, much of the stand area is in the stand initiation phase. These management units will be harvested again when stand volume reaches initial (pre-first cut) treatment volume (2,000 ft^3/acre). At that time all merchantable trees at and above the following species-specific diameter limits will be cut:

- eastern white pine, 10.5 inches
- spruce species and eastern hemlock, 9.5 inches
- paper birch and northern white-cedar, 7.5 inches
- all other species, 5.5 inches

Modified Diameter-Limit Cutting (MDL): The two replicates of this treatment are MU24 (26 acres) and MU28 (18 acres) (Fig. 2). The third modified diameter-limit cut was applied in MU24 in 1995 and in MU28 in 1996 (Fig. 3). Portions of the stands are in the stem exclusion and understory reinitiation stages of development.

Unlike the fixed diameter-limit treatment, where the harvest interval depends on stand dynamics, this treatment has a defined cutting cycle of 20 years. Furthermore, the diameter-limit classes are flexible, not proscriptively rigid as they are in the fixed diameter-limit treatment. Consequently, at the next harvest entry all merchantable trees above the following species-specific diameter-limit classes will be cut unless they are needed for a seed source or to provide wind protection for smaller trees:

- eastern white pine and spruce species, 14.5 inches
- eastern hemlock, 12.5 inches
- paper birch, 9.5 inches
- northern white-cedar, 7.5 inches
- all other species, 6.5 inches

Trees below the diameter limits may be harvested if they are expected to die before the next entry.

Experimental Control

Unmanaged Reference (REF): The reference replicates, MU32a (13 acres) and MU32b (6 acres), were originally one management unit, which was split in 1993 to take into account the distinctly different stages of stand development and to balance the experimental design. The stages of stand development were distinct because of an unrecorded natural disturbance event about the time the study was established that affected the area differently. MU32a is in the stand initiation and stem exclusion phases of development while MU32b is in the latter stages of stem exclusion and will soon enter the understory reinitiation phase. Neither management unit has been harvested since the late 1800s; prior to that, selective partial cuts were made.

Response Variables

Response variables are measured on a series of PSPs established at the beginning of the study. Currently there are 295 PSPs or, on average, one plot for each 1.4 acres of the experiment. These nested circular fixed-radius plots have a common center point. Plot size varies depending on the size of tree or variable measured. Within these plots are three permanent circular milacre plots for inventorying regeneration in the treated management units and four such plots in the reference. Response variables are measured before and after harvests. The current study plan calls for additional inventories at 10-year intervals between harvests. (S05 and S10 have no between-harvest inventories because of their cutting cycles.) Previously, that interval was 5 years. (S10 did have between-harvest inventories then.) It was changed to accommodate measuring additional response variables without adding substantially to the inventory workload. The current response variables are:

Species: Regardless of size, trees are recorded to species. Woody shrubs such as willow (*Salix* spp.), alder (*Alnus* spp.), and hazel (*Corylus* spp.) are not measured, even though they sometimes reach tree stature.

Regeneration: For each milacre plot the substrate is recorded as: undisturbed forest floor, disturbed forest floor, mineral soil, down coarse woody material, logging slash, rock, or water. If more than one substrate is present, the percentage of each is estimated to the nearest 10 percent. For tree species the number of seedlings >6 inches tall is counted according to height class: 0.5 to <1.0 foot, 1.0 to <2.0 feet, 2.0 to <4.5 feet, and ≥4.5 feet with d.b.h. <0.5 inches.

Understory vegetation: The milacre plots are also used to estimate percentage of cover of non-tree vegetation. Each milacre plot is visualized as a cylinder rising through the canopy, and the relative abundance for various taxa is classified within the cylinder (Witham et al. 1993). Non-tree taxa are recorded as: woody shrubs, herbaceous vegetation, grasses and sedges, ferns and similar plants, and mosses and lichens.

Diameter at breast height: Diameter at breast height is measured at 4.5 feet above the ground to the nearest 0.1 inch using a diameter tape. Tree size determines which plot it is measured on, as follows:

D.b.h. (inches)	Plot size (acres)
0.5 to <2.5	1/50
2.5 to <4.5	1/20
≥4.5	1/5

Diameter at breast height (continued)**:** Since the mid 1970s, trees for which d.b.h. is measured have been numbered individually and a horizontal line is painted on the side of the tree facing plot center. Thus individual trees are followed over time and d.b.h. is consistently remeasured at the same location on the stem. Under the current measurement regime, more than 40,000 trees are measured in a typical year. In September 2010, the one-millionth d.b.h. measurement of a numbered tree was taken (Fig. 5).

Spatial Distribution: On a subsample of at least 30 percent of the plots in each management unit, the location of each numbered tree ≥4.5 inches d.b.h. is determined in relation to plot center, to the nearest 0.1 foot and nearest 2° of azimuth. The same plots are remeasured in subsequent inventories to add ingrowth trees and follow mortality.

Tree Height and Crown Attributes: On the same subsample of plots used to establish spatial distribution, height and crown attributes are measured on the sampled (i.e., spatially located) trees, as follows:

Total height—Measured to the nearest 0.1 foot.

Height to base of live crown—Measured to the nearest 0.1 foot. In this study, the base of the live crown is the center of the lowest live branch where it intersects the bole of the tree. The lowest live branch is the lowest branch that appears to be contributing more than it receives from the rest of the crown.

Crown projection—Distance from the center of the bole of each measured tree to the edge of its crown is measured to the nearest 0.1 foot in the four cardinal directions.

Figure 5.—Project leader John Brissette takes the one-millionth measurement in the long-term silvicultural study on the Penobscot Experimental Forest in 2010, assisted by a student technician (center) and forester Rick Dionne. Photo by U.S. Forest Service.

Tree Condition: A condition code is assigned to each numbered tree at each inventory. The codes provide information about the tree's size class and general health and quality. Condition codes include such information as whether a tree is alive or dead (and the cause of mortality), whether it is ingrowth (first time measured as a sapling or pole-size tree) or was previously measured, and whether it is merchantable or cull. After trees ≥4.5 inches d.b.h. die, they stay in the inventory and the condition code reflects whether they are standing or down snags, and their state of decay.

DESIGN AND ANALYSIS

The study is laid out in a completely randomized experimental design (i.e., 2 replications of the 10 treatments). Management units are the experimental units. Response variables are measured on the PSPs. On average there are 15 PSPs per management unit.

The reference was not included in the original experimental layout. It was added in 1954, after the experimental treatments were assigned to management units but before all initial treatments were applied. It is not contiguous with the rest of the experiment. However, because it is the best reference area we have to compare with the treated management units, it is considered an experimental control in analyses.

Data collected in this study are entered into a relational database before the next field season; details can be found in Russell et al. (this volume). In addition, an archived online database is maintained and is readily available to researchers working on the study and cooperators interested in testing various hypotheses or building models of northern conifer stand dynamics (Brissette et al. 2012).

OUTCOMES AND FUTURE DIRECTION

Results from the long-term silvicultural experiment on the PEF have improved our understanding of forest ecology and influenced the way forests are managed both regionally and internationally. Unlike most earlier silvicultural studies, the PEF long-term experiment was replicated and included an array of silvicultural systems. Research was initially restricted to sapling-size and larger trees, but that deficiency was recognized early on and measures of regeneration were added in the mid-1960s. Researchers quantified the competitive advantage of balsam fir over red spruce due to fir's larger and less palatable seed (Abbott and Hart 1961), more frequent seeding, deeper rooting, and faster growth (Hart 1963). It became clear that natural regeneration of northern conifer stands was prolific, but questions remained about how to achieve desirable species mixtures. The spruce species were found to be less abundant than fir and hemlock under a range of selection and other partial cutting intensities, and hardwood-to-softwood ratios were higher in treatments with comparatively heavier removals (Brissette 1996).

Results of this study have been the basis of silvicultural guidance to forest managers. "The Silvicultural Guide for Spruce-Fir in the Northeast" (Frank and Bjorkbom 1973) has been used extensively by industrial, private, and government foresters throughout the northeastern United States and Atlantic Canada. In addition, management recommendations specific to uneven-aged silviculture were developed from the PEF selection treatments (Frank and Blum 1978). Findings after 20 years of treatment showed decreases in the amount of unmerchantable volume, increases in seedling density and proportions of spruce, and improved diameter distributions.

The uneven-aged (selection) system was emphasized during the initial planning of the PEF study due to the shade tolerance of the most important commercial species and the preponderance of Forest Service partial cutting research prior to World War II (Westveld 1946). Variants of even-aged systems were included in the experiment at the urging of David M. Smith from Yale University, who was asked to review a draft of the study plan. He told McLintock that "management and harvesting of spruce-fir types in this country would become pretty badly hog-tied in detailed refinements if an honest effort were made to superimpose the true selection principle… ." [2] A national paradigm shift to even-aged silviculture focusing on high-yield, low-cost wood production occurred around 1960 (Seymour et al. 2006), largely because uneven-aged silviculture was regarded by many foresters as unnecessarily complex, prone to high-grading, and ill-suited for maximizing wood production. Thus, Smith's suggestion to include even-aged treatments on the PEF proved to be an inspiration as studies of fertilization, PCT, strip clearcutting, whole-tree harvesting, and planting were initiated on the PEF between the 1960s and 1980s in direct response to the nationwide shift in forestry thinking. Because of the treatment design, the long-term silvicultural experiment on the PEF has demonstrated that northern conifer stands can be managed effectively with both uneven- and even-aged silvicultural systems, giving managers a broad range of options. That is not the case in most forest types.

The emphasis on even-aged silviculture began to wane in many parts of North America by the 1990s, when the idea of New Forestry ("a kinder and gentler forestry that better accommodates ecological values") (Franklin 1989: 38) started to influence how both researchers and managers approached silviculture. On the PEF, the descriptor "spruce-fir" gave way to the more inclusive (and more accurate) "northern conifers" and new response variables were added to the long-term study, including standing and downed snags; structural characteristics such as tree location, height, crown projection, and crown length; and ground cover. Treatment prescriptions started emphasizing wildlife trees and canopy emergents by excluding a significant portion of them from cutting.

[2] Smith, D.M. 1952 (November). Letter to T.F. McLintock. On file at the Penobscot Experimental Forest and available from the authors.

In 1994, the industrial owners of the PEF donated the property to the University of Maine Foundation with the hope that new research would be initiated by faculty and graduate students. In the donation document they stated their expectation that the PEF would "afford a setting for long-term research conducted cooperatively among U.S. Forest Service scientists, University researchers and professional forest managers in Maine; to enhance forestry education of students and the public; and to demonstrate how the timber needs of society are met from a working forest." [3] With greater involvement by University researchers, the number of short-term studies overlain on the Forest Service's long-term experiment has increased. These studies usually have a basic rather than applied focus and cover a range of topics important to sustainable forest management, including: wood decay (Smith et al. 2007), leaf area and growth efficiency (Kenefic and Seymour 1999a, Maguire et al. 1998, Seymour and Kenefic 2002), leaf morphology and gas exchange (Day et al. 2001), carbon storage (Hoover 2005), herbivory (Larouche et al. 2010), bird and insect diversity and habitat suitability (Johnston and Holberton 2009, Su and Woods 2001), and genetic diversity (Hawley et al. 2005).

Studies of dead standing trees have provided new insights into the dynamics of wildlife habitat. Snag longevity, for example, was found to be a function of species, size, stand density, and cause of death, and was greatest in unharvested stands and least in stands with short cutting cycles (Garber et al. 2005). Investigation of decayed down wood established the importance of this substrate for regeneration of spruce and hemlock (Weaver et al. 2009). The effect of silviculture on spatial arrangement of trees was also investigated. Regeneration events were found to increase aggregation and reduce species mingling, particularly when treatment shifted species composition toward hardwoods (Saunders and Wagner 2008).

Although non-tree vegetation received limited attention on the PEF in the past, an inventory of understory vegetation on the PSPs in the long-term study was recently completed. Understory species richness and diversity generally declined with decreasing silvicultural intensity (determined by BA removed and time since cutting); differences in diversity and composition of understory plants were related to canopy composition and forest floor disturbance (Bryce 2009). Nonnative invasive plants were uncommon in the experimental stands but abundant in adjacent old-field stands (Olson et al. 2011).

The long-term silvicultural experiment on the PEF provides a unique perspective on forest dynamics, a perspective that is increasingly more relevant with time. One of the advantages of long-term experiments is that scientists can document treatment responses that vary over time. For example, the diameter distributions of the PEF selection treatments were close to their goals in the 1970s and researchers predicted that the stands would remain "essentially balanced" (Frank and Blum 1978). However, analysis of data from later remeasurements revealed structural and compositional imbalances that were not apparent in earlier assessments (Kenefic and Brissette 2001, Seymour and Kenefic 1998). In addition, though increases in the proportion of spruce growing stock led Frank and Blum (1978) to conclude that efforts to favor those species were successful, we now know that this outcome was a function of accretion rather than recruitment (Kenefic et al. 2007). Spruce trees in the selection treatments are almost all more than a century old (Seymour and Kenefic 1998) and new saplings have been growing at a rate of less than 1 inch in diameter per decade.[4]

Similarly, growth rates of seedlings in the selection treatments have been slow; the shade-tolerant conifers can take as many as 35 years to reach 1.5 feet in height (Weaver 2007). Analysis of relationships between

[3] Unpublished document on file at the Penobscot Experimental Forest and available from the authors.

[4] Unpublished data on file at the Penobscot Experimental Forest and available from the authors.

overstory stocking and growth of understory trees in the selection treatments revealed that there was no level of canopy closure that favored spruce over its competitors (Moores et al. 2007). These findings tell a story much different from those of the 1970s, and raise concerns about long-term sustainability of structure and composition of the selection treatments. These concerns can be addressed only by continuing to implement planned treatments and measuring the results over the next few decades.

In general, understanding of how forests respond to disturbances increases with time, but we must acknowledge that the localized impacts of climate change are still largely speculative. Iverson and Prassad (2001) concluded from their models that spruce-fir forests will be extirpated from New England within the century. Dawson et al. (2011) contend that although such models help identify exposure to climate change, assessing consequences requires considering not only exposure but sensitivity and adaptive capacity as well. Sensitivity is the degree to which the persistence and fitness of a species or species group depends on a particular climate. Adaptive capacity refers to whether species or communities tolerate change, shift their habitats, migrate to new regions, or become extinct (Dawson et al. 2011).

Little is known about the sensitivity and adaptive capacity of northern conifers, but long-term experiments like the one on the PEF offer the best empirical evidence for evaluating the effects of climate change on these qualities. Studying phenotypic plasticity, genetic diversity, ecophysiology, and silvical traits like seed dispersal and microhabitat preferences can tell us much about the sensitivity and adaptive capacity of northern conifers. Many of these traits can be measured, and are being measured, in the PEF long-term experiment. In fact, many of these traits have been measured over the past 60 years (see Kenefic and Brissette, this volume) but not in the context of climate change. Evaluating how silvicultural treatments influence sensitivity and adaptive capacity will be a high priority for the PEF long-term silvicultural experiment over the next several decades.

SUMMARY

The long-term silvicultural study on the PEF has spanned the careers of four generations of researchers and has influenced the education and practices of untold numbers of foresters and other natural resource professionals, as well as landowners, from across the region. Field tours of the experiment are always dynamic events with many questions and much discussion. Two of the most frequently asked questions are: “What is the most important thing learned so far?” and “Why is it important to continue the study?”

Our answer to the first question is rather straightforward: *Healthy, productive forests are maintained through careful harvesting based on informed planning. Harvesting for immediate gain alone leaves behind a low-quality forest with few options for the future.*

Both even- and uneven-aged methods influence the composition and structure of northern conifer stands and thereby provide valuable timber, high-quality habitat, aesthetically pleasing views, and a broad range of management options for the future. However, management focused on short-term financial returns alone leaves stands that have few high-quality trees and require decades of growth before they once again provide a range of management options. In short, silviculture matters.

The answer to the second question is more subjective but perhaps more important: *Knowledge accumulated through continued research leads to better, more certain management decisions.*

Researchers turn data into knowledge. Managers turn knowledge into action. Knowledge based on short-term results is incomplete at best and often wrong. The value of knowledge increases as it accumulates in two important ways: greater precision for prescribing treatments and greater certainty that prescriptions will achieve desired results. The PEF study is now more than halfway through an even-aged rotation and the overstory of the uneven-aged treatments is still composed mostly of trees that were there when the experiment began. Consequently, we must continue to evaluate stand development patterns following the various treatments in order to provide managers the level of precision and certainty needed to ensure success.

This experiment represents a tremendous investment in time, effort, and dollars. It is also logical and appropriate to ask whether it has been worth it. We believe that it has, and that it continues to be worthy of our time and talents. Results of this study are of interest to a wide audience. Studies of underlying ecological processes and qualities like sensitivity and adaptive capacity with regard to climate change advance science and are presented via scientific meetings and peer-reviewed journal articles. Applied results such as management guidelines improve how forests are managed and are presented at practitioner-oriented meetings and in publications. Additionally, field tours of the experiment are a key component of the technology transfer program on the PEF. This experiment not only has influenced the practice of forestry in the northern conifer type, but more importantly, has helped advance understanding of tree and stand growth and the relationship between human and natural disturbance at a fundamental level, not specific to a forest type. We maintain that the value of this study will continue to increase as its results are used to address the always-evolving compelling questions of the day.

ACKNOWLEDGMENTS

Sustaining long-term field research over decades requires the effort and talent of many people, some of whom work on the study for entire careers and others of whom are involved for only a season. All leave their mark on the research. The principal investigators of the experiment are all named in the paper and we are grateful for their foresight and diligence. Their dedication allowed the study to pass into our hands and we are humbled by the knowledge that we will some day pass it on to others. We also thank all those, too many to name, who over the years contributed to the study, especially the field crews who collected the data and the data managers who made it usable for the researchers. We also thank Mary Beth Adams and Edwin Swift for their thoughtful reviews of an earlier draft of the manuscript.

LITERATURE CITED

Abbott, H.G.; Hart, A.C. 1961. **Mice and voles prefer spruce seed.** Station Paper 153. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 12 p.

Arbogast, C.A. 1957. **Marking guides for northern hardwoods under the selection system.** Station Paper 56. St. Paul, MN: U.S. Department of Agriculture, Forest Service, Lakes States Forest Experiment Station. 17 p.

Baker, J.B.: Bishop, L.M. 1986. **Crossett Demonstration Forest guide.** Gen. Rep. R8-GR6. Atlanta, GA: U.S. Department of Agriculture, Forest Service, Southern Region. 55 p.

Baskerville, G.L. 1960. **Conversions to periodic selection management in a fir, spruce, and birch forest.** Forest Research Division Tech. Note 86. Fredericton, NB: Canada Department of Resources and Development, Forestry Branch, Forest Research Laboratory. 19 p.

Baskerville, G.L. 1975a. **Spruce budworm: super silviculturist.** The Forestry Chronicle. 51: 138-140.

Baskerville, G.L. 1975b. **Spruce budworm: The answer is forest management. Or is it?** The Forestry Chronicle. 51: 157-160.

Blum, B.M. 1973. **Some observations on age relationships in spruce-fir regeneration.** Res. Note NE 169. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Blum, B.M.; Benzie, J.W.; Merski, E. 1983. **Eastern spruce-fir.** In: Burns, R.M., tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Hndbk. No. 445. Washington, DC: U.S. Department of Agriculture, Forest Service: 128-130.

Braun, E.L. 1950. **Deciduous forests of eastern North America.** Reprinted 1974. New York: Hafner Press. 596 p.

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

Brissette, J.C.; Frank, R.M., Jr.; Stone, T.L.; Skratt, T.A. 1999. **Precommercial thinning in a northern conifer stand: 18-year results.** The Forestry Chronicle. 75(6): 967-972.

Brissette, J.C.; Kenefic, L.S. 2008. **Silvicultural effects on composition, structure and growth of northern conifers in the Acadian Forest Region: revision of the Compartment Management Study on the Penobscot Experimental Forest.** In: Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed February 6, 2013).

Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012. **Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest.** Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed February 6, 2013).

Brissette, J.C.; Saunders, M.R.; Kenefic, L.S.; Sendak, P.E. 2006. **Long-term research on classical silvicultural approaches in the Acadian Forest: Penobscot Experimental Forest Part I.** In: Proceedings, Society of American Foresters 2006 national convention; 2006 October 25-29; Pittsburgh, PA. Bethesda, MD: Society of American Foresters: 922-931.

Brissette, J.C.; Swift, D.E. 2006. **Natural regeneration with shelterwood silviculture in the Acadian Forest Region.** In: Colombo, S.J., comp. The thin green line: a symposium on the state-of-the-art in reforestation: proceedings of the meeting; 2005 July 26-28; Thunder Bay, ON. Forest Research Information Paper 160. Sault Ste. Marie, ON: Ontario Ministry of Natural Resources, Ontario Forest Research Institute: 134.

Bryce, E.K. 2009. **Influence of silvicultural treatment, site characteristics, and land use history on native and nonnative forest understory plant composition on the Penobscot Experimental Forest in Maine.** Orono, ME: University of Maine. 123 p. M.S. thesis.

Cary, A. 1896. **Report of Austin Cary.** In: 3rd annual report, Maine Forest Commissioner. Augusta, ME: 15-203.

Crawford, H.S. 1984. **Effects of silvicultural practice on bird predation.** Society of American Foresters. Region IV Technical Conference. 1984 April 24-26; Burlington VT. Bethesda, MD: Society of American Foresters: 173-175.

Crawford, H.S.; Jennings, D.T. 1989. **Predation by birds on spruce budworm *Choristoneura fumiferana*: functional, numerical, and total responses.** Ecology. 70: 152-163.

Davis, R.B. 1966. **Spruce-fir forests on the coast of Maine.** Ecological Monographs. 36(2): 79-94.

Dawson, T.P.; Jackson, S.T.; House, J.I.; Prentice, I.C.; Mace, G.M. 2011. **Beyond predictions: biodiversity conservation in a changing climate.** Science. 332: 53-58.

Day, M.E.; Greenwood, M.S.; White, A.S. 2001. **Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age.** Tree Physiology. 21: 1195-1204.

Fajvan, M.A. 2006. **Research on diameter-limit cutting in central Appalachian forests.** In: Kenefic, L.S.; Nyland, R.D., eds. Proceedings of the diameter-limit cutting in northeastern forests conference. Gen. Tech. Rep. NE-342. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 32-38.

Fiedler, C.A. 1995. **The basal area- maximum diameter- q (BDq) approach to regulating uneven-aged stands.** In: Uneven-aged management: opportunities, constraints, and methodologies. MFCES Misc. Pub. No. 56. Missoula, MT: University of Montana, School of Forestry: 94-109.

Frank, R.M. 1975. **Revised study plan for Compartment Management Study: spruce-fir management, Penobscot Experimental Forest.** In: Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed February 7, 2013).

Frank, R.M.; Bjorkbom, J.C. 1973. **A silvicultural guide for spruce-fir in the northeast.** Gen. Tech. Rep. NE-6. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 29 p.

Frank, R.M.; Blum, B.M. 1978. **The selection system of silviculture in spruce-fir stands—procedures, early results, and comparisons with unmanaged stands.** Res. Pap. NE-425. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 15 p.

Frank, R.M.; Safford, L.O. 1970. **Lack of viable seeds in the forest floor after clearcutting.** Journal of Forestry. 68: 776-778.

Franklin, J.F. 1989. **Toward a new forestry.** American Forests. November/December: 37-44.

Garber, S.M.; Brown, J.P.; Wilson, D.S.; Maguire, D.A.; Heath, L.S. 2005. **Snag longevity under alternative silvicultural regimes in mixed species forests of central Maine.** Canadian Journal of Forest Research. 35: 787-796.

Guldin, J.M. 1987. **An ecological derivation of stand structure in balanced uneven-aged loblolly-shortleaf pine stands of the West Gulf region.** In: Phillips, D.R., ed. Proceedings of the 4th biennial southern silvicultural research conference; 1986 November 4-6; Atlanta GA. Gen. Tech. Rep. SE-42. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 496-502.

Guldin, J.M. 1991. **Uneven-aged BDq regulation of Sierra Nevada mixed conifers.** Western Journal of Applied Forestry. 6: 27-32.

Halliday, W.E.D. 1937. **A forest classification for Canada.** Forest Service Bull. 89. Ottawa, ON: Canada Department of Mines and Resources. Lands, Parks and Forests Branch. 5 p.

Hansen, G.D.; Nyland, R.D. 1987. **Effects of diameter distribution on growth of simulated uneven-aged sugar maple stands.** Canadian Journal of Forest Research. 17: 1-8.

Hart, A.C. 1962. **Revised working plan for the Compartment Management Study: spruce-fir management, Penobscot Experimental Forest.** In: Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed February 7, 2013).

Hart, A.C. 1963. **Spruce-fir silviculture in northern New England.** In: Proceedings, Society of American Foresters national convention; Boston, MA. Bethesda, MD: Society of American Foresters: 107-110.

Hawley, G.J.; Schaberg, P.G.; DeHayes, D.H.; Brissette, J.C. 2005. **Silviculture alters the genetic structure of an eastern hemlock forest in Maine, USA.** Canadian Journal of Forest Research. 35: 143-150.

Helms, J.A., ed. 1998. **The dictionary of forestry.** Bethesda, MD. Society of American Foresters. 210 p.

Hoover, C.M. 2005. **Carbon storage in northeastern U.S. forest soils.** In: Kenefic, L.S.; Twery, M.J., eds. Changing forests - challenging times: proceedings of the New England Society of American Foresters 85th winter meeting; 2005 March 16-18; Gen. Tech. Rep. NE-325. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 17.

Iverson, L.R.; Prasad, A.M. 2001. **Potential changes in tree species richness and forest community types following climate change.** Ecosystems. 4: 186-199.

Johnston, J.C.; Holberton, R.L. 2009. **Forest management and temporal effects on food abundance for a ground-foraging bird (*Catharus guttatus*).** Forest Ecology and Management. 258: 1516-1527.

Kenefic, L.S.; Brissette, J.C. 2001. **Long-term dynamics of structure and composition in uneven-aged northern conifer stands.** In: Forestry at the great divide: proceedings, Society of American Foresters national convention; 2001 September 13-17; Denver, CO. Bethesda, MD: Society of American Foresters: 405-407.

Kenefic, L.S.; Brissette, J.C. 2005. **Sapling recruitment and growth dynamics in uneven-aged northern conifer stands: A 25-year study.** In: Kenefic, L.S.; Twery, M.J., eds. Changing forests - challenging times: proceedings of the New England Society of American Foresters 85th winter meeting; 2005 March 16-18. Gen. Tech. Rep. NE-325. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 55.

Kenefic, L.S.; Brissette, J.C.; Sendak, P.E. 2004. **The effects of alternative diameter-limit cutting treatments: some findings from a long-term northern conifer experiment.** In: Ward, J.S.; Twery, M.J., eds. Forestry across borders: proceedings of the New England Society of American Foresters 84th winter meeting; 2004 March 23-26; Quebec City, Canada. Gen. Tech. Rep. NE-314. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 22-24.

Kenefic, L.S.; Nyland, R.D. 2005. **Diameter-limit cutting and silviculture in northeastern forests: a primer for landowners, practitioners, and policymakers.** NA-TP-02-05. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Area State and Private Forestry. 18 p.

Kenefic, L.S.; Nyland, R.D., eds. 2006. **Proceedings of the conference on diameter-limit cutting in northeastern forests.** Gen. Tech. Rep. NE-342. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 51 p.

Kenefic, L.S.; Sendak, P.E.; Brissette, J.C. 2005a. **Comparison of fixed diameter-limit and selection cutting in northern conifers.** Northern Journal of Applied Forestry. 22(2): 77-84.

Kenefic, L.S.; Sendak, P.E.; Brissette, J.C. 2006. **Turning data into knowledge for over 50 years: USDA Forest Service research on the Penobscot Experimental Forest.** In: Irland, L.C.; Camp, A.E.; Brissette, J.C.; Donohew, Z.R., eds. Long-term silvicultural and ecological studies: results for science and management. Global Institute of Sustainable Forestry Research Paper 005. New Haven, CT: Yale University: 26-33.

Kenefic, L.S.; Seymour, R.S. 1999a. **Leaf area prediction models for *Tsuga canadensis* in Maine.** Canadian Journal of Forest Research. 29: 1574-1582.

Kenefic, L.S.; Seymour, R.S. 1999b. **Patterns of tree growth and structural development in uneven-aged northern conifer stands in the Acadian Forest of Maine.** In: Emmingham, W.H., comp. Proceedings of the IUFRO interdisciplinary uneven-aged management symposium; 1997 Sept. 15-19. Corvallis, OR: Oregon State University, Forest Research Laboratory: 554-568.

Kenefic, L.S.; White, A.S.; Cutko, A.R.; Fraver, S. 2005b. **Reference stands for silvicultural research: a Maine perspective.** Journal of Forestry. 103(7): 363-367.

Kenefic, L.S.; Wilson, J.; Brissette, J.C.; Nyland, R.D.; Lilieholm, R.J. 2010. **Silvicultural rehabilitation of cutover mixedwood stands.** In: Proceedings of the Eastern Canada – USA Forest Science Conference; 2010 Oct. 14-16; Edmundston, NB. 30. Abstract.

Larouche, C.; Kenefic, L.S.; Ruel, J-C. 2010. **Northern white-cedar regeneration dynamics on the Penobscot Experimental Forest in Maine: 40-year results.** Northern Journal of Applied Forestry. 27(1): 5-12.

Leak, W.B.; Filip, S.M. 1975. **Uneven-aged management of northern hardwoods in New England.** Res. Pap. NE-332. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 15 p.

Leak, W.B.; Solomon, D.S.; Filip, S.M. 1969. A **silvicultural guide for northern hardwoods in the Northeast.** Res. Pap. NE-143. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 34 p.

MacLean, D.A. 1980. **Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion.** The Forestry Chronicle. 56: 213-221.

MacLean, D.A. 1984. **Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests.** The Forestry Chronicle. 60: 273-279.

Maguire, D.A.; Brissette, J.C.; Gu, L. 1998. **Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine.** Canadian Journal of Forest Research. 28: 1233-1240.

Marquis, D.A. 1978. **Application of uneven-aged silviculture on public and private lands.** In: Uneven-aged silviculture and management in the United States: combined proceedings of two in-service workshops; 1975 July 15-17; Morgantown, WV; 1976 October 19-21; Redding, CA. Gen. Tech. Rep. WO-24. Washington, DC: U.S. Department of Agriculture, Forest Service: 25-63.

McLintock, T.F. 1953. **Working plan for pilot operation study: spruce-fir management, Penobscot Experimental Forest.** In: Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012. Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed February 7, 2013).

McLintock, T.F.; Westveld, M. 1946. **Some financial aspects of removal of overmature balsam fir as a budworm control measure.** Mgmt. Pap. No. 1. Philadephia, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

McNab, W.H.; Avers, P.E. 1994. **Ecological subregions of the United States, part one: sections.** Rep. WO-WSA-5. Washington, DC: U.S. Department of Agriculture, Forest Service. 337 p.

McWilliams, W.H.; Butler, B.J.; Caldwell, L.E.; Griffith, D.M.; Hoppus, M.L.; Lausten, K.M.; Lister, A.J.; Lister, T.W.; Metzler, J.W.; Morin, R.S.; Sader, S.A.; Steward, L.B.; Steinman, J.R.; Westfall, J.A.; Williams, D.A.; Whitman, A.; Woodall, C.W. 2005. **The forests of Maine: 2003.** Res. Bull. NE-164. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 188 p.

Meyer, H.A. 1952. **Structure, growth, and drain in balanced uneven-aged forests.** Journal of Forestry. 50: 85-92.

Miller, G.W.; Smith, H.C. 1993. **A practical alternative to single-tree selection?** Northern Journal of Applied Forestry. 10: 32-38.

Moores, A.R.; Seymour, R.S.; Kenefic, L.S. 2007. **Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands.** Canadian Journal of Forest Research. 37(12): 2715-2723.

Nyland, R.D. 1987. **Selection system and its application to uneven-aged northern hardwoods.** In: Nyland, R.D., ed. Proceedings, managing northern hardwoods; 1986 June 23-25. Faculty of Forestry Misc. Publ. No. 13. Syracuse, NY: State University of New York, College of Environmental Science and Forestry: 49-80.

Nyland, R.D. 2002. **Silviculture concepts and applications.** 2nd ed. Boston, MA: McGraw-Hill Companies, Inc. 682 p.

Nyland, R.D. 2003. **Even- to uneven-aged: the challenges of conversion.** Forest Ecology and Management. 172: 291-300.

Nyland, R.D. 2005. **Diameter-limit cutting and silviculture: a comparison of long-term yields and values for uneven-aged sugar maple stands.** Northern Journal of Applied Forestry. 23: 111-116.

Nyland, R.D.; Alban, L.M.; Nissen, R.L., Jr. 1993. **Greed or sustention: silviculture or not.** In: Briggs, R.D.; Krohn, W.B. Nurturing the northeastern forest: proceedings of a joint meeting of the New England Society of American Foresters and the Maine Wildlife Society; 1993 March 3-5; Portland ME. Misc. Rep. 382. Orono, ME: Maine Agricultural and Forest Experiment Station: 37-52.

O'Hara, K.L. 1996. **Dynamics and stocking-level relationships of multi-aged ponderosa pine stands.** Forest Science, Monograph 33. 32 p.

Oliver, C.D. 1981. **Forest development in North America following disturbances.** Forest Ecology and Management. 3: 153-168.

Oliver, C.D.; Larson, B.C. 1996. **Forest stand dynamics.** Updated ed. New York: John Wiley & Sons. 520 p.

Olson, E.; Kenefic, L.S.; Dibble, A.C.; Brissette, J.C. 2011. **Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: influence of site, silviculture, and land use history.** Journal of the Torrey Botanical Society. 138(4): 453-464.

Osawa, A. 1989. **Causality in mortality patterns of spruce trees during a spruce budworm outbreak.** Canadian Journal of Forest Research. 19: 632-638.

Reynolds, R.R.; Baker, J.; Ku, T.T. 1984. **Four decades of selection management on the Crossett Farm Forties.** Arkansas Agricultural Experiment Station Bulletin 872. Fayetteville, AR: University of Arkansas. 43 p.

Roach, B.A. 1974. **Selection cutting and group selection.** AFRI Misc. Rep. 5. Syracuse, NY: State University of New York, College of Environmental Science and Forestry. 9 p.

Rowe, J.S. 1972. **Forest regions of Canada.** Publ. No. 1300. Ottawa, ON: Canadian Forestry Service, Department of the Environment. 172 p.

Saunders, M.R.; Wagner, R.G. 2008. **Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems.** Canadian Journal of Forest Research. 38: 498-517.

Schuler, T.M.; Adams, M.B.; Ford, W.M.; Kochenderfer, J.N.; Edwards, P.J. 2005. **Large area comparisons of forest management practices (1951-present).** In: Kenefic, L.S.; Twery, M.J., eds. Proceedings of the 85th annual winter meeting of the New England Society of American Foresters. Gen. Tech. Rep. NE-325. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 72.

Sendak, P.E.; Brissette, J.C.; Frank, R.M. 2003. **Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** Canadian Journal of Forest Research. 33: 2116-2128.

Seymour, R.S. 1992. **The red spruce – balsam fir forest of Maine: evolution of silvicultural practice in response to stand development patterns and disturbances.** In: Kelty, M.J.; Larson, B.C.; Oliver, C.D., eds. Ecology and silviculture of mixed species forests. Norwell, MA: Kluwer Publishers: 217-244.

Seymour, R.S. 1995. **The northeastern region.** In: Barrett, J.W., ed. Regional silviculture of the United States. 3rd ed. New York: John Wiley & Sons: 31-79.

Seymour, R.S. 1999. **Principles for developing and planning thinning prescriptions.** In: Proceedings: thinning in the Maine forest; 1999 November 15-16; Augusta, ME. Orono, ME: University of Maine: 5-12.

Seymour, R.S.; Guldin, J.; Marshall, D.; Palik, B. 2006. **Large-scale, long-term silvicultural experiments in the United States: Historical overview and contemporary examples.** Allgemeine Forst-und Jagdzeitung. 177: 104-112.

Seymour, R.S.; Kenefic, L.S. 1998. **Balance and sustainability in multi-aged stands: a northern conifer case study.** Journal of Forestry. 96(7): 12-16.

Seymour, R.S.; Kenefic, L.S. 2002. **Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands.** Canadian Journal of Forest Research. 32: 2032-2042.

Smith, D.M.; Larson, B.C.; Kelty, M.J.; Ashton, P.M.S. 1997. **The practice of silviculture.** 9th ed. New York: John Wiley & Sons. 537 p.

Smith, K.T.; Shortle, W.C.; Jellison, J.; Connolly, J.; Schilling, J. 2007. **Concentrations of Ca and Mg in early stages of sapwood decay in red spruce, eastern hemlock, red maple, and paper birch.** Canadian Journal of Forest Research. 37: 957-965.

Solomon, D.S.; Frank, R.M. 1983. **Growth response of managed uneven-aged northern conifer stands.** Res. Pap. NE-517. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 17 p.

Solomon, D.S.; Herman, D.A.; Leak, W.B. 1995. **Fiber 3.0: an ecological growth model for northeastern forest types.** Gen. Tech. Rep. NE-204. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 24 p.

Su, J.C.; Woods, S.A. 2001. **Importance of sampling along a vertical gradient to compare the insect fauna in managed forests.** Environmental Entomology. 30(2): 400-408.

Tian, S.; Ostrofsky, W.D. 2007. **Butt and root decay in precommercially thinned spruce-fir stands.** Northern Journal of Applied Forestry. 24(2): 129-133.

Troup, R.S. 1928. **Silvicultural systems.** London, UK: Oxford University Press. 199 p.

Wagner, R.G.; Seymour, R.S.; McConville, D.J. 2002. **Maine's commercial thinning research network.** In: Ward, J.S.; Twery, M.J., eds. Forestry across borders: proceedings of the New England Society of American Foresters 84th winter meeting; 2004 March 23-26; Quebec City, Canada. Gen. Tech. Rep. NE-314. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 43.

Weaver, J.K. 2007. **Substrate availability and regeneration microsites of tolerant conifers in mixed-species stands in Maine.** Orono, ME: University of Maine. 80 p. M.S. thesis.

Weaver, J.K.; Kenefic, L.S.; Seymour, R.S.; Brissette, J.C. 2009. **Decaying wood and tree regeneration in the Acadian Forest of Maine, USA.** Forest Ecology and Management. 257(7): 1623-1628.

Weiskittel, A.R.; Kenefic, L.S.; Li, R.; Brissette, J.C. 2011. **Long-term influence of precommercial thinning treatments on stand-level attributes in a northern conifer stand of central Maine.** Northern Journal of Applied Forestry. 28(2): 92-96.

Weiskittel, A.R.; Kenefic, L.S.; Seymour, R.S.; Phillips, L.M. 2009. **Long-term effects of precommercial thinning on stem dimensions, form and branch characteristics of red spruce and balsam fir crop trees in Maine, USA.** Silva Fennica. 43(3): 397-409.

Wendel, G.W.; Smith, H.C. 1990. ***Pinus strobus* L., eastern white pine.** In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: 1. Conifers. Agric. Hndbk. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 476-488.

Westveld, M. 1928. **Observations on cutover pulpwood lands in the Northeast.** Journal of Forestry. 26: 649-664.

Westveld, M. 1946. **Forest management as a means of controlling the spruce budworm.** Journal of Forestry. 44: 949-953.

Witham, J.W.; Moore, E.H.; Hunter, M.L., Jr.; Kimball, A.J.; White, A.S. 1993. **A long-term study of an oak pine forest ecosystem: techniques manual for the Holt Research Forest.** Tech. Bull. 153, Orono, ME: Maine Agricultural Experiment Station. 164 p.

APPENDIX I.

Conversion of English to metric values for units used in this paper.

Multiply	by	to obtain
Inches (in.)	2.54	Centimeters (cm)
Feet (ft)	0.3048	Meters (m)
Acres (ac)	0.4047	Hectares (ha)
Trees per acre (TPA)	2.471	Trees per hectare (TPH)
Square feet per acre (ft^2/ac)	0.2296	Square meters per hectare (m^2/ha)
Cubic feet per acre (ft^3/ac)	0.06997	Cubic meters per hectare (m^3/ha)

APPENDIX II.

Examples of recent short-term studies in the U.S. Forest Service Long-Term Silvicultural Experiment on the Penobscot Experimental Forest, 1994-2010.

Name	Topic	Date Completed	Degree	Advisor	Institution
Part 1. Graduate Student Research					
Daniel Gilmore	Crown structure, stem form, and leaf area relationships for balsam fir	1995	Ph.D.	Robert Seymour	University of Maine
Geoffrey Wilson	Modeling early regeneration processes in mixed-species forests	1997	M.S.	Douglas Maguire	University of Maine
Jeffrey Jaros-Su	Insect biodiversity in managed forests	1999	Ph.D.	Stephen Woods	University of Maine
Laura Kenefic	Leaf area, stemwood volume growth, and structure in mixed-species, multi-aged stands	2000	Ph.D.	Robert Seymour	University of Maine
Michael Day	Factors influencing net primary production in red spruce	2000	Ph.D.	Michael Greenwood	University of Maine
Kerry Sokol	Effects of long-term diameter-limit cutting on radial growth and genetic diversity	2001	M.S.	Michael Greenwood	University of Maine
Suzhong Tian	Effects of precommercial thinning on root structure	2002	Ph.D.	William Ostrofsky	University of Maine
Leah Phillips	Crop-tree growth and quality after precommercial thinning	2002	M.S.	Robert Seymour	University of Maine
Andrew Moores	Understory growth dynamics and mensuration techniques in uneven-aged, mixed-species stands	2003	M.S.	Robert Seymour	University of Maine
R. Justin DeRose	Leaf area index - relative density relationships in even-aged balsam fir - red spruce stands	2004	M.S.	Robert Seymour	University of Maine
Spencer Meyer	Leaf area as a growth predictor of balsam fir and red spruce	2004	M.S.	Robert Seymour	University of Maine
Margaret Ward	Age-related trends in red spruce needle anatomy and the relationship to declining productivity	2005	M.S.	Michael Greenwood	University of Maine

Appendix II continued on next page

Appendix II (continued)

Name	Topic	Date Completed	Degree	Advisor	Institution
Michael Saunders	Dynamics of forest structure under different silvicultural regimes	2006	Ph.D.	Robert Wagner	University of Maine
Stephanie Adams	Age-related decline in photosynthesis in red spruce	2006	M.S.	Michael Day, Michael Greenwood	University of Maine
Brent Horton	Reproductive behavior of the white-throated sparrow	2007	Ph.D.	Rebecca Holberton	University of Maine
Jamie Weaver	Regeneration and substrate availability in partially cut stands	2007	M.S.	Laura Kenefic	University of Maine
Jason Johnston	Effects of forest management and food availability on condition and breeding of hermit thrushes	2007	Ph.D.	Rebecca Holberton	University of Maine
Robert Lindemuth	Sampling methods for estimating basal area and volume in partially harvested stands	2007	M.S.	Thomas Brann	University of Maine
Ashley Thomson	Comparative phylogeography of North American birches	2009	M.S.	Christopher Dick	University of Michigan
Catherine Larouche	Regeneration of northern white-cedar in partially cut mixedwood stands	2009	Ph.D.	Jean-Claude Ruel, Laura Kenefic	Laval University
Elizabeth Bryce	Influence of silviculture and site on native and nonnative forest understory plant distribution	2009	M.S.	Laura Kenefic	University of Maine
Katherine Spencer	Red spruce photosynthesis and maturation	2009	M.S.	Michael Day	University of Maine
Matthew Olson	Temporal and spatial patterns of tree regeneration	2009	Ph.D.	Robert Wagner	University of Maine
Christopher Zellers	Growth and financial performance of eastern white pine reserve trees	2010	M.S.	Robert Seymour	University of Maine
Kate Zellers	Patterns of eastern white pine regeneration as influenced by reserve trees	2010	M.S.	Robert Seymour	University of Maine

Appendix II continued on next page

Appendix II (continued)

Principal Investigator(s)	Topic	Date completed	Institution
Part 2. Examples of Additional Short-Term Research			
John Brissette	Red spruce and hemlock stem volume	1997	U.S. Forest Service, Northern Research Station (NRS)
Robert Shepard	Wood properties in thinned and unthinned stands	1997	University of Maine
Doug Maguire et al.	Crown structure and growth efficiency of red spruce	1998	University of Maine
Laura Kenefic, Robert Seymour	Age-size relationships in managed uneven-aged stands	1998	U.S. Forest Service, NRS University of Maine
Alison Dibble et al.	Understory vegetation and red spruce regeneration	1999	U.S. Forest Service, NRS University of Maine
Gary Hawley et al.	Genetic implications of diameter-limit cutting	2000	University of Vermont U.S. Forest Service, NRS
Mark Ducey et al.	Point relascope sampling of down woody material	2003	University of New Hampshire U.S. Forest Service, NRS
Shawn Garber et al.	Snag longevity in managed stands	2005	Oregon State University University of Maine
Coeli Hoover	Carbon sequestration in thinned stands	2006	U.S. Forest Service, NRS
Aaron Weiskittel et al.	Effect of precommercial thinning on tree and stand characteristics	2009	University of Maine U.S. Forest Service, NRS
Bruce Cook et al.	Ecosystem structure and dynamics	ongoing	NASA
John Bradford et al.	Relationship of climate and silviculture to tree growth response	ongoing	U.S. Forest Service, NRS
Laura Kenefic et al.	Rehabilitation options for cutover mixedwood stands	ongoing	U.S. Forest Service, NRS University of Maine
Sam Droege, Jim Guldin	Native pollinators	ongoing	U.S. Geological Survey U.S. Forest Service, SRS
Walter Shortle, Jody Jellison	Biology and biochemistry of wood decay	ongoing	U.S. Forest Service, NRS University of Maine

SIXTY YEARS OF RESEARCH, 60 YEARS OF DATA: LONG-TERM U.S. FOREST SERVICE DATA MANAGEMENT ON THE PENOBSCOT EXPERIMENTAL FOREST

Matthew B. Russell, Spencer R. Meyer, John C. Brissette, and Laura S. Kenefic

Abstract.—The U.S. Department of Agriculture, Forest Service silvicultural experiment on the Penobscot Experimental Forest (PEF) in Maine represents 60 years of research in the northern conifer and mixedwood forests of the Acadian Forest Region. The objective of this data management effort, which began in 2008, was to compile, organize, and archive research data collected in the U.S. Forest Service silvicultural experiment and several auxiliary studies. Due to the hierarchical nature of these data, a relational database management system (RDMS) was used (Microsoft Office Access). The resulting data management system affords new opportunities for novel research through data mining and increased collaboration among researchers; many of the data have since been published online (Brissette et al. 2012a, 2012b). Data management efforts such as these bridge data collection and data analysis, and play an important role in preserving the integrity of long-term studies. The RDMS used in this project is contemporary and widely used, but data storage systems will continue to evolve. It is important that U.S. Forest Service data management efforts continue and that new systems are adopted as needed.

INTRODUCTION

The U.S. Department of Agriculture, Forest Service (USFS) silvicultural experiment on the Penobscot Experimental Forest (PEF) in Maine has generated 60 years of research in the northern conifer and mixedwood forests common to the Acadian Forest Region of Atlantic Canada and adjacent Maine (Braun 1950, Rowe 1972). Research began in the 1950s when the USFS initiated a study consisting of an array of silvicultural treatments applied to replicated experimental units (Sendak et al. 2003). Since then, many auxiliary studies have been implemented on the PEF, several of which are conducted by University of Maine faculty and students. Many of these studies are short-term; others include several years of measurements. These auxiliary studies were built upon the foundation of the long-term silvicultural experiment. Consequently, data from these studies are related and allow for synthesis and comprehensive analyses to address a range of intriguing questions. Adequate management of data records is an essential component of any long-term research program (Burton 2006), but is often overlooked due to limited resources and the short-term nature of most projects.

Methods and data management practices for the USFS's PEF database have evolved tremendously over these 60 years. Punch cards were used during the 1970s, but were phased out in the early 1980s when data transferred to electronic formats (e.g., computer tapes). Data were maintained for a time on the University of Maine mainframe computer system using FORTRAN programs. In the 1990s, the USFS PEF data were converted to ASCII files. These methods were appropriate for their time, though they are now outdated and inefficient.

By the early 2000s, nearly 60 years of PEF data were stored in 3,605 ASCII data files in 255 folders, and contained 374 megabytes of information. As a result of the numerous files and folders, data were not readily accessible to researchers. The USFS recognized that the size and complexity of the PEF database warranted organization in a relational database management system (RDMS).

Serving as a tool for understanding the dynamics of northern conifer forests, data management is crucial for maintaining the integrity and value of research conducted on the PEF. This report describes a project initiated in 2008 to archive research data collected in the USFS silvicultural experiment and auxiliary studies. Specific objectives were to (1) organize and compile existing data, (2) test the functionality of an RDMS for archiving these data and making them available to users, and (3) develop and document a process for new data to be appended to the database. Many of the data have subsequently been published and are available online through the USFS Research Data Archive (Brissette et al. 2012a, 2012b).

METHODS

The Relational Database

Research institutions have increasingly relied on the RDMS model to archive experiment data in a hierarchical structure. Such systems can be customized to meet the needs and design requirements of the information being stored. The RDMS appeared to be an ideal tool for an experiment like that of the USFS on the PEF for several reasons. First, the RDMS allows various types of data to be related under a single framework. As an example, one data table may describe the silvicultural treatments, while another includes information about the experimental units to which each treatment is applied. In addition, each experimental unit contains a network of permanent sample plots, each of which has spatial data. With an RDMS, plots can be related to the experimental unit, and the experimental unit can be related to the silvicultural treatment (Fig. 1). Second, through

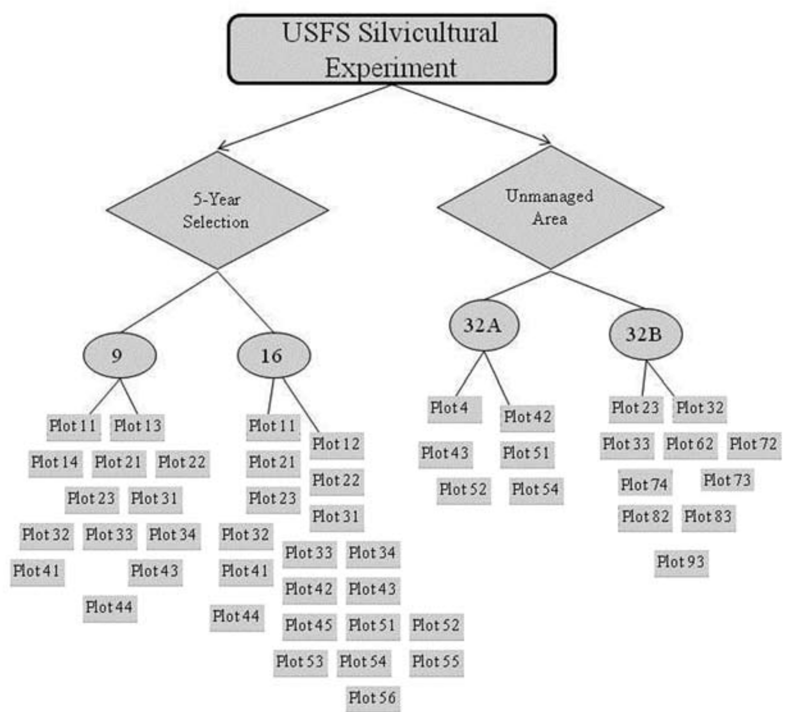


Figure 1.—Schematic displaying how U.S. Forest Service research on the Penobscot Experimental Forest fits into the structure of a relational database management system.

powerful querying capabilities, analysts can rapidly manipulate, summarize, or extract data of interest. By drawing from different tables, queries allow users to interpret data without changing the underlying data structure. Lastly, the RDMS has the ability to store large amounts of data, which reside as a single, easily replicated, and shared file on a personal computer or server. In contrast to typical spreadsheet or other "flat" data management systems, an RDMS reduces data storage capacity by extracting redundant information and making use of hierarchical relationships.

With large data sets such as the USFS's PEF experiment, data would be difficult to manage collectively as individual text files or spreadsheets. In the past, if researchers were interested in analyzing long-term data collected from a specific experimental unit, dozens of files from various inventories would first need to be compiled. Additional files that explained changing data collection methods and other associated metadata would similarly need to be compiled in order to interpret the data. This process of assembling data represented a cumbersome and time-consuming process for the analyst, and increased the probability of making errors. In addition, RDMS software is configured to work well with external software packages such as those used for statistical analyses by including fully featured input and output. RDMS software and database connection tools are available to work well with other operating systems such as Linux/UNIX and Apple operating systems (e.g., see R Development Core Team 2010).

Compiling and Archiving 60 Years of Information

Data collected on the PEF as part of the long-term USFS silvicultural experiment through the 2006 field season were used to develop the base structure and organization of the database. Data were aggregated into groups according to the type of study. Groups were organized according to the kinds of treatments applied in the experiment and the types of data collected. Data that were part of the long-term USFS experiment were classified in one group while auxiliary studies were grouped in another. Datasets were normalized when possible, meaning that data were arranged and restructured to meet the assumptions of conventional relational database design, thus reducing redundant storage of information. Management of data followed general guidelines established for ecological studies (Borer et al. 2009). Data were archived in a Microsoft Office Access database. Non-proprietary ASCII files of these data were also archived.

U.S. Forest Service Long-term Silvicultural Study

Data records for the long-term USFS experiment on the PEF were previously stored solely in ASCII files. One file existed for overstory tree data collected in each experimental unit (called a management unit, or MU) at each inventory. Tree species, diameter, and status were universally recorded in these files. Given that the same variables were collected in all inventories, these data were first grouped by management unit. For example, data from the 22 inventories that had occurred in MU 9 were previously stored in 22 separate files with related information. These were consolidated into one unified table in the database. After the files for each MU were aggregated, data were collapsed even further into a single table that contained all tree data collected on all MUs at all inventories. Tree regeneration data were organized in a similar manner as the overstory tree data.

Each MU contains an average of 15 permanent sample plots, totaling more than 600 plots in the USFS experiment on the PEF. These plots differed in terms of the inventory design used and the level of measurement detail (Fig. 2). Measurement protocols differ between "compartments" (replicated MUs in the long-term experiment), "units" (nonreplicated MUs used for other research), and the "management intensity demonstrations" (MUs managed for demonstration purposes). The measurement protocols for these areas evolved during the study (Table 1).

Other files, such as those containing spatial distribution and tree height and crown data for the

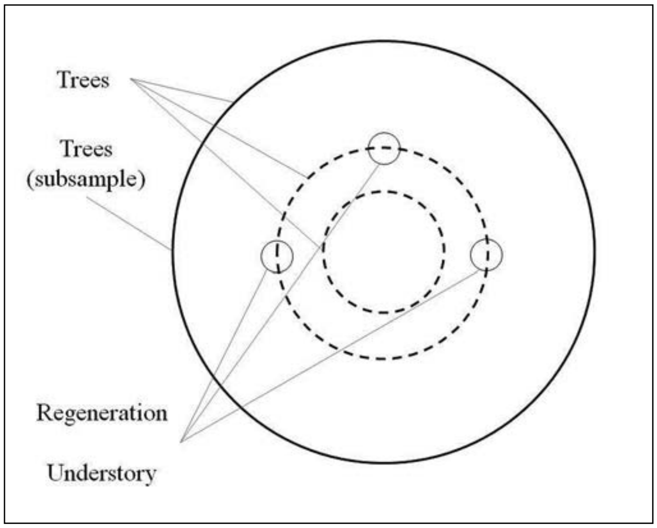


Figure 2.—U.S. Forest Service permanent sample plot schematic displaying 1/5th-, 1/20th-, 1/50th-, and 1/1000th-acre nested plots and the types of data associated with each as archived in the USFS's Penobscot Experimental Forest database (key information archived in these tables is described in Table 2).

compartments resided in separate Microsoft Office Excel spreadsheets. Similar to the tree data, these data existed in separate files for each MU. Given that identical variables were measured across the MUs, files of these types could be merged. Altogether, several key data tables were archived, and serve as the basis of the USFS silvicultural experiment on the PEF (Table 2).

Much of the supplementary information for the silvicultural experiment was obtained from scanned historical documents. Descriptions of silvicultural treatments, information on plot sizes, and tree species codes are examples of information obtained this way.

After data through the 2006 field season were compiled and archived in Access, field data collected in 2007 and subsequent years were used to test the functionality of the database in terms of checking and appending subsequent remeasurement data.

Auxiliary Studies

A wealth of information existed in the USFS archives concerning auxiliary studies, i.e., those expanding upon the foundation of the long-term experiment but not directly a part of it. For example, complete metadata and tree-level data from a precommercial

Table 1.—Overview of general historical data collection methods for trees in compartments, units, and the management intensity demonstration areas (MIDs) in the U.S. Forest Service's long-term silvicultural study on the Penobscot Experimental Forest (1950-2010)

	Plot size (ac)		Minimum diameter at breast height measured (in)	
	Before 2000	2000 and after	Before 2000	2000 and after
Compartments	1/5, 1/20	1/5, 1/20, 1/50	0.5	0.5
Units	1/5, 1/20	1/5	1-in class	5-in class
MIDs	varied	1/5, 1/20, 1/50	0.5 or 1.0	0.5

Table 2.—Key data tables for the U.S. Forest Service's long-term silvicultural experiment, as archived in the Penobscot Experimental Forest Microsoft Office Access database (local-use only)

Data table	Key information
Management units	MU ID, silvicultural treatment, acreage, status
Plots	MU ID, plot ID, spatial coordinates, depth to water table
Trees	MU ID, plot ID, tree ID, species, diameter at breast height, status
Trees (subsample)	MU ID, plot ID, tree ID, height, height to crown, crown width, spatial location
Regeneration	plot ID, species, count of stems by height class
Understory	plot ID, ground cover class percentages

thinning study (Brissette et al. 1999) were archived and well documented, as were data from a study of tree age. Some studies had limited data or metadata (e.g., for a study of growth efficiency on Study 58 plots and a logging technology study in MUs 2A and 2B). Auxiliary data that were well documented were imported directly into the database.

Additional data from other auxiliary studies were obtained from individual researchers. Examples included studies of tree leaf area (Kenefic and Seymour 1999, Maguire et al. 1998) and additional tree size measurement data sets (Saunders and Wagner 2008) (Table 3). Many of these data sets were archived following the overall database design used for the long-term silvicultural experiment; data manipulation was minor and done only to ensure consistency across all data tables archived within the database.

Table 3.—Data sets for completed and ongoing studies included in the U.S. Forest Service's Penobscot Experimental Forest local-use Microsoft Office Access database at the time of the 60th anniversary in 2010. Data from USFS and S58 have since been published online (Brissette et al. 2012a, 2012b).

ID	Experiment name
USFS	Silvicultural Experiment
REGEN	Regeneration Study
BRYCE	Understory Vegetation and Cover
CORE	Tree Core Analysis
MOORE	Light/Seedling Experiment (Spruce, Fir, Hemlock)
SAUND	Tree Measurements
WEAV	Seedling/Downed Woody Debris Study
S58	Study 58
PHLPS	Study 58 Stem Analysis Measurements
REHAB	Rehabilitation Study
LEAP	Land Use Effects on Amphibian Populations[a]
KZELL	White Pine Study
GAP	Expanding Gap Silvicultural Study[a]
CZELL	White Pine Study
CTRN	Maine Commercial Thinning Research Network[a]
WPINE	White Pine Quality under Varying Silviculture
LKFOL	Leaf Area of Eastern Hemlock
DMFOL	Growth Efficiency of Red Spruce
WEATH	PEF Weather Data/Weather Station
DAMAG	PEF Harvest Damage Survey
2020	Agenda 2020 Vegetation Competition Study[a]

[a] Study overview only

RESULTS

At the time of the PEF's 60th anniversary in 2010, the USFS PEF data were archived and resided as a fully integrated Microsoft Office Access database of 80 megabytes in size. An additional 120 megabytes of supplementary information was linked to this database. This information included references to external files, such as maps (including maps of management units, plots, and soils) and key publications of PEF research. This database is for local use by researchers on the PEF; Russell and Meyer (2009)[1] serves as a guide for researchers using the database and details procedures for documenting future data. Many of the data have since been published and are publicly available via the Web (Brissette et al. 2012a, 2012b). The local-use database laid the groundwork for a smooth, timely transition between the multitude of ASCII files and full online access. It is a valuable resource for researchers and staff on the PEF, and allows management of data prior to publication. Those seeking to obtain data from this database should follow the appropriate procedures for acquiring data through the Northern Research Station.

Twenty tables were initially archived within the local-use database. These tables included data collected as part of the silvicultural experiment, as well as auxiliary datasets (Table 3). In 2009, the "trees" data table contained more than 900,000 records with information on the species, diameter, and status of trees measured on permanent sample plots since the early 1950s.

Several reference tables were included in the database to aid in interpreting and analyzing data. Examples of these tables include comprehensive tables of species codes used for all the experiments, coefficients for estimating tree volume (Honer 1967), and a list of all inventory and harvest dates for the MUs.

[1] Russell, M.B.; Meyer, S.R. 2009. Penobscot Experimental Forest: a guide for data management and the Microsoft Access database. 61 p. Internal report available by request from M.B. Russell, University of Minnesota, College of Food, Agricultural and Natural Resource Sciences, Department of Forest Resources, 1530 Cleveland Ave. N., St. Paul, MN 55108.

Relationships were identified to associate data types in one table to similar types of data in another (Fig. 3). This step had important implications for using the database for querying tables and interpreting data. These data relationships form the backbone of the RDMS and allow the powerful query language to summarize similar data.

Action queries proved to be an effective and efficient tool for the database in several ways. Data collected after 2006, for example, were appended to existing data tables through action querying to take advantage of the structure of the database. In addition, several queries were designed to summarize stand-level statistics by using the underlying trees data table. These statistics included total and species-specific number of trees, basal area, and volume per acre for each of the inventories in the silvicultural experiment, as well as diameter distributions.

DISCUSSION

The RDMS proved to be an effective tool for archiving and managing 60 years of research data collected in the USFS long-term experiment on the PEF. The RDMS structure allows data in one table to be associated with data in another, and is an ideal instrument for archiving forest inventory information. In the example of the USFS silvicultural experiment on the PEF, the "management units" table contains a list of areas of land that are managed in the different USFS experiments on the PEF, while the "plots" table is a list of measurement plots used in each MU. The ability of the RDMS to associate data of different types in a hierarchical fashion makes it well-suited to managing long-term forest inventory data sets such as those of the PEF.

Querying functions allow users to interpret and analyze data found in the underlying data tables. By using the relationships defined among the different data tables, queries can be built that pull data from different source tables; this process allows users to summarize data sets quickly and repeatedly. For example, the "trees" table in the local-use database for the long-term silvicultural experiment can be queried to compute stand-level basal area, volume, and tree

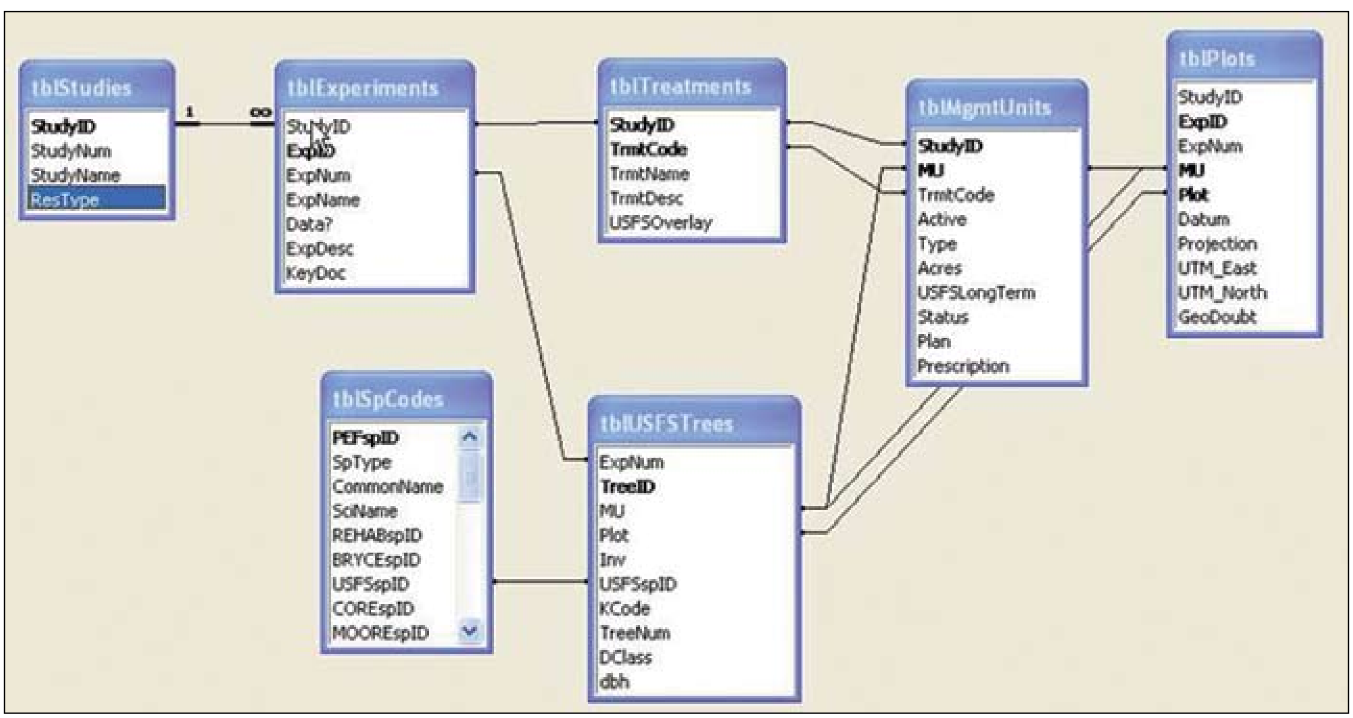


Figure 3.—Relationships window displaying associations of data tables within the U.S. Forest Service's Penobscot Experimental Forest local-use database.

diameter distributions across MUs, years, treatments, or other parameters. Users can readily graph stand development patterns throughout the duration of the study. A researcher may wish to routinely analyze trends in basal area among the differing selection system stands (Fig. 4). Once the analyst designs a query, it is instantaneously updated as new data are included in the database. This feature greatly facilitates analyses that are conducted annually.

Storing data in non-proprietary formats is an effective data management practice (Borer et al. 2009) and was accomplished as part of these efforts. Whereas Microsoft Office Access is proprietary software that (1) is subject to continuous updates, (2) could potentially become unavailable in the future, and (3) could be replaced by other newer and improved types of software, ASCII, or text files, can always be read. Similarly, analysis scripts have been maintained that

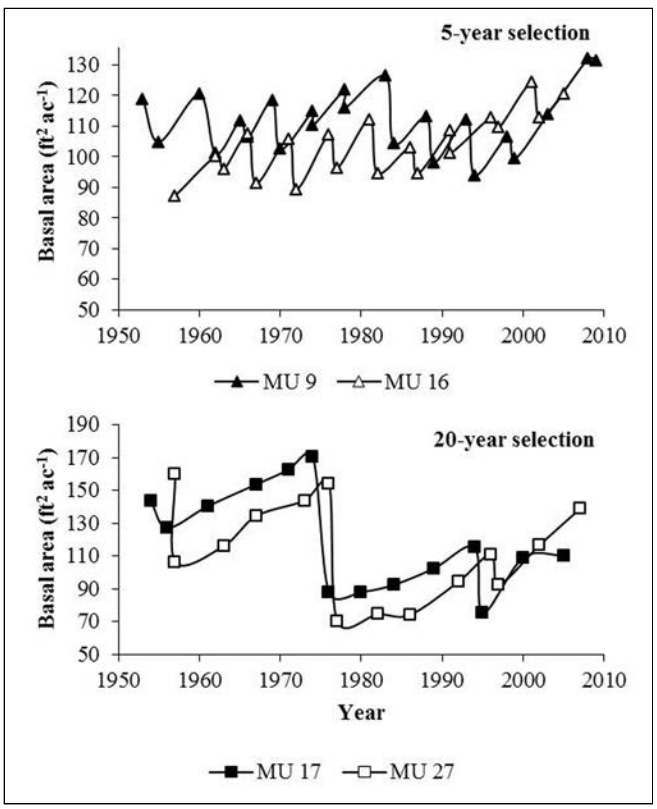


Figure 4.—Trends in basal area per acre (trees ≥0.5 in diameter at breast height) for management units treated with the selection system on 5- and 20-year cutting cycles, as archived in the U.S. Forest Service's Penobscot Experimental Forest database.

allow a user to import USFS PEF data into statistical packages such as R (R Development Core Team 2010), MATLAB® (MathWorks, Inc., Natick, MA), and SAS (SAS Institute, Inc., Cary, NC). To preserve the relationships between different data tables in the RDMS, structured query language (SQL) scripts have been maintained of essential queries for importing data into other database systems, such as MySQL or PostgreSQL. Although currently the data are primarily managed within the Access RDMS, connectivity with other operating systems is offered. The open-source R statistical package is recommended for users seeking to use these coded scripts because of its compatibility with multiple operating systems and well-developed database connectivity packages (R Development Core Team 2010). Online USFS PEF data are in an Oracle® database; both raw data and summary statistics can be downloaded.

The ability to append data has tremendous value to the USFS long-term experiment. Data that are cohesively managed with a consistent structure provide a data format that can be easily maintained. For new data types and data from auxiliary experiments, new data tables can be created and incorporated into the existing database structure.

Opportunities

As an artifact of today's technological age, computer technologies change and data management software continually evolves. Employing contemporary software used by scientists and managers is central to the research integrity of the USFS's PEF data sets. In future years, the design and structure of the database should be evaluated to determine whether or not it is effectively meeting users' needs. Similarly, new avenues of research and data management have arisen for the USFS's PEF database. First, there are opportunities for spatially explicit data summary and analysis. Spatial technologies and geographic information systems software are now widely used, and technologies for bridging observed tree data with spatial data sets are available. Second, the database adds value to the long-term experiment by providing a unified data set that can be readily used by researchers for forest growth and yield modeling, threat assessment, and other associated areas. Finally, opportunities for collaborations with new researchers have been established through Web-based PEF data-sharing sites (e.g., http://www.fs.usda.gov/rds/archive/Product/RDS-2012-0008 and http://www.fs.usda.gov/rds/archive/Product/RDS-2012-0009). Such sites showcase the USFS's data from the PEF and increase the real and perceived value of the experiments.

CONCLUSIONS

Sixty years of research data from USFS experiments on the PEF have been compiled, archived, and made available to researchers. The relational database model proved effective given the design of the long-term silvicultural experiment and associated auxiliary studies. New opportunities and collaborations continue to arise as a result of these data management efforts.

LITERATURE CITED

Borer, E.T.; Seabloom, E.W.; Jones, E.B.; Schildhauer, M. 2009. **Some simple guidelines for effective data management.** Bulletin of the Ecological Society of America. 90(2): 205-214.

Braun, E.L. 1950. **Deciduous forests of eastern North America.** New York: Hafner. 596 p.

Brissette, J.C.; Frank, R.M.; Stone, T.L.; Skratt, T. 1999. **Precommercial thinning results in a northern conifer stand: 18-year results.** The Forestry Chronicle. 75(6): 967-972.

Brissette, J.C.; Kenefic, L.S.; Russell, M.B. 2012a. **Precommercial thinning x fertilization study data from the Penobscot Experimental Forest.** Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0009. (Accessed June 17, 2013).

Brissette, J.C.; Kenefic, L.S.; Russell, M.B.; Puhlick, J.J. 2012b. **Overstory tree and regeneration data from the "Silvicultural Effects on Composition, Structure, and Growth" study at Penobscot Experimental Forest.** Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. Available at http://dx.doi.org/10.2737/RDS-2012-0008. (Accessed June 17, 2013).

Burton, P.J. 2006. **The need for long-term research installations and datasets.** In: Irland, L.C.; Camp, A.E.; Brissette, J.C.; Donohew, Z.R., eds. Long-term silvicultural and ecological studies: results for science and management. GISF Res. Pap. 005. New Haven, CT: Yale University: 136-138.

Honer, T.G. 1967. **Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada.** Ottawa, ON: Canadian Department of Forestry and Rural Development, Forest Management Research and Services Institute. Info. Rep. FMR-X-5.

Kenefic, L.S.; Seymour, R.S. 1999. **Leaf area prediction models for *Tsuga canadensis* in Maine.** Canadian Journal of Forest Research. 29: 1574-1582.

Maguire, D.A.; Brissette, J.C.; Gu, L. 1998. **Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine.** Canadian Journal of Forest Research. 28: 1233-1240.

R Development Core Team. 2010. **R data import/export.** Vienna, Austria: R Foundation for Statistical Computing. Available at http://cran.r-project.org/doc/manuals/R-data.html. (Accessed October 25, 2010).

Rowe, J.S. 1972. **Forest regions of Canada.** Publ. 1300. Ottawa, ON: Canadian Forest Service, Department of the Environment. 172 p.

Saunders, M.R.; Wagner, R.G. 2008. **Height-diameter models with random coefficients and site variables for tree species of Central Maine.** Annals of Forest Science. 65(2): 1-10.

Sendak, P.E.; Brissette, J.C.; Frank, R.M. 2003. **Silviculture affects composition, growth, and, yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** Canadian Journal of Forest Research. 33(11): 2116-2128.

THE ACADIAN FOREST ECOSYSTEM RESEARCH PROGRAM: AN EXAMPLE OF NATURAL DISTURBANCE-BASED SILVICULTURE IN THE NORTHEAST

Mike R. Saunders, Robert S. Seymour, and Robert G. Wagner

Abstract.—The Acadian Forest Ecosystem Research Program (AFERP) began in 1994 as one of the nation's first trials of natural disturbance-based silviculture. The study tests the ecological impacts of two versions of expanding-gap silvicultural systems that are designed to emulate the spatial extent and frequency of natural disturbances in northeastern North America. The AFERP is now well into its second decade of monitoring. Inventory systems for overstory trees, saplings, herbaceous plants, tree regeneration, coarse woody debris, forest floor depth, and canopy light interception are described in this paper.

INTRODUCTION

Over the past 20 years, there has been a strong shift away from production-oriented management on public lands in the United States and Canada towards silvicultural practices guided by principles of disturbance ecology to increase ecosystem resilience and conserve biodiversity (Long 2009, Seymour et al. 2006). Inherently, these new practices are conceptually and practically much more complex, often requiring extensive dendrochronological reconstructions of stand and landscape age structures to effectively emulate natural disturbance patterns for forest types in each region (D'Amato and Orwig 2008, North and Keeton 2008). However, both voluntary and regulated implementation of these systems has proceeded even without extensive research on economic or ecological sustainability of the practices (Gamborg and Larsen 2003, Long 2009). Earlier experiments by the U.S. Department of Agriculture, Forest Service and Canadian Forest Service were limited in focus, treatment types, or experimental design, and did not fully inform policy makers of repercussions of the shift in emphasis (Seymour et al. 2006).

The resulting paucity of pertinent research spawned numerous innovative large-scale management experiments by the U.S. and Canadian Forest Services, universities, and other organizations starting in the early 1990s (Puettmann 2005, Seymour et al. 2006). In northeastern North America, there are two notable experiments: the Vermont Forest Ecosystem Management Demonstration Project (FEMDP) (Keeton 2006, North and Keeton 2008) and the Acadian Forest Ecosystem Research Program (AFERP) (Saunders and Wagner 2005, Seymour et al. 2006). These stand-level experiments use silvicultural systems that are designed to emulate wind disturbance, senescence, and other tree- to gap-level disturbances that historically affected 1-5 percent yr^{-1} of forest lands throughout the region (D'Amato and Orwig 2008, Lorimer and White 2003, Runkle 1982, Seymour et al. 2002).

The AFERP is the older experiment of the two with initial harvests occurring during winter 1995-96. Rather than using size-based structural control (e.g., a diameter distribution), the AFERP uses area control; all harvests are located within expanding gaps that are based loosely on the German "Femelschlag" system (Troup 1928). These treatments lead to distinctly irregular age and size structures, and may serve as a technique in a wide array of forest types to convert single-cohort stands to multi-aged stands more capable of sustaining selection-based forestry. Specifically, the

AFERP has three primary goals (Saunders and Wagner 2005): (1) develop alternative silvicultural techniques and systems based on regional disturbance ecology, (2) evaluate ecosystem-scale influences of forest management practices, and (3) enhance understanding about forest ecosystems in the Acadian ecoregion.

Saunders and Wagner (2005) reported on results from the first 10 years of the AFERP, giving a very brief overview of the experimental design and inventory systems of the study. Since that publication, the experimental gaps within the AFERP have been expanded. Planning for these harvests revealed that one of the treatments was conceptually flawed and would not test the expanding gap concept. Changes were made to the treatment design to rectify this oversight. Further, several modifications to inventory systems have been made to make each more efficient. This paper documents those changes in detail.

METHODS

Study Area

The AFERP study is located on nine 9.4- to 11.3-ha sites within the Penobscot Experimental Forest (PEF) (see Kenefic and Brissette's "History" [this volume] for a description of the PEF). Although much of the PEF was originally heavily dominated by conifers, these sites have had a significant hardwood component for at least the past 50 years[1] and are generally of higher quality. Tree species with average, pretreatment basal areas greater than 1 m^2 ha^{-1} include (in decreasing order of dominance): eastern hemlock (*Tsuga canadensis* [L.] Carr.), red maple (*Acer rubrum* L.), eastern white pine (*Pinus strobus* L.), balsam fir (*Abies balsamea* [L.] Mill), northern white-cedar (*Thuja occidentalis* L.), paper birch (*Betula papyrifera* Marsh.), red spruce (*Picea rubens* Sarg.), and trembling aspen (*Populus tremuloides* Michx.). Sixteen other tree species are also present across the sites.

Topography in the AFERP sites is generally flat to rolling with slopes less than 20 percent. Soils are a fine-scaled mix of Spodosols and Histosols. Drainage is quite variable, ranging from moderately well drained to poorly drained. Based on stand growth projections, site qualities generally exceed 21 m for balsam fir (50 year base age) (Arsenault 2011).

Prior to initial harvests, sites did not differ significantly in basal area, density, or stand volume, although there were some minor compositional differences among the stands (Arsenault et al. 2011). Stand volume, basal area, and tree density averaged 283.6 m^3 ha^{-1}, 37.6 m^2 ha^{-1}, and 2,404 trees ha^{-1}, respectively (Arsenault et al. 2011).

Experimental Design

Treatments

Three treatments were implemented in three blocks using a randomized block design across the nine sites. Blocks are associated with initial harvest date, during the winter of either 1995-96, 1996-97, or 1997-98 (Table 1). Treatments were an unharvested, unmanaged experimental control and two expanding-gap silvicultural systems. Both use a common 10-year cutting cycle over a 100-year rotation.

The more intensive large-gap, or 20:10, treatment was described in detail by Saunders and Wagner (2005). Briefly, the 20:10 is an extended group shelterwood with reserves with 20 percent of the area harvested during each of the first five cutting cycles (i.e., a 10-year regeneration period) (Fig. 1). Initial gaps are approximately 0.2 ha in size. Study areas are scheduled to "rest" during the last five cutting cycles, although thinning and other intermediate treatments may occur if deemed necessary. The goal of this system is a mid-succession stand with a significant component of species that are intermediate in shade tolerance (i.e., white pine, paper birch, yellow birch [*Betula alleghaniensis* Britt.]).

[1] Seymour, R.S. [N.d.] FES 536: Forest stand dynamics (class files). On file with R.S. Seymour, University of Maine, School of Forest Resources, 5755 Nutting Hall, Orono, ME 04469-5755.

Table 1.—Schedule of completed AFERP measurements and harvests, 1995-2010, by year and block number. With a few exceptions as noted, inventories were completed by replicate block defined as follows: Block 1 = research areas 1-3, Block 2 = research areas 4-6, and Block 3 = research areas 7-9. Planned intervals between inventories for a block are also given.

	Inventory						
Year	Overstory & saplings	Coarse woody debris	Seedlings & herb. plants	Forest floor	Canopy light interception	Retention trees*	Harvest (winter)
1995	1,2	1,2§	1,2	1	1,2	1	
1996		2§		2			1
1997	3	3	3	3	3	2	2
1998		1	1		1	1,3	3
1999		2	2		2		
2000	1,3†	3	3		3	1	
2001	2					2	
2002	3					3	
2003							
2004							
2005	1	1	1			1	
2006	2	2	2			2	1
2007	3	3	3			3	2
2008							3
2009							
2010	1,2‡						
Planned Interval (yr)	5	10	5	20	5	5	

* Before 2005, retention trees were only measured in 20:10 replicates.
§ Inventory started in 1995, but only the control replicate was finished. Inventory on other replicates was completed in 1996.
† Inventory only included 20:10 replicate in block 3.
‡ Inventory only included 20:10 and control replicates in block 2.

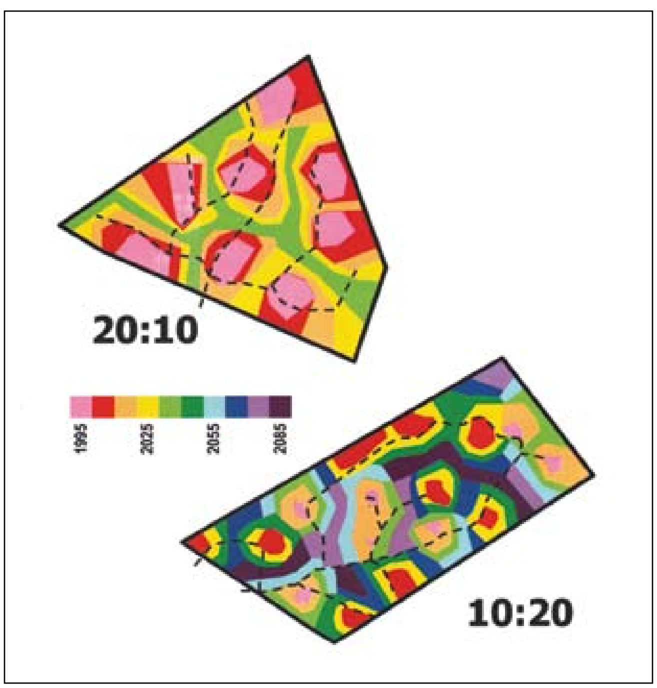


Figure 1.—Conceptual gap expansion diagrams for the two harvest treatments in the AFERP, color coordinated by year of entry. Initial entries into the 20:10 treatment (above) are in light red and expansion proceeds outward to the multi-colored strips. Initial entries into the 10:20 treatment (below) are the light and dark red areas, in 1995 and 2005, respectively. Successive expansions of these initial gaps occur every 20 years, alternating by gap cohort (i.e., 1995 gaps or 2005 gaps). In both treatments, gaps are coalesced to avoid narrow strips and patches that could be inoperable in a future cycle. Expansions release regeneration whenever possible and use natural or anthropogenic breaks in a stand (i.e., streams, wet areas, skid trails) to define their boundary. Skid trails are shown as black dashed lines.

The small-gap, or 10:20, treatment was refined during the 2005-2007 harvests to better reflect the original intent of the project. The 10:20 is an "expanding" group selection with 10 percent of the area harvested each cycle (Fig. 1). Initial gaps average 0.1 ha in size, and are expanded on alternative cutting cycles (i.e., a 20-year regeneration period); therefore two "cohorts" of gaps exist in each study area. This system encourages regeneration of shade-tolerant species, namely eastern hemlock, red spruce, sugar maple (*Acer saccharum* Marsh.), and balsam fir, and should accelerate the study area to a late-successional status.

Gap retention targets

Both systems use a permanent retention target of 10 percent of the experiment-wide, pretreatment basal area, or roughly 3.75 m^2 ha^{-1}. During gap creation and expansion, there are two possible retention scenarios depending on the amount of regeneration present (Fig. 2). If the gap or expansion has a sufficient stocking of large (at or above breast height or 1.37 m) and well-distributed seedlings and saplings—indicative of the understory reinitiation stage of stand development (Oliver and Larson 1996)—the gap or expansion is treated with a one-stage removal of the overstory (Fig. 2, top row), thereby lowering the residual basal area to the permanent 10 percent target. If the gap or expansion has an insufficient amount of regeneration (i.e., "nonregenerated"), the overstory removal will proceed in two stages to provide seed source and adequate shade for regeneration development (Fig. 2, bottom row). Initially, basal area will be reduced to a target of 30 percent, or 11.25 m^2 ha^{-1}. In the following gap expansion, 10 or 20 years for the 20:10 and 10:20 treatments, respectively, the basal area is then reduced to the final 10 percent target.

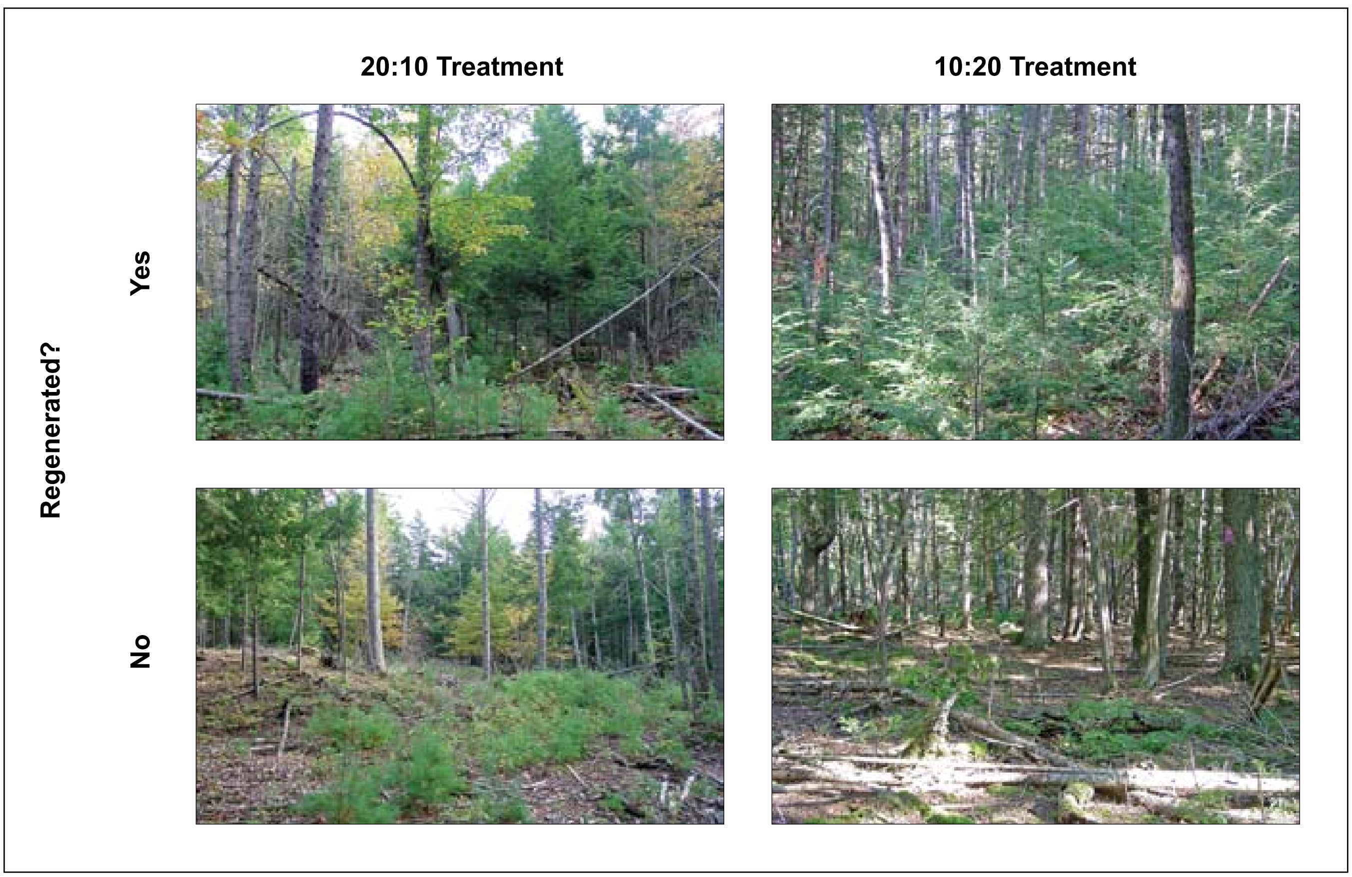


Figure 2.—Examples of regenerated gaps (top) and nonregenerated gaps (bottom) for both the 20:10 treatment (left) and 10:20 treatment (right). The 20:10 pictures are taken 10 years post-harvest; the 10:20 pictures were taken preharvest. Photos courtesy of Mike Saunders, Purdue University.

Retention targets are meant to act as a flexible guide. Retention in individual openings may vary among replicates, but on average will be approximately 10 percent and 30 percent for regenerated and nonregenerated areas, respectively.

Special areas

Within several of the replicates, there are temporary and perennial streams, vernal pools, seeps, and other wetland features. These features are protected by a "special area" designation that extends 10 m away from the resource. Harvesting these areas is included within the 10 or 20 percent area control for a treated replicate, but retention guidelines are much higher, 60 percent of pretreatment basal area or 22.50 m^2 ha^{-1}. Further, for special areas protecting a stream, both sides of the stream cannot be harvested in the same entry. Mature canopy cover is thereby kept above the stream and the need for new stream crossings is minimized.

Inventory Systems

There are several types of inventories conducted across the AFERP research areas, including overstory and sapling plots, coarse woody debris transects, seedling and herbaceous plant quadrats, forest floor sampling, canopy light interception readings, retention tree measurements, and a census of harvested stems. Most inventories are spatially linked to a 50 m by 50 m grid that overlays each research area (Fig. 3a). All inventories had preharvest measurements in 1995-97, with most post-harvest measurements in 1998-2002 (Table 1). Planned resampling cycles are from 5-20 years, depending on inventory (Table 1). Data from nearly all inventories are contained within a geo-referenced database maintained by the School of Forest Resources and at the University of Maine.

Overstory and saplings

The purpose of this inventory is to monitor the growth and structural development in each of the replicates. Overstory and sapling plots are installed on 20 randomly selected grid points. Overstory trees are defined as woody vegetation ≥9.5 cm in diameter at breast height (d.b.h.) and measured on circular 0.05-ha plots. Saplings are defined as woody vegetation between 1.5 and 9.5 cm d.b.h. and measured on circular, nested 0.01-ha subplots (Fig. 3c). All overstory trees and saplings are spatially located within these plots and permanently tagged. Species, d.b.h., tree condition (e.g., live, dead, cull, broken top), canopy stratum, and light field (*sensu* Bechtold 2003) are recorded for both trees and saplings. For saplings, origin (i.e., seedling on mineral soil or forest floor, seedling on nurse log, or stump sprout), and overhead character (i.e., beneath contiguous overstory or within canopy gap) are also recorded.

Coarse woody debris

The purpose of this inventory is to monitor the biomass, volume, and spatial distribution of coarse woody debris by type and decay class within each replicate. Because individual pieces are tracked, decay rates and transitions between types may be estimated as well. In 2005, this inventory replaced a more costly and less efficient area-based sampling design; see Fraver et al. (2002) for a description of the prior system.

Coarse woody debris is defined within the AFERP as all standing snags and down wood >4.5 cm in diameter. Both snags and down wood are surveyed on 50-m or 100-m transects randomly oriented upon nearly every grid point in each research area (Fig. 3a). Transects are centered on the grid point and allowed to intersect one another. Transects that would otherwise extend beyond research area boundaries are either terminated or reflected back into the research area. Between 2,398 and 3,516 m of transects are installed per research area.

Transects are considered nested because coarse woody debris is measured in different size classes at different points along the transect (Fig. 3b). For 100-m transects, both snags and down wood ≥4.5-cm in diameter are sampled from 0-5 m, 45-55 m, and 95-100 m along the transect. Everywhere

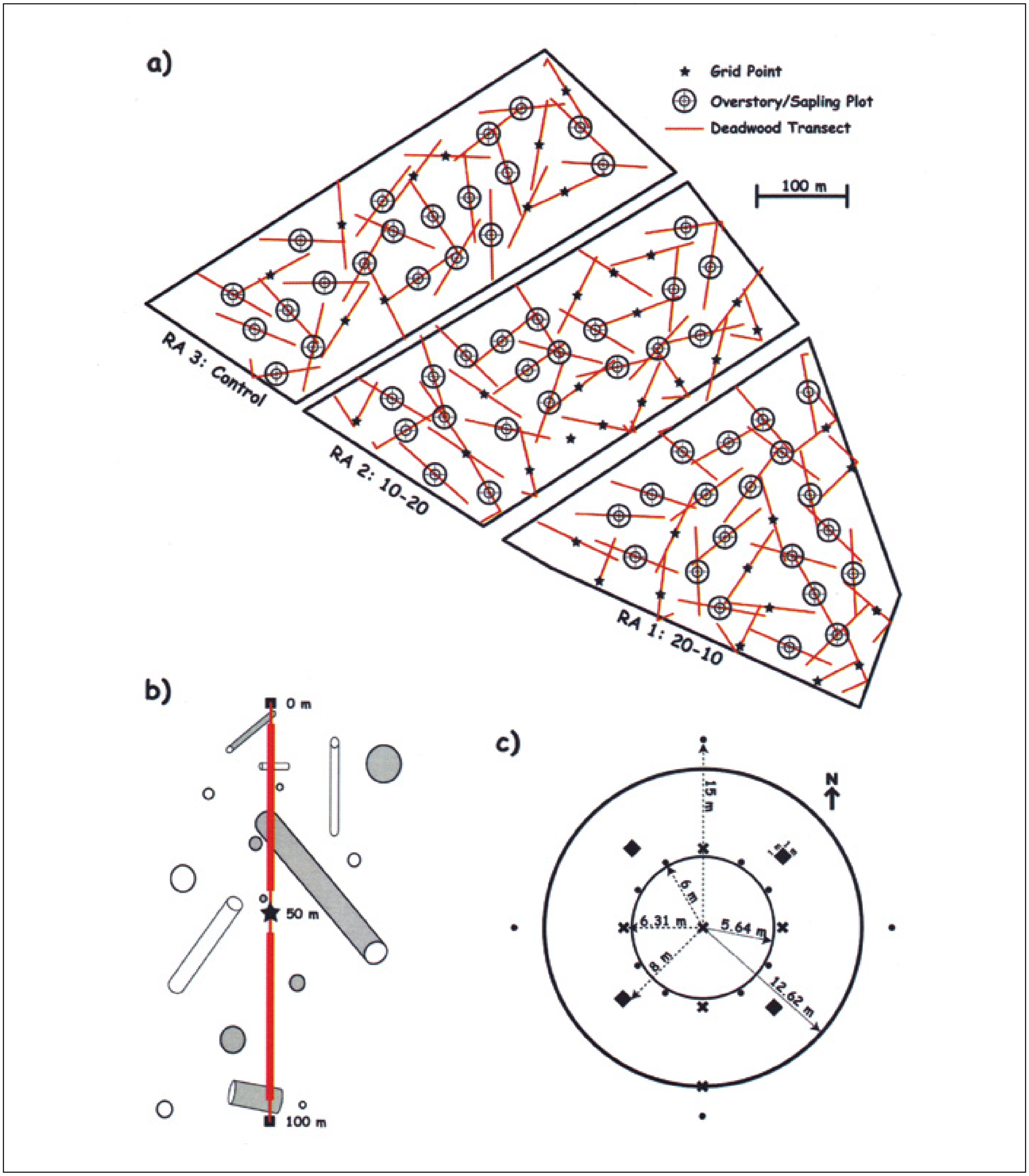


Figure 3.—Overview of the inventory systems for the AFERP. (a) Spatial layout of overstory plots and deadwood transects across the network of gridpoints in the first replicate block. (b) Schematic drawing of a 100-m-long nested, deadwood transect showing zones where sampling includes material ≥9.5 cm (thick red lines) and ≥4.5 cm (thin red lines). Items sampled include all down woody items crossing the transect line that are ≥0.3 m in length (gray cylinders) and standing snags that are measured "in" using a 4-m BAF variable radius prism centered on the transect perpendicular to the snag (gray circles). (c) Schematic drawing to scale of an 0.05-ha overstory plot, with a nested 0.01-ha sapling plot, four 1-m^2 herbaceous and seedling quadrats (black diamonds), 12 forest floor sampling points (black circles), and six canopy light interception points (X's).

else, snags and down wood must measure ≥9.5 cm in diameter. To be sampled, down wood must intersect the transect and have a diameter exceeding the size threshold. Snags are sampled when their d.b.h. exceeds the size threshold for that part of the transect, and they can be counted as "in" from a 4-m basal area factor (BAF) prism held above a point on the transect perpendicular to the snag location (i.e., at the shortest point between the snag and the transect). Down wood with a diameter greater than its length and snags shorter than breast height are not sampled.

For snags, species (if it can be determined), decay class (Cline et al. 1980), origin (i.e., windsnap, windthrow, logging), d.b.h., height, and spatial location are recorded. Attributes such as cavities and history (e.g., dead tree from overstory inventory) are also noted.

For down wood, species, decay class (Maser et al. 1979), origin, and transect intersection location are recorded. To estimate volume using line transect-based estimators (van Wagner 1968), diameter at transect intersection, diameter at large end, diameter at small end, horizontal (i.e., straight-line) length, curved length, number of pieces, and hollowness are measured. Lengths and diameters are taken only on that portion of a piece with a diameter greater than the 4.5- or 9.5-cm threshold. Finally, suspension class (i.e., proportion of length not contacting the mineral soil or duff), history, and other special features are noted.

Seedlings and herbaceous plants

The purpose of this inventory is to both monitor changes in the herbaceous plant community and quantify tree regeneration up to 1.5 cm in d.b.h. Measurements take place on four 1-m^2 quadrats systematically located within the 0.05-ha overstory plots (Fig. 3c, black diamonds).

In each quadrat, ferns, grasses, sedges, rushes, forbs, shrubs, and tree seedlings are identified to species whenever possible. Mosses and lichens are identified to genus only. In cases in which identification to species in the field is not possible, collections from outside of the quadrat are made if numerous other individuals of the species are present. For all plants, percentage cover is estimated to the nearest 0.1 percent for 0.1-5 percent cover, the nearest 1 percent for 5-10 percent cover, the nearest 5 percent for 10-25 percent cover, and the nearest 10 percent for greater than 25 percent cover. Number of stems is recorded for ferns, forbs, shrubs, and tree seedlings.

Forest floor

The purpose of this inventory is to quantify changes in forest floor organic horizons by stratum depth and mass. Forest floor depth measurements are taken at eight locations within the 0.05-ha overstory plots (Fig. 3c, inner small black circles). In addition, 15 cm by 15 cm removal subplots are taken at four locations surrounding each overstory plot (Fig. 3c, outer small black circles); organic matter layer depth is measured to the nearest 0.1 cm on each side of the removal subplot. Collected material from each subplot is oven-dried at 70 ºC for 48-72 hours and weighed to the nearest 0.01 g to determine mass. All samples are then archived for future use.

Canopy light interception

The purpose of these measurements is to estimate changes in leaf area index and gap fraction in response to treatments. Measurements are taken twice per summer, once in July and once in August, with a LiCOR LAI-2000 plant canopy analyzer (LiCOR, Inc. 1992) at six precise locations within each 0.05-ha overstory plot (Fig. 3c, X's). Readings are taken on completely overcast days or on completely cloudless days in either early morning or late afternoon hours when diffuse light conditions predominate. Canopy masks (180º) are used to block out the southern portion of the sky for all readings. After downloading, average leaf area index and gap fraction of each overstory plot are calculated using the central 43º cone (rings 1-3) (Puettmann and Reich 1995), although all mean contact frequency (CT#_) and gap fraction (GAP_) values are saved for recalculation of leaf area or gap fraction for any masking scheme.

Retention trees

The purpose of this inventory is to quantify the growth and fate of trees retained during harvest operations. This inventory is not associated with plots or a grid, focusing on individual trees instead. Further, this inventory is not fully implemented. Records exist since 1995-97 for trees that meet the 10 percent long-term target in the 20:10 treatment (n=535). Trees are being added from the 10:20 treatment areas and for meeting the 30 percent target for nonregenerated gaps. In total, 907 individuals are now being monitored.

Each monitored tree is tagged and spatially located. Species, d.b.h., tree condition, height, lowest live crown (as defined by lowest whorl), canopy stratum, and light field are recorded. Presence of cavities, foliose lichen, and other special structural features are noted.

Harvested trees

The purpose of these measurements is to quantify the volume and quality of harvested material. This is a recent addition to the monitoring protocols as these data were not collected in the initial harvests in 1995-97. Before each harvest, the species and d.b.h. of marked stems are recorded within each gap. For trees greater than 20 cm in d.b.h., merchantable height to the nearest 1.22 m (15 cm minimum inside bark diameter) and number of clear faces in the 2.59-m (including trim) butt log are recorded to approximate the quality of sawtimber and veneer being removed.

Other inventories

Several other kinds of data have been collected since the experiment began, largely for short-term studies that documented various community responses to the initial gap harvests. Nearly all these data have been spatially referenced with Universal Transverse Mercator coordinates. Results and methodology of some of these studies have been published elsewhere (Miller et al. 2007, 2008; Thomas et al. 2009) although several exist only as unpublished theses. For example, Schofield (2003) collected herbaceous vegetation and tree regeneration data in 4-m^2 quadrats placed along north-south transects bisecting 45 harvest gaps, 23 recent (i.e., <25 years) natural gaps, and 23 closed-canopy areas across the experiment. Data collected were similar to the aforementioned inventory of seedlings and herbaceous plants, but also included spatial location in the gap, overstory basal area, canopy gap fraction, and increment cores and cross-sectional disks (i.e., tree cookies) from gap edge trees to determine gap age and origin. In a study of gap harvest impacts on the amphibian community, Strojny (2004) measured volume, decay class, and abundance of down wood ≥10 cm within 17 harvest gaps, 19 natural gaps, and 6 closed-canopy areas using 10-m line transects. Lastly, Olson (2009) superimposed 4-m^2 vegetation quadrats in a repeating pattern, cyclical sampling design (sensu Scheller and Mladenoff 2002) upon the coarse woody debris transects to investigate the spatial pattern of both herbaceous communities and tree regeneration in response to overstory basal area and canopy gap fraction.

Two other data sources are of note. For several of the research areas, stand histories have been reconstructed based on dendrochronological analysis of increment cores collected from trees in the overstory inventory.[2] Cores have been archived for future use. Second, airborne light detection and ranging data have been collected for five of the nine sites at a first return point density of >5 on a 1 m by 1 m grid. Raw and post-processed data are available from the lead author.

DISCUSSION

Puettmann et al. (2009) suggested that forests must be managed as complex adaptive systems in which silviculturists must produce forests with heterogeneous structures, composition, and functions in order to be resilient to changing biotic and abiotic conditions. Silvicultural research, they argued, thus must be designed to investigate aspects of scale and scaling

[2] Seymour, R.S. [N.d.] FES 536: Forest stand dynamics (class files). On file with R.S. Seymour, University of Maine, School of Forest Resources, 5755 Nutting Hall, Orono, ME 04469-5755.

to quantify nonlinear thresholds, local feedbacks, and other emergent properties (Puettmann et al. 2009).

The AFERP is a model example of this approach to forestry management and research. The AFERP uses silvicultural systems that can create quite heterogeneous stand structures and can be adapted to local conditions. Although inventory systems were initially designed to experimentally compare treatments with analysis of variance techniques (Seymour et al. 2006), redesigns over the past 5 years were done to explicitly investigate spatial patterns over multiple scales (e.g., Olson 2009). Retention tree inventories, for example, can be used to investigate tree growth in response to neighborhood competition; kriging can be used on the deadwood data to estimate relative salamander abundance.

Although the basic monitoring remains focused on vegetation, the AFERP continues to invite researchers interested in other biotic communities. This experiment, along with its more traditional PEF counterpart, the U.S. Forest Service Compartment Study (Brissette and Kenefic, this volume), will continue to be invaluable to both managers and researchers for years to come.

LITERATURE CITED

Arsenault, J.A. 2011. **Modeling gap-based silviculture systems with spatially independent growth models.** West Lafayette, IN: Purdue University, Department of Forestry and Natural Resources. 144 p. M.S. thesis.

Arsenault, J.A.; Saunders, M.R.; Seymour, R.S.; Wagner, R.G. 2011. **First decadal response to treatment in a disturbance-based silviculture experiment in Maine.** Forest Ecology and Management. 262: 404-412.

Bechtold, W.A. 2003. **Crown position and light exposure classification—an alternative to field-assigned crown class.** Northern Journal of Applied Forestry. 20: 154-160.

Cline, S.P.; Berg, A.B.; Wight, H.M. 1980. **Snag characteristics and dynamics in Douglas-fir forests, western Oregon.** Journal of Wildlife Management. 44: 773-786.

D'Amato, A.W.; Orwig, D.A. 2008. **Stand and landscape-level disturbance dynamics in old-growth forests in western Massachusetts.** Ecological Monographs. 78: 507-522.

Fraver, S.; Wagner, R.G.; Day, M. 2002. **Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A.** Canadian Journal of Forest Research. 32: 2094-2105.

Gamborg, C.; Larsen, J.B. 2003. **'Back to nature' - A sustainable future for forestry?** Forest Ecology and Management. 179: 559-571.

Keeton, W.S. 2006. **Managing for late-successional/ old-growth characteristics in northern hardwood-conifer forests.** Forest Ecology and Management. 235: 129-142.

LiCOR, Inc. 1992. **LAI-2000 plant canopy analyzer: operating manual.** Lincoln, NE.

Long, J.N. 2009. **Emulating natural disturbance regimes as a basis for forest management: a North American view.** Forest Ecology and Management. 257: 1868-1873.

Lorimer, C.G.; White, A.S. 2003. **Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions.** Forest Ecology and Management. 185: 41-64.

Maser, C.M.; Anderson, R.G.; Cormack, K., Jr.; Williams, J.T.; Martin, R.E. 1979. **Dead and down woody material.** In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handbk. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 78-95.

Miller, K.M.; Wagner, R.G.; Woods, S.A. 2007. **Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine.** Canadian Journal of Forest Research. 37: 2175-2187.

Miller, K.M.; Wagner, R.G.; Woods, S.A. 2008. **Arboreal arthropod associations with epiphytes following gap harvesting in the Acadian forest of Maine.** The Bryologist. 111(3): 424-434.

North, M.P.; Keeton, W.S. 2008. **Emulating natural disturbance regimes: an emerging approach for sustainable forest management.** In: Lafortezza, R.; Chen, J.; Sanesi, G.; Crow, Th.R., eds. Patterns and processes in forest landscapes. New York: Springer, Inc.: 341-372.

Oliver, C.D.; Larson, B.C. 1996. **Forest stand dynamics.** Update edition. New York: John Wiley & Sons, Inc. 520 p.

Olson, M.G. 2009. **Spatial and temporal patterns of tree regeneration in the Acadian Forest of central Maine.** Orono, ME: University of Maine, School of Forest Resources. 120 p. Ph.D. dissertation.

Puettmann, K.J. 2005. **Do innovative experiments lead to innovative silvicultural systems?** In: Peterson, C.E.; Maguire, D.A., eds. Balancing ecosystem values: innovative experiments for sustainable forestry. Gen. Tech. Rep. PNW-625. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 49-53.

Puettmann, K.J.; Reich, P.G. 1995. **The differential sensitivity of red pine and quaking aspen to competition.** Canadian Journal of Forest Research. 25: 2172-2183.

Puettmann, K.J.; Coates, K.D.; Messier, C. 2009. **A critique of silviculture: managing for complexity.** Washington, DC: Island Press. 188 p.

Runkle, J.R. 1982. **Patterns of disturbance in some old-growth mesic forests of eastern North America.** Ecology. 63: 1533-1546.

Saunders, M.R.; Wagner, R.G. 2005. **Ten-year results of the Forest Ecosystem Research Program – successes and challenges.** In: Peterson, C.E.; Maguire, D.A., eds. Balancing ecosystem values: innovative experiments for sustainable forestry. Gen. Tech. Rep. PNW-625. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 147-152.

Scheller, R.M.; Mladenoff, D.J. 2002. **Understory species patterns and diversity in old-growth and managed northern hardwood forests.** Ecological Applications. 12(5): 1329-1343.

Schofield, D.A. 2003. **Vegetation dynamics and tree radial growth response in harvest gaps, natural gaps, and closed canopy conditions in Maine's Acadian Forest.** Orono, ME: University of Maine, Department of Forest Ecosystem Sciences. 147 p. M.S. thesis.

Seymour, R.S.; White, A.S.; deMaynadier, P.G. 2002. **Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies.** Forest Ecology and Management. 155: 357-367.

Seymour, R.S.; Guldin, J.; Marshall, D.; Palik, B. 2006. **Large-scale, long-term silvicultural experiments in the United States: historical overview and contemporary examples.** Allgemeine Forst-und Jagdzeitung. 177: 104-112.

Strojny, C. 2004. **Effects of harvest gaps and natural canopy gaps on amphibians within a northeastern forest.** Orono, ME: University of Maine, Department of Wildlife Ecology. 88 p. M.S. thesis.

Thomas, S.L.; Wagner, R.G.; Halteman, W.A. 2009. **Influence of harvest gaps and coarse woody material on click beetles (Coleoptera: Elateridae) in Maine's Acadian Forest.** Biodiversity and Conservation 18(5): online 07 March 2009.

Troup, R.S. 1928. **Silvicultural systems.** Oxford, UK: Claredon Press. 200 p.

van Wagner, C.E. 1968. **The line intersect method in forest fuel sampling.** Forest Science. 14: 20-26.

THE COOPERATIVE FORESTRY RESEARCH UNIT COMMERCIAL THINNING RESEARCH NETWORK: 9-YEAR RESULTS

Robert S. Seymour, Spencer R. Meyer, and Robert G. Wagner

Abstract.—The Commercial Thinning Research Network (CTRN) was established throughout the spruce-fir forest of Maine beginning in 2000 with substantial funding from the University of Maine's Cooperative Forestry Research Unit. One of six replicates of the precommercially thinned stand condition in the CTRN is located in compartment 23A in the U.S. Department of Agriculture, Forest Service's long-term silviculture experiment on the Penobscot Experimental Forest (PEF), in which the experimental treatments are the timing of the first thinning entry and relative-density reduction. This paper presents 9-year results of this study, including detailed stand trajectories for the plots in compartment 23A. Contrary to expectations, there was no difference in periodic annual volume increment among the early-thinning treatments, owing to a much greater-than-expected growth response from the heavily thinned (50 percent reduction) plots. The study has provided valuable calibration data for the Forest Vegetation Simulator, and has informed landowner thinning decisions for a large area of northern Maine that was regenerated in the 1970s and 1980s during the spruce budworm salvage era. The study is actively maintained and future publications will document the effects of the 10-year delayed treatments.

INTRODUCTION

The Cooperative Forestry Research Unit

The Cooperative Forestry Research Unit (CFRU) is a partnership between Maine forest landowners and managers and the University of Maine. The purpose of the CFRU is to help member organizations advance forest management practices in Maine through applied scientific research. Member organizations contribute annual dues to support research projects that are guided by an advisory committee. In 2013, the CFRU had 31 members (representing approximately 8 million acres), including private industrial, private nonindustrial, and public forest landowners; wood processors; and other private contributors.

The Commercial Thinning Research Network

The Commercial Thinning Research Network (CTRN) is a statewide system of study sites created with substantial funding from the CFRU to study questions surrounding commercial thinning of Maine's spruce-fir resource. The CTRN was installed in 2000-2001 and consists of two experiments, each replicated at six sites (Fig. 1). The research questions for the two experiments are:

1. For naturally regenerated spruce-fir stands that have never received precommercial thinning (PCT), what is the influence of (a) method of commercial thinning and (b) residual density on subsequent stand response?
2. For naturally regenerated spruce-fir stands that have received PCT, what is the influence of (a) timing of first commercial thinning entry and (b) residual density on subsequent stand response?

The Penobscot Experimental Forest (PEF) study site hosts one replicate of the second experiment type, hereafter referred to as the "PCT Study."

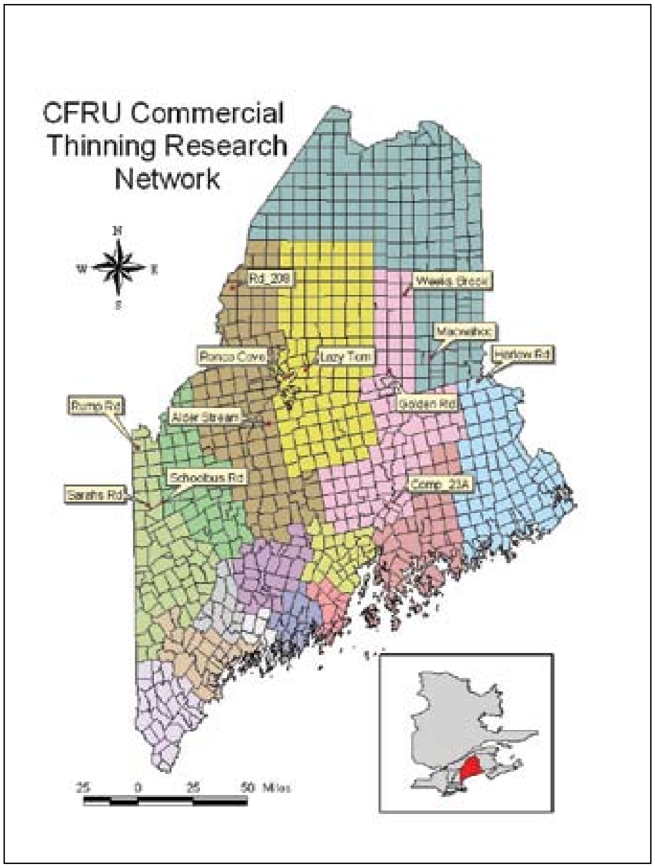


Figure 1.—Location of the 12 original CFRU Commercial Thinning Research Network study sites in Maine.

METHODS

Treatment Prescriptions

In the PCT-origin stands of the CTRN, treatments were designed to answer two important questions regarding the (a) timing and (b) intensity of first commercial thinning entry (Table 1).

The "immediate" treatment should be interpreted as implementing a commercial thinning as soon as the stand is commercially harvestable, typically when the average height of all trees is about 35 feet if it has been precommercially thinned.

Treatments were 33 percent and 50 percent removal based on the original relative density, calculated from the diagram of Wilson et al. (1999). Relative density is the ratio of the current density (trees per acre) to the maximum number of trees possible based on the current average tree volume. Trees to be cut were marked with paint for the harvester operators. Marking generally favored the largest, most vigorous crop trees, while attempting to maintain fairly uniform spacing of residuals and discriminating against smaller merchantable firs. One exception is that balsam fir (*Abies balsamea*) over 9 inches in diameter at breast height (d.b.h.) were generally removed, based on the increasing likelihood of heart rots and susceptibility to the balsam woolly adelgid (*Adelges piceae*).

Treatment plots are nominally 1.0 acres with a 0.2-acre measurement plot in the center (Fig. 2). Forwarder trails are spaced 100 feet apart with only one forwarder trail running through the sample plot. In the first two entries, small, single-grip processors used "ghost trails" spaced between forwarder trails to conduct thinnings.

Table 1.—Treatment prescriptions used in the PCT-origin stands. (Codes used in the subsequent text and analysis begin with the relative density reduction followed by the timing. For example, the 33 percent relative density removal waiting 5 years is coded "LT5.")

	Relative density (RD) reduction (code)	
Timing (code)	33% (LT)	50% (HT)
Immediate (0)	Evenly space residual stand and reduce RD by 33% in 2001-2002	Evenly space residual stand and reduce RD by 50% in 2001-2002
Wait 5 years (5)	Evenly space residual stand and reduce RD by 33% in 2006-2007	Evenly space residual stand and reduce RD by 50% in 2006-2007
Wait 10 years (10)	Evenly space residual stand and reduce RD by 33% in 2011-2012	Evenly space residual stand and reduce RD by 50% in 2011-2012
Never	Untreated control (NT)	

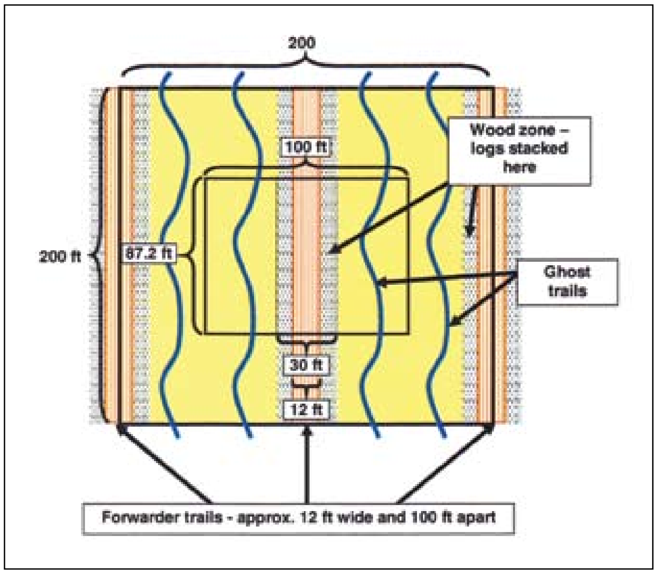


Figure 2.—Treatment and sample plot design for CFRU Commercial Thinning Research Network study sites.

Measurement Protocol

All trees ≥4.6 inches in d.b.h. have been measured annually since the study's inception on seven 0.20-acre (87.2 feet by 100 feet) sample plots per site that are centered within the 0.92-acre (200 feet by 200 feet) treatment plots. Measurements are status (live or dead, with apparent cause of mortality), d.b.h., total height, and crown height of every tree. All logs removed from the plots during thinning were measured for length, diameter, and species.

Initial Stand Conditions

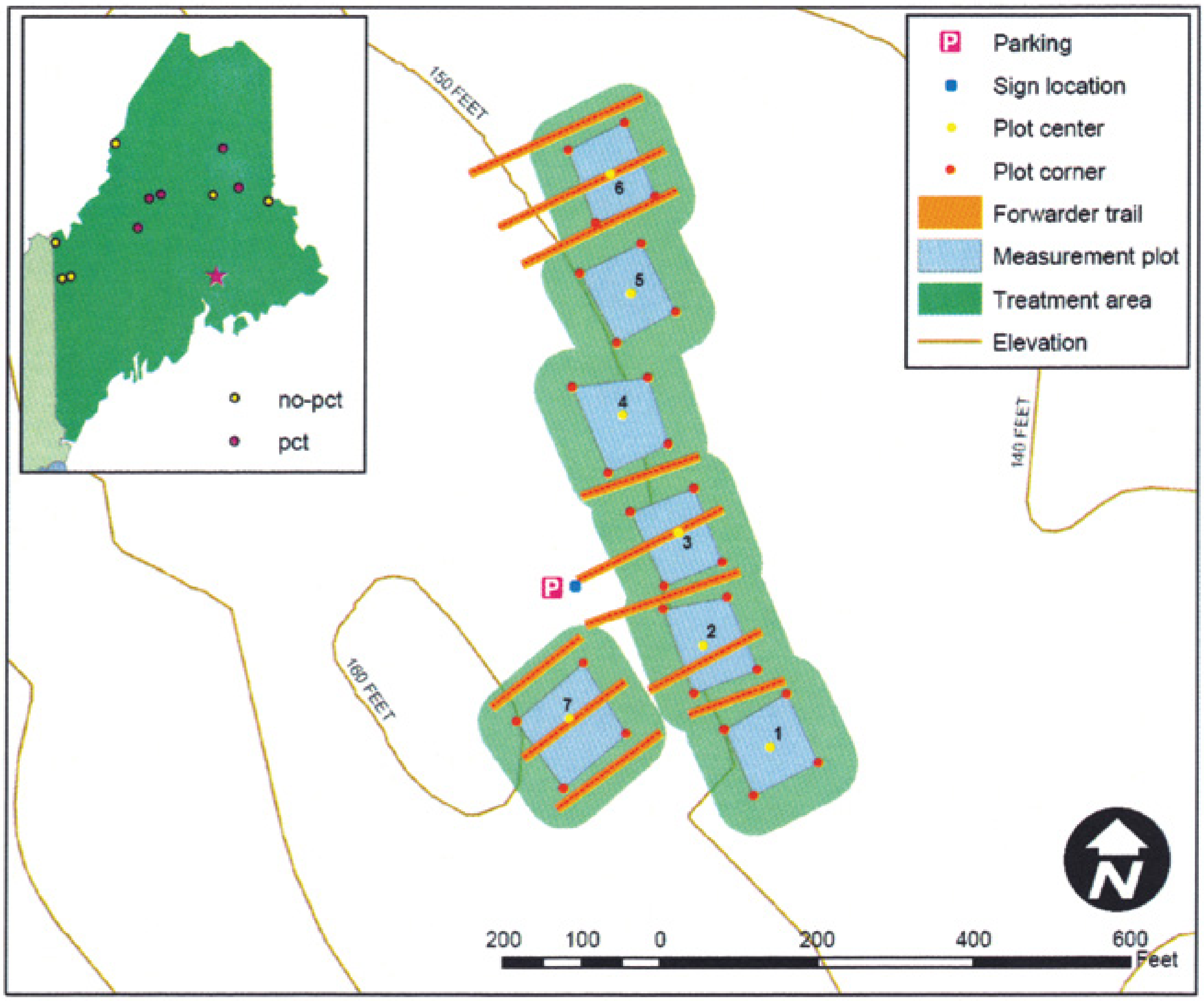
All stands were originally precommercially thinned during the 1980s to a spacing of about 8 feet by 8 feet (600-800 trees per acre). Stand age at the time of our first commercial thinning in 2001 ranged from 23 to 40 years; site index is high, ranging from 60 to 80 (height in feet at a breast-height [bh] age of 50). All sites are dominated by balsam fir, some more than others (Table 2). The remaining stocking is mostly red spruce (*Picea rubens*), with occasional white spruce (*Picea glauca*) and other conifers such as eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*).

PEF Study Site Description

The study stand, compartment 23A, is one of two replicates of the three-stage shelterwood treatment in the U.S. Department of Agriculture, Forest Service's long-term experiment on the PEF (Fig. 3). It originated after a shelterwood removal cutting that released small-sapling-size regeneration in 1972 (see Brissette and Kenefic, this volume). After the removal cutting, all stems >2.5 inches in d.b.h. were felled, resulting in a very uniform even-aged condition. Precommercial thinning was done in 1981 to a 2 m by 3 m spacing (slightly lower density than 8 feet by 8 feet). The first commercial thinnings were done in the winter of 2001-2002, the second treatments were completed

Table 2.—Preharvest stand metrics for the PCT-origin sites, averages or totals of all trees with d.b.h. ≥4.6 inches. (Site Index is the height of the tallest 40 trees per acre at a bh age of 50, from the equations in the appendix of Wilson et al. [1999]. QMD is the quadratic mean d.b.h.; volumes are from Honer's [1967] equations; merchantable limits are 4.6 inches d.b.h. to a 3.0-inch top diameter inside bark; relative density is from the equations in Wilson et al. [1999]; balsam fir percentage is based on the relative basal areas.) Site abbreviations from Figure 1 are Alder Stream (AS), Lake Macwahoc (LM), Lazy Tom (LT), the Penobscot Experimental Forest (PEF), Ronco Cove (RC), and Weeks Brook (WB).

Site	Age at bh (yr)	Site index	Basal area (ft^2 per acre)	Density (trees per acre)	QMD (inches)	Height (ft)	Total stemwood volume (ft^3)	Merchantable stemwood volume (ft^3)	Relative density	Balsam fir
AS	28	74	109	539	6.1	33	1,926	1,454	0.29	82%
LM	40	60	125	656	6.0	39	2,427	1,774	0.36	100%
LT	28	70	122	778	5.4	34	2,154	1,406	0.34	73%
PEF	29	67	101	606	5.5	35	1,854	1,254	0.29	69%
RC	23	80	113	736	5.3	31	1,802	1,169	0.29	97%
WB	29	67	124	831	5.3	35	2,273	1,477	0.36	92%



Penobscot Exp. For. Site Information		Plot Information		
Site name	PEF, Penobscot Exp. For., Compartment 23A Site	Plot	TrtmntDate	Treatment
Township	Bradley	1		Control
County	Penobscot	2	2001-2002	33%
Landowner	University of Maine	3	2001-2002	50%
History	PCT - 1983	4	2011-2012	33%
Plots established	August 2001	5	2011-2012	50%
Commercial Thinning(s)	February 2002, February 2007	6	2006-2007	50%
Location	45-51'-17" N, 68-38'-07" W	7	2006-2007	33%
For more information contact the Cooperative Forestry Research Unit at (207) 581-2893				

CFRU

Cartographer: Benjamin Gannon
Date: August 16, 2007
Projection: UTM Zone 19 North
Datum: NAD 1983

Figure 3.—Treatment map for the CFRU Commercial Thinning Study installation in compartment 23A of the PEF.

in the winter of 2006-2007, and the final (10-year) treatment was completed during the winter of 2011-2012.

Analysis

All data are contained in a master Microsoft Office Access database which is updated annually. Data included here include the preharvest measurements from 2001, along with the annual measurements from 2002 through 2011. Because trees are generally measured early in the growing season, this analysis thus includes nine growing seasons, broken into two periods corresponding to the timing of the 5-year treatments: 2002 through 2006, and 2007 through 2010. Data from the 5- and 10-year treatments were treated as unthinned controls during the years prior to thinning. The 10-year treatments were treated after the last measurement used here, so these plots are effectively the same as the controls during this period. Accretion is the volume increment on trees that are merchantable at the beginning of the growth period. Ingrowth is the ending-period volume of trees that grew across the 4.6-inch d.b.h. threshold. All volumes are merchantable, inside-bark cubic feet, from Honer's (1967) equations; merchantable limits include trees ≥4.6 inches in d.b.h. to a 3.0-inch top diameter inside bark. Statistical analyses were done with Systat's version 12 General Linear Model procedure (Systat Software Inc., San Jose, CA).

RESULTS AND DISCUSSION

Commercial Harvests

The first harvests (the "immediate" treatment, done in 2001-2002) yielded significant volumes of commercial products, ranging in value from about $500 to nearly $1,200 per acre on a mill-delivered basis (Fig. 4).

Over all sites, volume removals averaged between 8 and 10 cords per acre in the first entries in 2001. The year-5 entries removed 26 percent more volume than the first, undoubtedly owing to the higher stocking levels and taller trees removed with essentially the same prescription (Table 3).

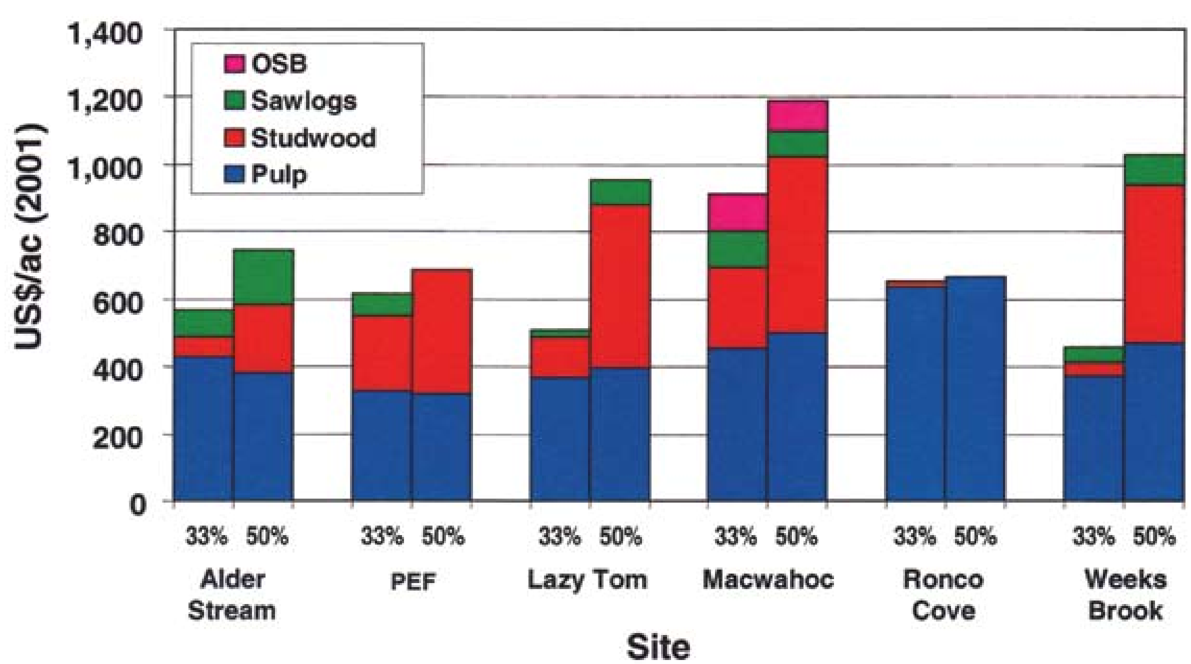


Figure 4.—Mill-delivered value by product class from thinning each of the six sites at 33 percent and 50 percent relative density reductions from first thinning (2001).

Table 3.—Merchantable harvests (cubic feet per acre, cords in parentheses) from the commercial thinning treatments averaged over all six sites, by timing and removal rate

Timing	LT (33%)	HT (50%)
Immediate	673 (7.9)	890 (10.5)
Year 5	934 (11.0)	1039 (12.2)

Nine-Year Stand Development and Growth Responses

Over all sites, yields increased from 1,694 ft^3 (19.9 cords) per acre in 2002 to 2,934 ft^3 (34.5 cords) in 2011, a 73 percent increase (Fig. 5). Net periodic annual increment (PAI) averaged 128 ft^3 (1.5 cords) per acre during the first 5 years, increasing to 143 ft^3 (1.7 cords) during the next 4 years. Over the 9-year period, yields of many plots more than doubled. These stands are exceptionally productive by any relevant standard. The only exception is the LM site, where the 5-year treatments suffered post-thinning mortality losses, as evidenced by the level or declining yields in two plots in the oldest site (>age 40, Fig. 5).

The overall analyses of variance (Table 4) revealed significant effects of treatment on the positive growth components, although this effect is due entirely to the lower growth of the "heavy thinning, wait 5 years" (HT5) treatment (Fig. 6). When each growth period was analyzed separately, accretion was not different among treatments during the first 5 years, averaging 116 ft^3 (1.4 cords) per acre per year. During this period, but not the second, there was a significant difference in ingrowth, with the unthinned controls exceeding the treated plots. Evidently, many small (<4.6 inches d.b.h.) trees were harvested in the early treatments, thus preempting their subsequent ingrowth.

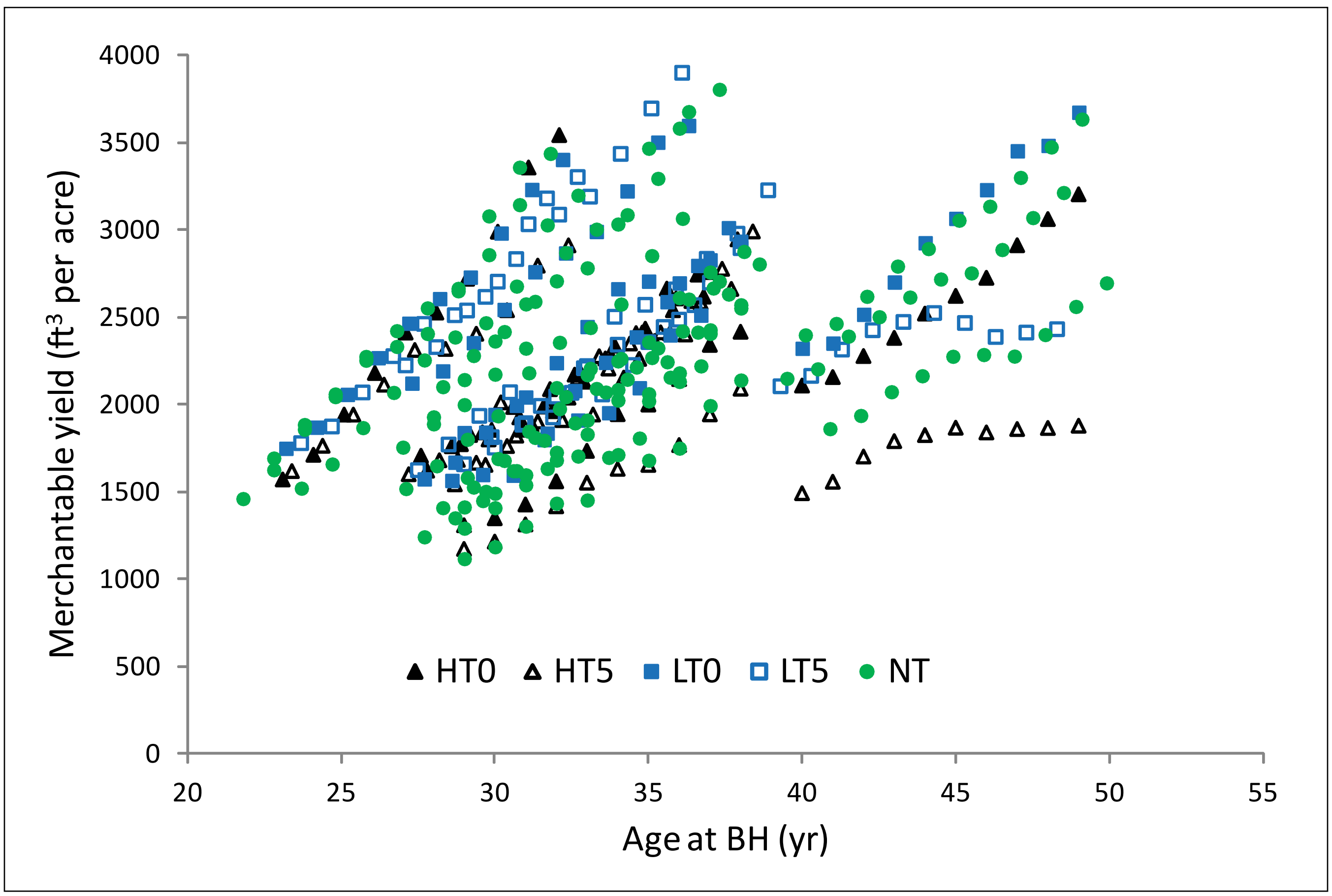


Figure 5.—Nine-year stand development of all 42 plots in the CTRN PCT study, grouped by thinning treatment. Yields include standing volumes plus removals in prior thinnings, if any.

Table 4.—Analyses of variance of four growth components using treatment and growth period as main effects and site as a blocking factor. P-values in italics are the probability of no differences in each growth component (columns) resulting from each factor. Data are least-squares means (in ft³ per acre per year); means followed by the same letter do not differ at p = 0.10 using Tukey's Honestly-Significant-Difference test.

Factor		Accretion	Ingrowth	Mortality	Net PAI
Treatment	*p-value*	*0.002*	*0.001*	*0.097*	*0.003*
LT0		153.5 b	8.6 a	15.6 a	162.1 a
HT0		133.4 b	6.1 a	5.9 a	139.5 ab
LT5		137.6 b	11.6 ab	22.3 a	149.3 a
HT5		99.7 a	12.7 ab	17.7 a	112.4 b
NT (control)		137.6 b	14.3 b	6.8 a	152.5 a
Growth period	*p-value*	*<0.001*	*<0.001*	*0.959*	*<0.001*
2002-2006		116.0 a	15.0 a	13.5 a	131.0 a
2007-2010		148.9 b	6.4 b	13.7 a	155.3 b
Site	*p-value*	*<0.001*	*<0.001*	*0.001*	*<0.001*
Ronco Cove (RC)		176.8 a	14.1 bc	6.8 a	190.9 a
Alder Stream (AS)		156.1 ab	8.3 b	5.0 a	164.4 b
Weeks Brook (WB)		136.6 bc	18.1c	11.0 ab	154.7 b
Lake Macwahoc (LM)		114.2 cd	1.6 a	23.6 b	115.8 c
Lazy Tom (LT)		107.5 d	8.9 b	26.3 b	116.4 c
PEF		103.4 d	13.3 bc	8.8 a	116.8 c

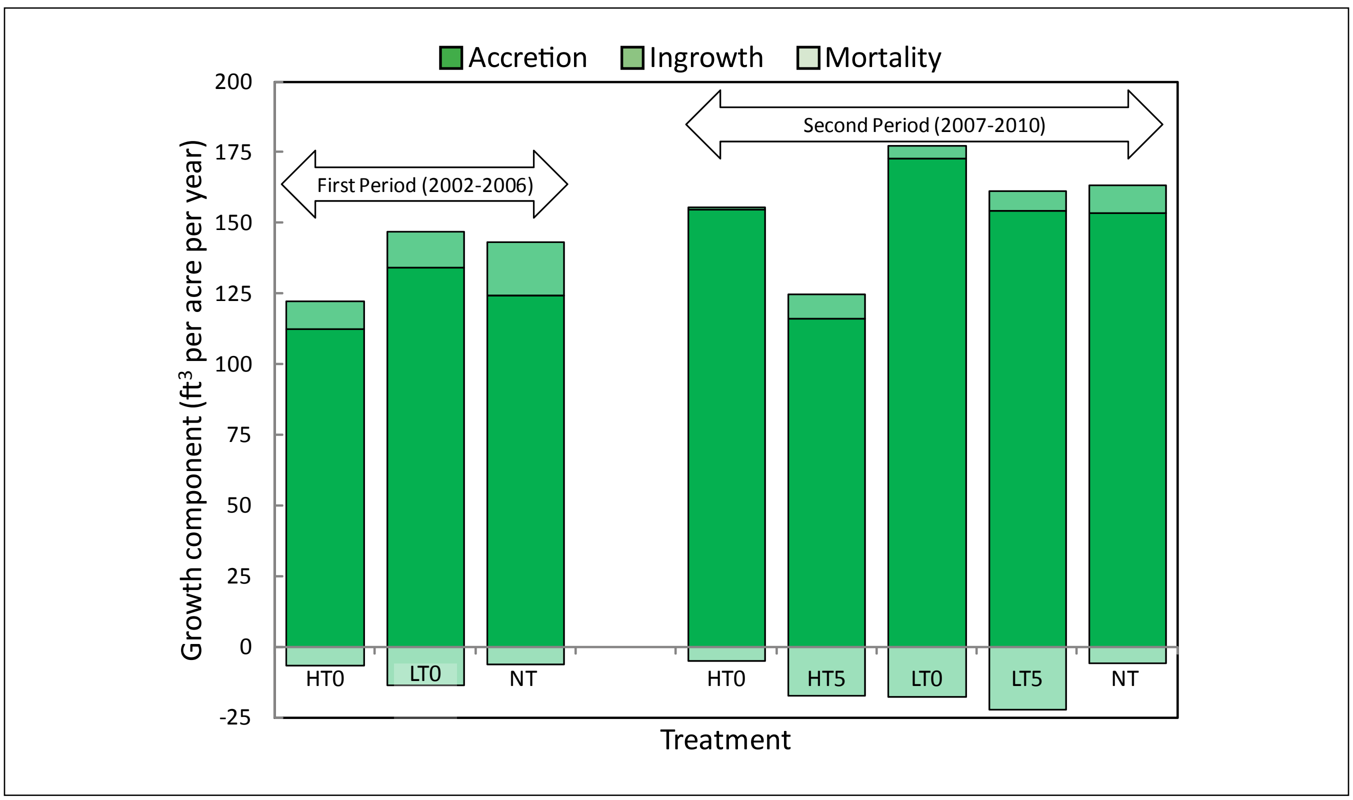


Figure 6.—Growth components (merchantable ft³ per acre per year) by thinning treatment and growth period, averaged over the six PCT sites. The positive height of the bars (accretion plus ingrowth) is the gross growth; gross growth minus the negative bars (mortality) is net growth.

Except with the HT5 treatment, growth increased significantly over the course of the study. Net PAI was 24 ft^3 greater during the second period than the first (Table 4). The treatment effect on mortality was marginally significant overall, yet no mean separations reached this significance threshold. Note that mortality was very low on the unthinned controls during both periods (Fig. 6), suggesting that these stands are not yet self-thinning.

Growth was quite different among the six sites (Table 4), reflecting differences in their site indices (Table 2). The extraordinary growth (>2 cords per acre per year) and high site index (80 feet) of the Ronco Cove site are especially noteworthy. The net PAIs of the top three sites (Table 4) exceed the highest PAIs reported in the Green River spacing study (Pitt and Lanteigne 2008), and the Ronco Cove site approaches the highest PAIs reported by Pelletier and Pitt (2008) for white spruce plantations with a high site index in northwestern New Brunswick.

When relative density at the midpoint of the growth period was added to the analysis of variance model (Table 4) as a covariate, treatment effects became highly significant (Fig. 7). This difference is due entirely to the relatively lower growth of the unthinned control plots at a given relative density. The different slopes fitted to each treatment separately suggest an interaction between treatment and relative density, but this interaction was significant only at p = 0.29. Clearly the thinned treatments are more growth-efficient at a given density, likely owing to their improved light environment. The pattern illustrated in Figure 7 is the main reason that Saunders et al. (2008) needed to perform extensive treatment-related growth calibrations to the Forest Vegetation Simulator for analyzing various commercial thinning regimes.

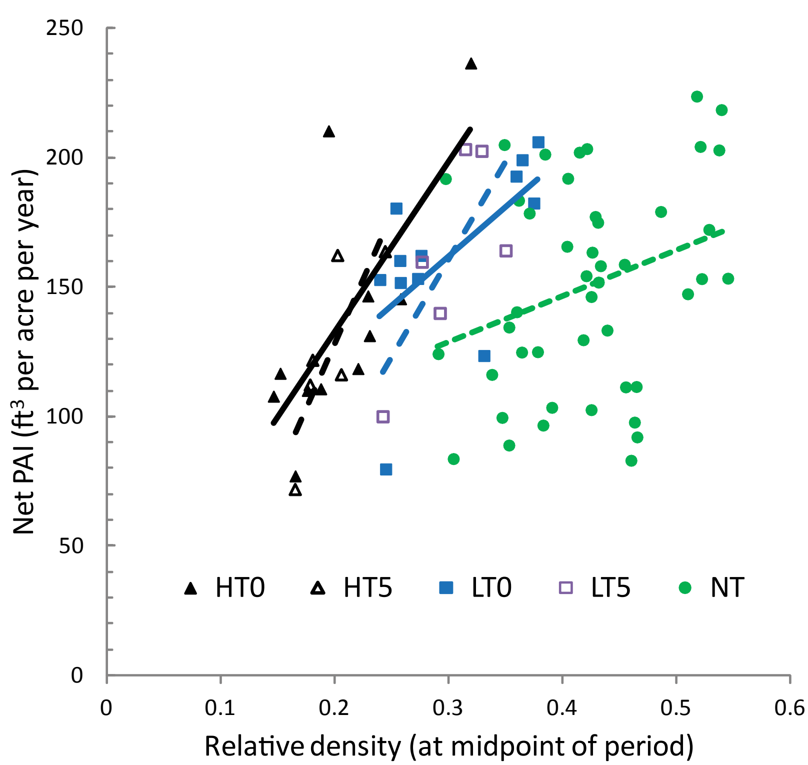


Figure 7.—Net PAI over relative density at the midpoint of the growth period, by treatment. Lines represent separate least-squares regressions fitted to each treatment.

Stand Development of the PEF Site in Compartment 23A

When the PEF plots are graphed on the Wilson et al. (1999) density management diagram (Fig. 8), we see that the 50 percent removal (H) treatments left residual stands at a density of 240-260 trees per acre, or a spacing of about 13 feet between crop trees. The 33 percent (L) treatments left about 100 more trees per acre (340-355), a spacing of 11 feet. Plots 1 (the control) and 4 (unthinned until 2012) began the study at a relative density of about 0.3 and have grown to nearly 0.5 over the 9-year period. No evidence of self-thinning or density-dependent mortality is yet apparent.

Growth components by treatment (Fig. 9) are somewhat lower than the overall study averages. During the first growth period, the L0 treatment grew much more than its heavier counterpart (H0), but during the second period, three large (8 inches, 12 inches, and 13 inches d.b.h.) balsam firs died standing on this plot. We suspect they were attacked by the balsam woolly adelgid, which has not been observed on the other five installations.

FUTURE WORK

Although these results are interesting, conclusive findings must await future measurements and include the outcome of the 10-year delayed treatments implemented during the winter of 2012-2013. We hope to maintain this study until stands reach rotation age. Mean annual increments are still much lower than periodic growth, suggesting the culmination is at least 10-20 years in the future. The CTRN was also expanded in 2009-2010 to include three more stands of PCT origin with lower site indices and more spruce stocking, and thus more representative of the entire spruce-fir region than the six fir-dominated stands with high site indices reported here.

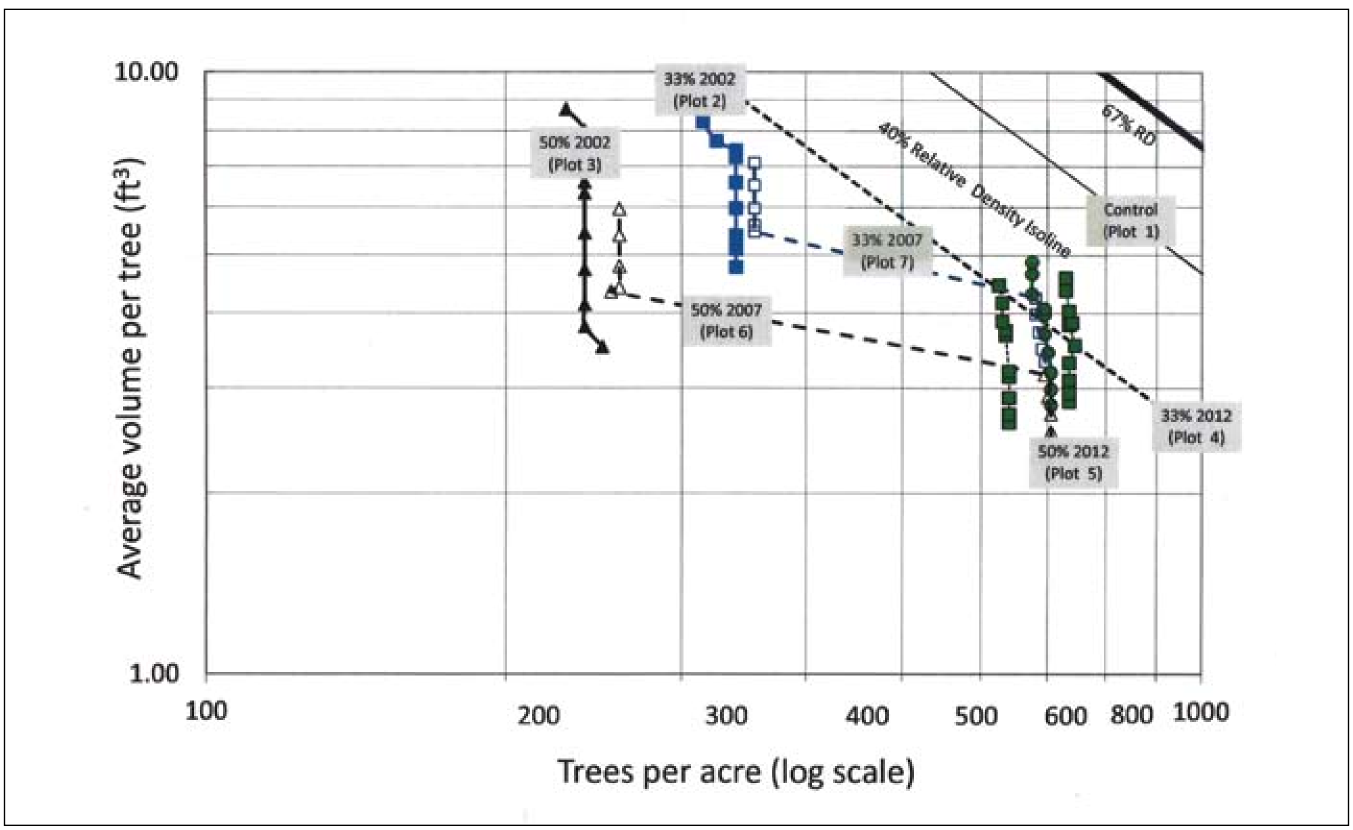


Figure 8.—Nine-year stand development of the PEF site plotted on the density management diagram of Wilson et al. (1999). Treatment symbols are identical to previous figures.

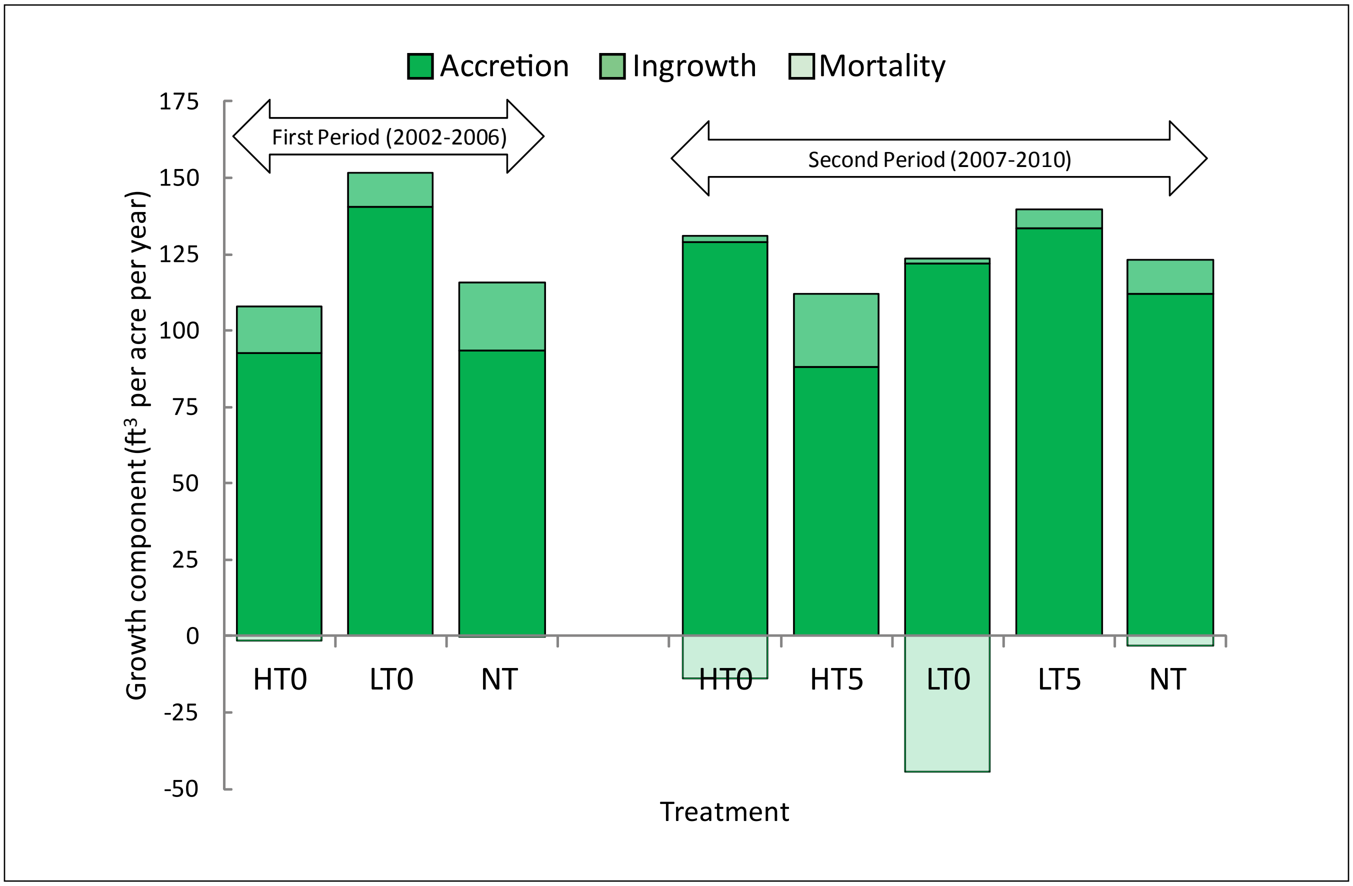


Figure 9.—Growth components (merchantable ft³ per acre per year) by thinning treatment and growth period for the PEF site. The positive height of the bars (accretion plus ingrowth) is the gross growth; gross growth minus the negative bars (mortality) is net growth.

LITERATURE CITED

Honer, T.G. 1967. **Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada.** Information Report FMR-X-5. Ottawa, ON: Department of Forestry and Rural Development. 21 + 133 p.

Pelletier, G.; Pitt, D.G. 2008. **Silvicultural responses of two spruce plantations to midrotation commercial thinning in New Brunswick.** Canadian Journal of Forest Research. 38: 851-867.

Pitt, D.G.; Lanteigne, L. 2008. **Long-term outcome of precommercial thinning in northwestern New Brunswick: growth and yield of balsam fir and red spruce.** Canadian Journal of Forest Research. 38: 592-610.

Saunders, M.; Wagner, W.G.; Seymour, R.S. 2008. **Thinning regimes for spruce-fir stands in the northeastern United States and eastern Canada.** Orono, ME: University of Maine, Cooperative Forestry Research Unit. 186 p.

Wilson, D.S.; Seymour, R.S.; Maguire, D.A. 1999. **Density management diagram for northeastern red spruce and balsam fir forests.** Northern Journal of Applied Forestry. 16: 48-56.

SILVICULTURAL OPTIONS FOR EARLY-SUCCESSIONAL STANDS IN MAINE: 6-YEAR RESULTS OF THE SILVICULTURAL INTENSITY AND SPECIES COMPOSITION EXPERIMENT

Andrew S. Nelson, Robert G. Wagner, and Mike R. Saunders

Abstract.—The Silvicultural Intensity and Species Composition (SIComp) experiment was installed in 2003 on a recently clearcut mixedwood site within the Penobscot Experimental Forest in east-central Maine. This study was initiated because the response of early-successional stands to various intensities of silviculture was poorly understood in the region. The goal of SIComp is to shift stand development and composition in multiple directions through a factorial combination of three silvicultural intensities (low, medium, and high) and three objectives for species composition (hardwood, mixedwood, and conifer). To date, the experiment has documented the survival, growth, and yield of hybrid poplar and planted white spruce plantations, the effects of precommercial thinning in juvenile aspen stands, the response of early-successional stands to conifer release treatments, and alternative approaches for managing young mixedwood stands. Current investigations are focused on mechanistic responses to the heterogeneous growing conditions created by the varied treatments in the experiment. Energy (labor, petroleum, and pesticide) inputs required to establish and maintain the experiment also will be incorporated into models estimating net carbon balance and value of the various treatments over time.

INTRODUCTION

Young, naturally regenerated stands dominated by shade-intolerant hardwoods mixed with conifer species compose approximately 13 percent of the forest land in Maine (McWilliams et al. 2005). The majority of these stands originated after the large-scale, post-budworm clearcuts during the 1980s and subsequent partial harvesting that continues today. Although these stands are prevalent in the region, their response to silviculture has not been well studied, which limits our ability to implement appropriate silvicultural systems to promote desirable composition and increase stand productivity. Additionally, without a firm understanding of early-successional stand responses to silviculture, current growth and yield models cannot accurately project stand development; therefore, the contribution of these stands to increasing regional wood fiber demands is poorly understood. In response to these concerns, the Silvicultural Intensity and Species Composition (SIComp) experiment was established in 2003 on a recently clearcut mixedwood site on the Penobscot Experimental Forest (PEF) in east-central Maine. Experimental plots were put on different trajectories by manipulating tree species composition and applying various intensities of silviculture, with the overall goal of documenting the resulting dynamics of young Acadian Forest stands.

Long-term silvicultural experiments in Maine are limited, but the various experiments on the PEF have served as a basis for understanding the response of northern conifer stands to traditional silviculture (U.S. Department of Agriculture, Forest Service Compartment Study), ecological silviculture (Acadian Forest Ecosystem Research Program Expanding Gap Experiment), and intermediate treatments such as precommercial and commercial thinning (Commercial Thinning Research Network). The SIComp experiment complements these other long-term studies on the PEF. Long-term silvicultural experiments in the region provide a basis for comparing the effectiveness of various treatments, such as clearcutting, shelterwood, and selection systems, and intensities of management on residual stand structure and regeneration dynamics (Brissette 1996). Responses to these various treatments will typically vary depending on species composition (Sendak et al. 2003). For example, clearcut-harvested stands in northern and central Maine typically regenerate to aspen (*Populus* spp.) and birch (*Betula* spp.), but future composition and structure may differ depending on the density of conifer advance regeneration.

The intensity of silviculture applied to a stand is directly related to the desired financial investment. In early-successional mixedwood stands in Maine, unmanaged stands often remain dominated by shade-intolerant hardwood species and growth rates may be inhibited by high stem densities. With a comparatively modest financial investment, desirable species can be promoted and growth rates can be increased with treatments such as conifer release (Newton et al. 1992) or hardwood thinning (Rice et al. 2001). Additional silvicultural investment, such as enrichment planting, can increase stand productivity and accelerate composition to mid- to late-successional species (Greene et al. 2002, Paquette et al. 2006). Currently, there are no long-term experiments in the Acadian region documenting the response of early-successional stands to different intensities of silviculture. Without these long-term data, it is difficult to assess the potential benefits of different treatments in early-successional stands.

The lack of information on the responses of early-successional stands to silviculture was the impetus for the establishment of SIComp. The three major objectives of the study are to: (1) quantify the growth and yield response of early-successional stands in central Maine to varying intensities of silviculture under different compositional objectives, (2) document the mechanisms affecting the dynamics and productivity of these young forest stands, and (3) compare the energy requirements and financial returns associated with implementation and eventual harvest under differing silvicultural intensities and compositional objectives. These objectives are long-term and require interdisciplinary collaboration. Currently, productivity is being investigated by modeling allometry, resource availability, and ecophysiological response in relation to the various growing conditions created by the treatments. Ongoing efforts to document the energy inputs (labor, petroleum, and pesticides) of the different treatments will provide managers with the costs and financial returns associated with the silvicultural strategies being tested.

Shortly after the study was established, the wide range of micro-environmental conditions created by the experiment allowed Kanoti (2005) to determine how silvicultural intensity can influence the natural regeneration (germination and survival) of Acadian tree species. He hypothesized that silviculture could be used to mitigate the possible negative effects of climate change on soil temperature and moisture regimes in a way that can encourage the germination and establishment of Acadian Forest tree species. Results showed that moisture availability was the most important factor influencing germination success. Drought tolerance decreased in the following order: trembling aspen (*Populus tremuloides* Michx.) > red spruce (*Picea rubens* Sarg.) = hybrid larch (*Larix* x *eurolepis* Henry) > Norway maple (*Acer platanoides* L.) = paper birch (*B. papyrifera* Marsh.) = white pine (*Pinus strobus* L.) > balsam fir (*Abies balsamea* L.) = red maple (*Acer rubrum* L.). Additionally, Kanoti (2005) found that predator protection and sowing date strongly influenced emergence success, with a fall sowing date being detrimental to exotic species. After seedlings emerged, greater densities of grass competition and overstory density reduced survival of many of the species.

The importance of understanding the response of early-successional stands in Maine to various silvicultural intensities is increasing, yet no long-term silvicultural studies have previously addressed these issues. Additionally, given the young age of the SIComp experiment, details of the study have not been documented elsewhere. Therefore, the goals of this paper were to: (1) describe the experimental design of the SIComp experiment, and (2) present initial findings on the difference in composition and individual tree size among species and treatments 6 years after the experiment was started.

METHODS

Study Area

This study was installed within the PEF near the towns of Bradley and Eddington (44°49'N, 68°38'W) between 2003 and 2004. Natural forest composition on the PEF is dominated by shade-tolerant conifer species, including balsam fir, eastern hemlock (*Tsuga canadensis* L.), and red spruce, and shade-intolerant hardwood species, such as trembling aspen, bigtooth aspen (*Populus grandidentata* Michx.), red maple, and paper birch (Sendak et al. 2003). Soils at the forest are of Wisconsin glacial till origin and the soil classifications at the study site range from loamy, mixed, active, acid, frigid, shallow, Aeric Endoquepts to coarse-loamy, isotic, frigid, Aquic Haplothods. The climate of eastern Maine is cool and humid. February is the coldest month on average (–7.1 °C) and July is typically the warmest (20.0 °C). Mean precipitation is 1070 mm, and the average growing season lasts approximately 160 days (Sendak et al. 2003).

In 1995, the 9.2-ha site of the experiment was clearcut with approximately 2.3 m^2 ha^{-1} of residual basal area. Following harvest, the site naturally regenerated to shade-intolerant hardwoods (trembling aspen, bigtooth aspen, red maple, and paper birch) and smaller balsam fir, red spruce, white pine (*Pinus strobus* L.), and white spruce (*Picea glauca* [Moench] Voss). Shortly after harvest, Norway (*Picea abies* [L.] Karst.), red, black (*Picea mariana* [Mill.]), and white spruce were planted to increase the density of desirable conifer species, but much of the planting failed due to hare clipping during the first winter.

Study Design

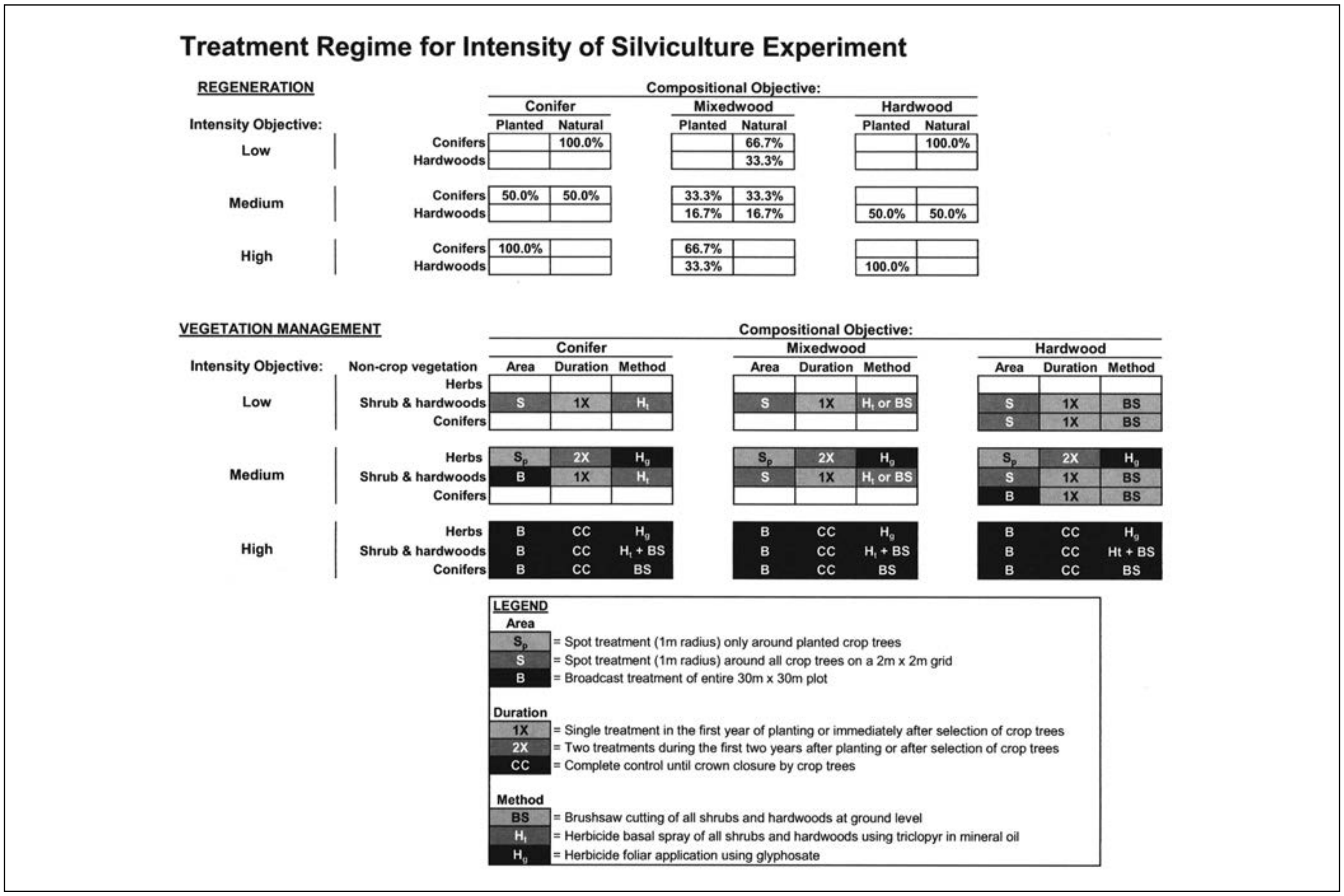
The SIComp experiment is based on a mix of treatments needed to achieve the desired level of silvicultural intensity and tree species composition (Table 1). A specific set of regeneration and vegetation management treatments was then designed to achieve each treatment objective (Fig. 1). The treatment objectives consisted of three levels of silvicultural intensity (low, medium, and high) crossed with three species compositional objectives (conifer, mixedwood, and hardwood), plus an untreated control. Prior to the installation of the treatments, a vegetation survey across the site revealed a patchy pattern of conifer composition that required blocking of the treatment plots by species composition. Therefore, the experimental design is a 3 x 3 +1 factorial, restricted-randomized complete block design, with four replicates of each treatment. Abbreviations for the array of treatments are: low conifer (LC), low mixedwood (LM), low hardwood (LH), medium conifer (MC), medium mixedwood (MM), medium hardwood (MH), high conifer (HC), high mixedwood (HM), high hardwood (HH), and untreated control (C).

Each of the ten treatments was replicated four times for a total of forty 30 m by 30 m treatment plots (Fig. 2). In each low- and medium-intensity treatment plot, manipulations were applied to individual crop-trees within each 2 m by 2 m growing space in the treatment plot (i.e., an average of 225 spaces per plot). Depending on treatment, these growing spaces were assigned one of four crop-tree types: naturally regenerated hardwood, planted hybrid poplar (*Populus* clones), naturally regenerated conifer, or planted white spruce (Fig. 3). Naturally regenerated hardwoods and conifers were selected from high-quality, large individuals in each growing space using the following orders of priority: hardwoods—bigtooth aspen > trembling aspen > paper birch > sugar maple (*Acer saccharum* Marsh.) > red maple; conifers—eastern white pine > balsam fir > spruce species.

Table 1.—Description of the different levels of silvicultural intensity applied to treatment plots in the SIComp experiment.

Silvicultural intensity	Control of species colonization (regeneration)	Control of relative species performance (vegetation management)	Control of spacing among desired trees (thinning)
Zero	None	None	None
Low	Selection among natural regeneration for desired tree species at desired spacing; "holes" without desired trees not filled	Minimum control of neighboring woody plants needed to maintain desired trees in main canopy (i.e., one-time release)	None
Medium	Selection among natural regeneration for desired tree species; "holes" fill-planted with desired tree species where needed to achieve desired spacing	Periodic control of neighboring woody plants around all desired trees that overtop or threaten to overtop desired trees	After crown closure of desired species, periodic thinning of desired trees to maintain a 0.3 spacing:height ratio
High	Genetically improved stock of desired tree species planted at desired spacing	Complete removal of all non-crop plants (woody and herbaceous) just before planting and through early stand development until crown closure of desired species	Periodic thinning of desired trees to maintain a 0.3 spacing:height ratio throughout life of stand

Silvicultural intensity	Pure conifer	Conifer/hardwood	Pure hardwood
Zero		Natural succession (no composition target)	
Low	Naturally regenerated balsam fir and red spruce depending on relative abundance; "holes" without desired conifers not managed	Naturally regenerated conifers (balsam fir and red spruce) and hardwoods (aspen, red maple, or sugar maple) at 67:33 mixture depending on relative abundance	Naturally regenerated aspen, red maple, or sugar maple depending on relative abundance; "holes" without desired hardwoods not managed
Medium	Naturally regenerated balsam fir and red spruce depending on relative abundance; "holes" fill-planted with white spruce	Naturally regenerated conifers (balsam fir and red spruce) and hardwoods (aspen, red maple, sugar maple) at 67:33 mixture; "holes" fill-planted with white spruce and hybrid poplar	Naturally regenerated aspen, red maple, or sugar maple depending on relative abundance; "holes" fill-planted with hybrid poplar
High	Planted white spruce	White spruce and hybrid poplar planted in 67:33 mixture	Planted hybrid poplar



Treatment Regime for Intensity of Silviculture Experiment

REGENERATION

Intensity Objective:		Conifer: Planted	Conifer: Natural	Mixedwood: Planted	Mixedwood: Natural	Hardwood: Planted	Hardwood: Natural
Low	Conifers		100.0%		66.7%		100.0%
	Hardwoods				33.3%		
Medium	Conifers	50.0%	50.0%	33.3%	33.3%		
	Hardwoods			16.7%	16.7%	50.0%	50.0%
High	Conifers	100.0%		66.7%			
	Hardwoods			33.3%		100.0%	

Compositional Objective: Conifer, Mixedwood, Hardwood

VEGETATION MANAGEMENT

Intensity Objective:	Non-crop vegetation	Conifer: Area	Conifer: Duration	Conifer: Method	Mixedwood: Area	Mixedwood: Duration	Mixedwood: Method	Hardwood: Area	Hardwood: Duration	Hardwood: Method
Low	Herbs									
	Shrub & hardwoods	S	1X	H_t	S	1X	H_t or BS	S	1X	BS
	Conifers							S	1X	BS
Medium	Herbs	S_p	2X	H_g	S_p	2X	H_g	S_p	2X	H_g
	Shrub & hardwoods	B	1X	H_t	S	1X	H_t or BS	S	1X	BS
	Conifers							B	1X	BS
High	Herbs	B	CC	H_g	B	CC	H_g	B	CC	H_g
	Shrub & hardwoods	B	CC	H_t + BS	B	CC	H_t + BS	B	CC	Ht + BS
	Conifers	B	CC	BS	B	CC	BS	B	CC	BS

Compositional Objective: Conifer, Mixedwood, Hardwood

LEGEND

Area
- S_p = Spot treatment (1m radius) only around planted crop trees
- S = Spot treatment (1m radius) around all crop trees on a 2m x 2m grid
- B = Broadcast treatment of entire 30m x 30m plot

Duration
- 1X = Single treatment in the first year of planting or immediately after selection of crop trees
- 2X = Two treatments during the first two years after planting or after selection of crop trees
- CC = Complete control until crown closure by crop trees

Method
- BS = Brushsaw cutting of all shrubs and hardwoods at ground level
- H_t = Herbicide basal spray of all shrubs and hardwoods using triclopyr in mineral oil
- H_g = Herbicide foliar application using glyphosate

Figure 1.—Treatments applied to achieve the various silvicultural objectives of the SIComp experiment.

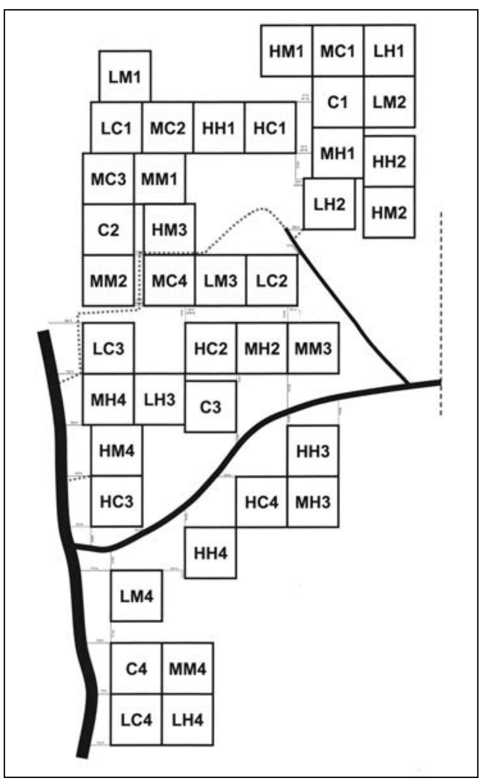


Figure 2.—Layout of the SIComp 30 m by 30 m treatment plots across the 9.2-ha clearcut site on the PEF. Treatment abbreviations are: C – untreated control, LC – low conifer, LM – low mixedwood, LH – low hardwood, MC – medium conifer, MM – medium mixedwood, MH – medium hardwood, HC – high conifer, HM – high mixedwood, and HH – high hardwood.

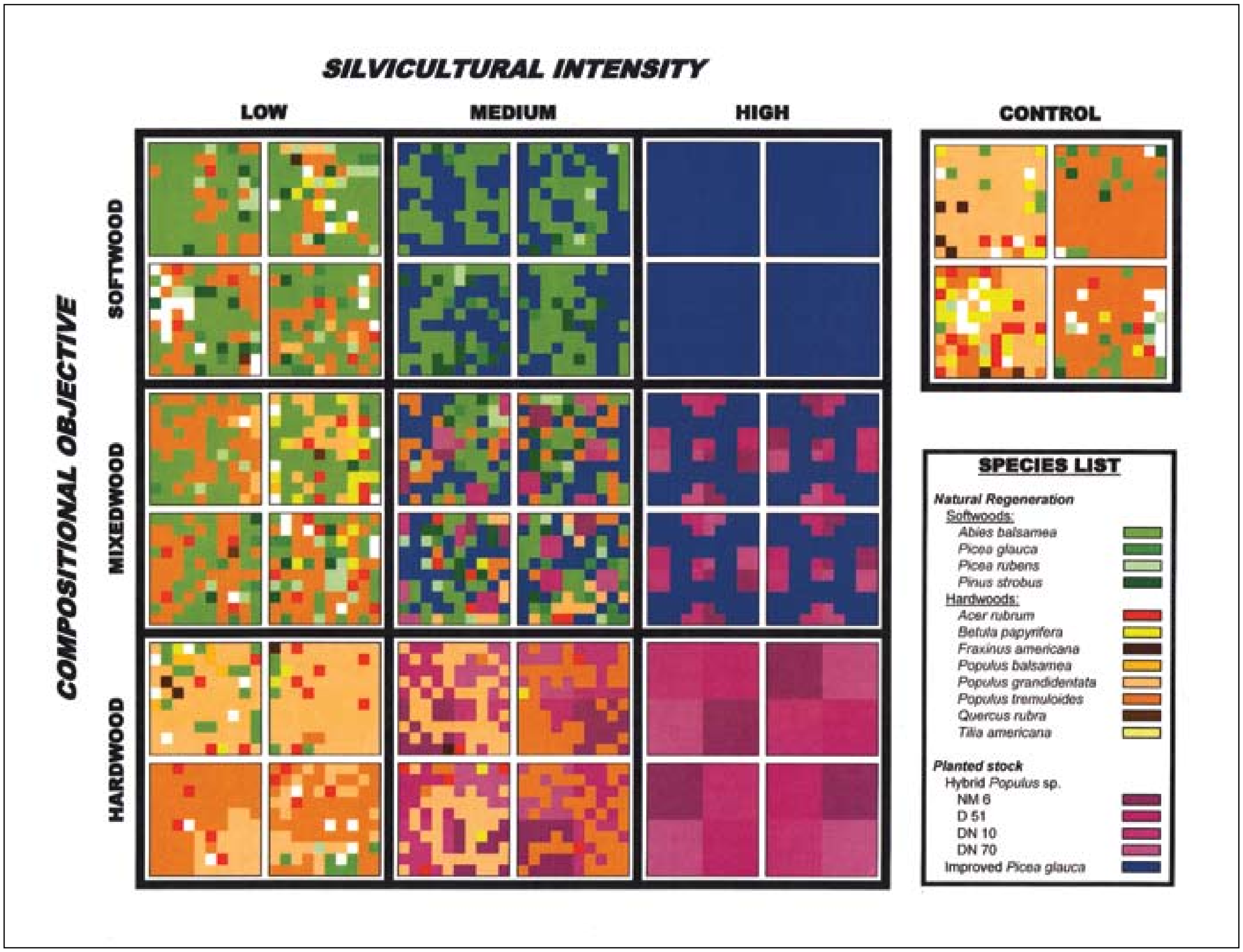


Figure 3.—Growing space allocation map for the SIComp experiment at study inception. The figure depicts each 2 m by 2 m growing space within measurement plots (20 m by 20 m) for each of the four replicates of a treatment. Cells are color-coded to species.

For both naturally regenerated crop-tree types, all woody vegetation within a 1-m radius around crop-trees was chemically or mechanically controlled in 2004. Hardwood competitors around conifer trees were killed using a basal application of 20 percent Garlon 4® (triclopyr ester) (Dow AgroSciences, Indianapolis, IN) mixed with Bark Oil Blue® (UAP Distribution Inc., Greeley, CO) (Table 2). Aspen trees of root-sucker origin were common across the site, so hardwood competitors around hardwood crop-trees were removed with motorized brushsaws to avoid potential herbicide damage to crop-trees through shared root systems with controlled trees. All conifer competitors were killed using brushsaws.

Growing spaces assigned to fill-planted hybrid poplar and white spruce in the medium- and high-intensity treatments were treated with herbicides (triclopyr basal-bark applications and glyphosate foliar treatments) and manually cleared of all pre-existing woody and herbaceous vegetation. In 2003 the high-intensity treatments underwent a follow-up broadcast application of 2.80 acid equivalent (a.e.) kg ha^{-1} glyphosate (Accord® Concentrate, Dow AgroSciences) to control herbs, and residual sprouting by shrub and tree regeneration. Planted growing spaces within the MC, MM, HC, and HM treatments were then planted in spring 2004 with containerized white spruce obtained from a J.D. Irving, Ltd., tree nursery in

Table 2.—Species composition (calculated as a proportion of total basal area) 6 years after the start of the experiment by treatment and for all treatments combined shown as least squares means. Treatment abbreviations are: C – untreated control, LC – low conifer, LM – low mixedwood, LH – low hardwood, MC – medium conifer, MM – medium mixedwood, MH – medium hardwood, HC – high conifer, HM – high mixedwood. The between-treatment standard error is also shown.

	Proportion of basal area (%)										
Species	C	LC	LM	LH	MC	MM	MH	HC	HM	HH	Standard error
Paper birch	22.5	1.8	3.7	8.5	7.8	9.7	13.3	-	-	-	5.6
Gray birch	4.4	3.4	2.9	17.8	1.4	13.3	6.5	-	-	-	8.8
Bigtooth aspen	19.8	13.8	12.7	10.0	2.6	4.8	16.2	-	-	-	6.3
Trembling aspen	13.2	2.1	1.9	9.5	1.1	2.3	8.6	-	-	-	4.0
Red maple	17.6	12.3	8.8	23.9	5.2	13.0	27.0	-	-	-	6.6
Other hardwood species	10.4	12.1	10.3	21.0	15.9	11.3	21.8	-	-	-	7.0
Balsam fir	8.8	48.6	53.1	8.5	44.1	30.1	1.9	-	-	-	7.7
Red spruce	1.2	3.1	3.2	0.1	0.3	2.5	-	-	-	-	1.2
Natural white spruce	0.2	1.4	1.8	-	0.3	-	0.9	-	-	-	0.5
Eastern white pine	1.6	1.4	1.4	0.6	4.1	5.7	1.5	-	-	-	1.1
Planted white spruce	-	-	-	-	17.1	6.3	-	100.0	80.7	-	3.2
Hybrid poplar	-	-	-	-	-	0.6	2.2	-	19.3	100.0	1.8

New Brunswick, Canada. The white spruce seedlings were 2+0 half-sib individuals grown in MP67 multi-pots with a 65-cm^3 rooting volume and planted with a Pottiputki® (a device with a hollow tube and duck-billed end that levers open a hole in soil suitable for seedling planting; BCC, Landscrona, Sweden).

Planted growing spaces within the MH, MM, HH, and HM treatments were planted with hybrid poplar cuttings obtained from the Woody Biomass Program at the State University of New York's College of Environmental Science and Forestry. Four hybrid poplar clones were planted with dibbles using a split-plot design with equal proportions of each clone. Knowing asymmetry would occur early with the fast-growing hybrid poplars in the HM treatment, we spatially grouped the hybrid poplar into 4-10 individuals each to minimize early interactions with the spruce (Fig. 3). Three *Populus deltoides* x *Populus nigra* clones (D51, DN10, and DN70) and one *Populus nigra* x *Populus maximowiczii* clone (NM6) were selected because it was unclear which variety would perform best under Maine soil and climatic conditions.

Stubborn natural vegetation in the high-intensity plots required various treatments to ensure the success of the plantations. In 2004, a subsequent 1.68 a.e. kg ha^{-1} glyphosate broadcast was applied, but natural vegetation persisted. Following planting, a broadcast pre-emergent herbicide mixture was applied in 2005 using backpack sprayers with a waving-wand method. The prescription consisted of 1.40 active ingredient (a.i.) kg ha^{-1} of isoxabin (Gallery® 75, Dow AgroSciences), 3.36 a.i. kg ha^{-1} of orayzalin (Surflan A.S.™, Dow AgroSciences), and 0.56 a.i. kg ha^{-1} of oxyfluorfen (Goal® 2XL, Dow AgroSciences). The initial treatment was not completely successful in controlling all vegetation, requiring a subsequent 1.68 a.e. kg ha^{-1} glyphosate broadcast application. Annually thereafter, all competition in the high-intensity plots has been controlled with applications of glyphosate (2 to 5% concentration in water), which will be applied until crop-trees in all plots reach crown closure. Seedlings were protected from herbicide exposure using plastic bags for each application until they reached sufficient size for a directed application. Vegetation control in the southern plots has been relatively successful, but the northern plots still support high densities of sedge (*Carex* spp.). Replanting of both poplar and spruce occurred during spring 2005 because of high initial mortality likely due to the poorly-drained soils across the site.

Measurements

Within each treatment plot is a nested 20 m by 20 m measurement plot where 100 crop-trees were initially selected (Fig. 4). Two types of measurements are made annually from late spring to early summer (May-June). The crop-tree inventory measures the height, height to the base of the live crown, diameter at breast height (d.b.h.), basal diameter, and survival of the 100 crop-trees in each measurement plot. The composition plot inventory consists of five 16-m^2 circular plots which are used to document changes in species composition and stand structure. Each of four composition plots is located 1.14 m inward from a measurement plot corner; the fifth is in the middle of the measurement plot. All woody vegetation ≥1.37 m tall within the subplot is tallied annually by species and d.b.h. is measured. For trees and shrubs <1.37 m tall, species and number of stems are recorded.

Crown diameter, stem form, and damage rating of the crop-trees are measured periodically. Crown widths are measured in the north-south and east-west directions. Stem form is evaluated on the butt log (bottom 3 m) of the trees and placed into one of four categories: no defect, correctable form (e.g., minor crook), questionable form (e.g., moderate crook or minor sweep), or cull (e.g., major crook, sweep, or presence of forks). In conjunction with stem form, damage is periodically measured. Damage to the foliage and main stem including crown dieback, cracks or damage to bole, and decay are examined during this assessment.

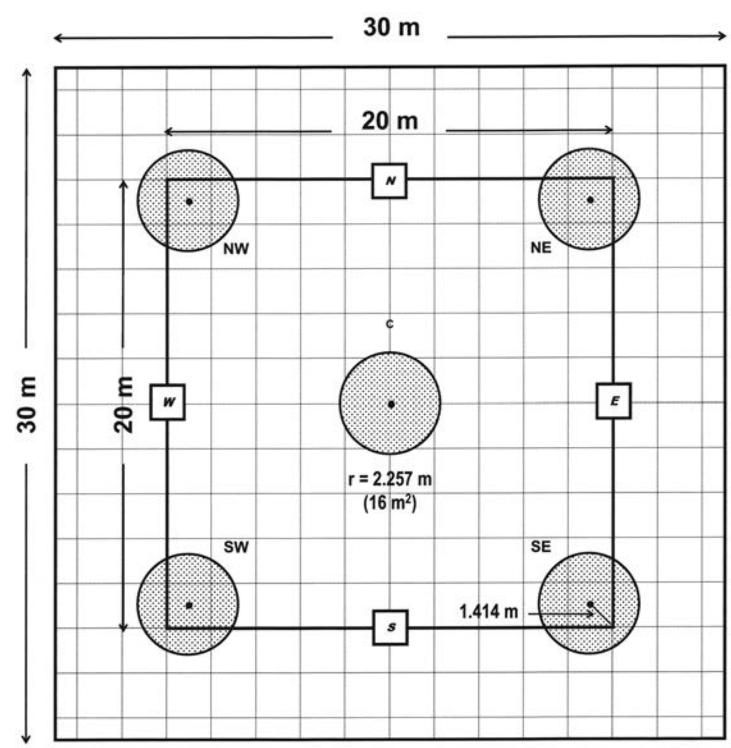


Figure 4.—Layout of 20 m by 20 m measurement plots within each 30 m by 30 m treatment plot. The five shaded areas are compositional plots and total 80 m^2. One crop or “pseudo-crop” tree is designated within each cell of the 2 m by 2 m grid (light dotted lines).

Since the start of the experiment, all of the energy inputs required to install and maintain the experiment have been measured. The energy inputs are herbicide a.i. (kg ha^{-1}), petroleum (L ha^{-1}), and labor (h ha^{-1}).

Analysis

In this paper, the composition plot inventory from the sixth post-treatment growing season (2009) was used to calculate species composition (calculated as proportion of basal area) and mean d.b.h. by species and treatment. These two variables were analyzed with analysis of variance by species, where the independent variable in the models was treatment. Significance was assessed at the $\alpha = 0.05$ level, and all analyses were performed in R version 2.13.2 (R Development Core Team 2011). Additionally, the energy inputs (herbicide, petroleum, and labor) were summed over the 6 years of the experiment and expressed as a unitless energy index to document the energy requirements of the various treatments.

FINDINGS

Tree Composition and Performance 6 Years Post-treatment

Annual measurements of the SIComp experiment have documented the responses of individual crop-trees as well as stand-level compositional and structural changes to the wide range of early silvicultural treatments. Species composition and mean tree d.b.h. by species from the sixth post-treatment season (2009) composition plot inventory are shown in Tables 2 and 3. The treatments were successful in promoting the desired species composition (expressed as a proportion of total basal area by species) after 6 years. The untreated control (C) and naturally regenerated hardwood treatments (LH and MH) were dominated by hardwood species, primarily trembling and bigtooth aspen, paper birch, and red maple (Table 2). The naturally regenerated conifer treatments (LC and MC) were dominated by balsam fir, but hardwood species were also well represented, especially bigtooth aspen and red maple with 13.8 percent (± 6.3%) and 12.3 percent (± 6.6%) in the LC treatment and 2.6 percent (± 6.3%) and 5.2 percent (±6.6%) in the MC treatment, respectively.

Balsam fir was the dominant species in the LM treatment, accounting for 53.1 percent (± 7.7%) of the composition, followed by bigtooth aspen (12.7% ± 6.3%) and red maple (8.8% ± 6.6%). Similarly, balsam fir was the most prevalent species in the MM treatment (30.1% ± 6.3%), followed by gray birch (*Betula populifolia*; 13.3% ± 8.8%), red maple (13.0% ± 6.6%), and paper birch (9.7% ± 5.6%). The

Table 3.—Least squares mean d.b.h. (cm) of the most common species 6 years after treatment. Treatment abbreviations are: C – untreated control, LC – low conifer, LM – low mixedwood, LH – low hardwood, MC – medium conifer, MM – medium mixedwood, MH – medium hardwood, HC – high conifer, HM – high mixedwood, and HH – high hardwood. The between-treatment standard error (cm) is also shown.

	Mean tree d.b.h. (cm)										Standard error
Species	C	LC	LM	LH	MC	MM	MH	HC	HM	HH	
Paper birch	1.1	0.6	0.6	1.3	0.6	1.5	1.0	-	-	-	0.4
Gray birch	1.4	0.2	0.4	0.3	0.2	0.4	0.5	-	-	-	0.4
Bigtooth aspen	3.8	6.3	6.3	3.5	1.9	7.2	4.8	-	-	-	1.6
Trembling aspen	2.5	4.0	3.0	7.8	0.6	3.4	3.5	-	-	-	1.6
Red maple	2.6	1.5	1.5	2.5	0.9	1.4	1.6	-	-	-	0.6
Balsam fir	1.9	3.5	3.2	1.7	3.3	3.3	0.6	-	-	-	0.4
Red spruce	1.3	2.2	1.7	0.1	1.5	3.9	-	-	-	-	1.1
Natural white spruce	0.2	1.4	3.3	-	0.4	-	0.3	-	-	-	0.9
Eastern white pine	2.7	1.3	2.5	0.5	2.2	4.8	0.3	-	-	-	1.0
Planted white spruce	-	-	-	-	0.8	1.0	-	1.2	1.1	-	0.2
Hybrid poplar	-	-	-	-		0.6	0.6	-	6.1	4.6	0.8

high-intensity treatments (HC, HM, and HH) were all successful in maintaining species composition, but in the HM treatment the proportion of white spruce had shifted to 80.7 percent (± 3.2%) from the initial proportion of 68.0 percent, likely due to the low hybrid poplar survival.

Across the treatments, bigtooth and trembling aspen had the largest d.b.h. among all species (Table 3). Both of these species had larger stem diameters in the LH, MH, LM, and MM treatments than the C treatment. The d.b.h. of paper birch, gray birch, and red maple in the low- and medium-intensity treatments was similar to the C treatment. Among conifer species, d.b.h. of balsam fir was slightly larger in the low and medium treatments compared to the C treatment, but red spruce diameter was similar across treatments. Hybrid poplar d.b.h. was greater in the high treatments than the medium treatments, suggesting that fill-planting these shade-intolerant clones with natural regeneration reduced their performance. In contrast, d.b.h of the planted white spruce did not differ between the silvicultural intensities.

Energy Investment through 2009

The energy input index shown in Figure 5 represents the sum of labor, herbicide, and petroleum inputs for each of the 10 treatment of the SIComp experiment through the 2009 spot-application of Accord® Concentrate in the high-intensity treatments. Among treatments, the high-intensity plots had the greatest consumption of energy, most of which was from initial labor to prepare the sites for planting and the subsequent annual control of competing vegetation. In the low- and medium-intensity treatments, energy investments have been greater in the conifer and mixedwood treatments than the hardwood treatments. The dominance of early-successional hardwood species following the 1995 clearcut required greater energy investment to shift species composition.

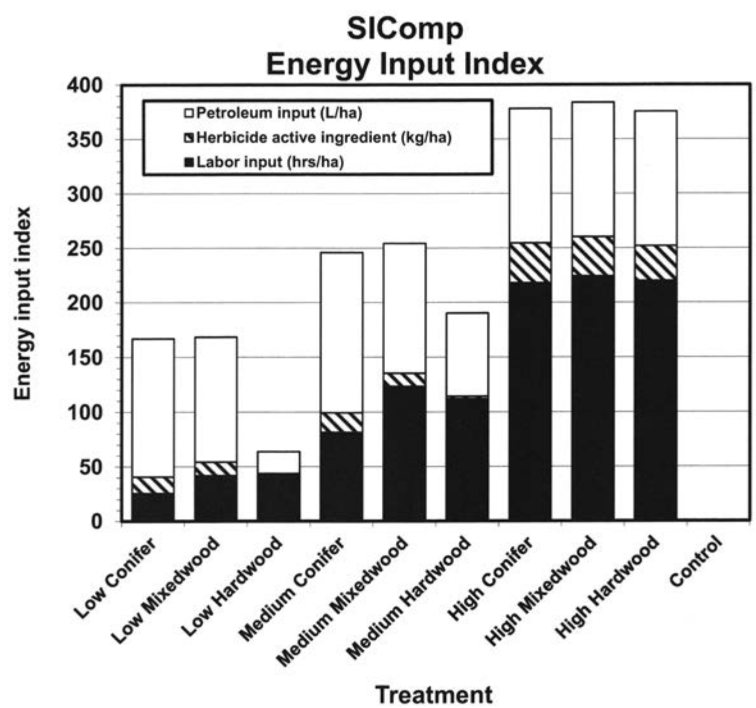


Figure 5.—Energy input index (a unitless measure of energy requirements to initiate and maintain the experimental design) for each of the 10 treatments maintained in the SIComp study through the sixth year of the study. The index is the sum of labor, herbicide, and petroleum inputs.

FUTURE DIRECTIONS

The SIComp experiment is still in its early stages of development. However, the study has already documented substantial differences in the response of young stands to various silvicultural treatments to achieve a range of objectives. It has provided opportunities to use the extreme range of environments created by the treatments to study germination success. Ongoing research will afford other valuable research opportunities, including gaining a better understanding of mechanisms driving forest productivity and carbon accumulation, and collecting data for improving regional growth and yield models. The novel experimental design and unique growing conditions created by the treatments provide a basis for future work on multiple levels. A potential future investigation on the tree level may focus on investigating whether sink or source ecophysiological mechanisms are responsible for the differences observed in productivity. Such an investigation could be linked to environmental conditions and resource availability to assess whether the responses are more closely related to species composition or site-related factors. Plans also call for incorporating the energy data into financial and carbon balance analyses. These analyses will allow us to determine the value of the various species compositions and identify treatments that maximize stand value and carbon sequestration.

ACKNOWLEDGMENTS

The installation and maintenance of the SIComp experiment has been supported by the U.S. Department of Agriculture, Forest Service, Agenda 2020 Project (grant number 03-CA-11242343-031); University of Maine Cooperative Forestry Research Unit; Northeastern States Research Cooperative (NSRC Theme 3) (grant numbers 10-DG-11242307-049, 09-DG-11242307-055); and the Henry W. Saunders' Chair, School of Forest Resources, University of Maine. We would like to thank Keith Kanoti, Rick Dionne, John Brissette, Matthew Olson, and the numerous technicians involved in the establishment and measurement of the experiment over the years.

LITERATURE CITED

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

Greene, D.F.; Kneeshaw, D.D.; Messier, C.; Lieffers, V.J.; Cormier, D.; Doucet, R.; Coates, K.D.; Groot, A.; Grover, G.; Calogeropoulos, C. 2002. **Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir).** The Forestry Chronicle. 78(2): 281-295.

Kanoti, K-G. 2005. **Factors influencing the germination, emergence, and early survival of boreal, temperate and exotic Acadian forest tree species in central Maine.** Orono, ME: University of Maine. 143 p. M.S. thesis.

McWilliams, W.H.; Butler, B.J.; Caldwell, L.E.; Griffith, D.M.; Hoppus, M.L.; Laustsen, K.M.; Lister, A.J.; Lister, T.W.; Metzler, J.W.; Morin, R.S.; Sader, S.A.; Stewart, L.B.; Steinman, J.R.; Westfall, J.A.; Williams, D.A.; Whitman, A.; Woodall, C.W. 2005. **The forests of Maine: 2003.** Resour. Bull. NE-164. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 188 p.

Newton, M.; Cole, E.C.; White, D.E.; McCormack, M.L., Jr. 1992. **Young spruce-fir forests released by herbicides. II. Conifer response to residual hardwoods and overstocking.** Northern Journal of Applied Forestry. 9(4): 130-135.

Paquette, A.; Bouchard, A.; Cogliastro, A. 2006. **Survival and growth of under-planted trees: a meta-analysis across four biomes.** Ecological Applications. 16(4): 1575-1589.

R Development Core Team. 2011. **R: a language and environment for statistical computing.** Vienna, Austria: R Foundation for Statistical Computing. Available at www.R-project.org. (Accessed February 18, 2013).

Rice, J.A.; MacDonald, G.B.; Weingartner, D.H. 2001. **Precommercial thinning of trembling aspen in northern Ontario: Part 1 - Growth responses.** The Forestry Chronicle. 77(5): 893-901.

Sendak, P.E.; Brissette, J.C.; Frank, R.M. 2003. **Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** Canadian Journal of Forest Research. 33(11): 2116-2128.

VASCULAR FLORA OF THE PENOBSCOT EXPERIMENTAL FOREST, WITH PROVISIONAL LISTS OF LICHENS AND BRYOPHYTES

Alison C. Dibble

Abstract.—A compilation of plant lists from all available sources since the 1950s represents the flora of the Penobscot Experimental Forest (PEF), Bradley, Maine. More than 300 taxa of vascular plants in 71 families and 186 genera are included. Approximately 85 percent of the taxa are native to Maine. Ten of 45 nonnative species are considered invasive. Infraspecific taxa have not necessarily been resolved, though 14 subspecies are included as they represent the species in the region. Two rare plants, *Carex oronensis* and *Clematis occidentalis*, have been documented. Omitted taxa overlap known species (e.g., "*Salix* sp." in which a single species is indicated), or are thought to be misidentifications. Sixty-two lichen and 49 bryophyte species are included provisionally. More species could be found in surveys for (1) ruderal plants in disturbed ground; (2) species found in the 1960s that are unknown today at the PEF; (3) expected, common species of spruce-fir that have not been documented; (4) graminoids, which seem underrepresented; and (5) species in riparian zones and wetlands. The plant checklist could be especially useful in documenting shifts in the flora that might be attributable to climate change. Nomenclature in a new flora of New England differs from the U.S. Department of Agriculture, Natural Resources Conservation Service database in significant ways; both sources should be considered in vegetation research in the PEF.

INTRODUCTION

Plant lists have value for estimating species diversity, summarizing large data sets, pointing out rare species and invasive plants, and stimulating additional study of an area, among many other uses (Palmer et al. 1995). This report is the first comprehensive vascular plant list for the Penobscot Experimental Forest (PEF) in Bradley, Penobscot County, Maine. The PEF is a long-term research site of the Northern Research Station of the U.S. Department of Agriculture (USDA), Forest Service, and is owned by the University of Maine Foundation. Ongoing research is conducted jointly and separately by the Forest Service and the university. The plants have been studied since the 1950s (Kenefic et al. 2006), yet plant species mentioned in peer-reviewed publications have not been compiled into a plant list for the 1,618-ha forest until now. Vegetation has been reported especially regarding changes in overstory composition and tree regeneration in response to silvicultural experiments (Brissette 1996, Kenefic et al. 2006). Earliest studies focused entirely on valuable timber species, and by the late 1960s, 105 woody plant species were on a list (Safford et al. 1969). Recent studies not only have included silvicultural treatments but also have broadened the focus, emphasizing the herb layer (Dibble et al. 1999, Schofield 2003), epiphytic lichens (Miller et al. 2007, 2008), and invasive plants (Bryce 2009). Observations and surveys apart from the system of Continuous Forest Inventory (CFI) plots (also called permanent sample plots or PSPs) have included some of the roadsides, successional forest, and former agricultural land.

Any flora can have significance for conservation planning in that emphasis tends to fall on species that are seldom collected. Once their rarity is recognized, attention might flow toward further understanding of habitat requirements for such species, and management activities can help assure their continued occurrence within an area. However, common and abundant species could be consequential if they are affected by disease or insect attack, with profound consequences for ecosystem processes, functions, and biodiversity (Ellison et al. 2005). Examples are the attack of American chestnut (*Castanea dentata*) by blight (*Cryphonectria parasitica* [Murrill] Barr), and the decimation of eastern hemlock (*Tsuga canadensis*) by hemlock woolly adelgid (*Adelges tsugae* Annand).

Checklist and atlas preparation have been developing in recent years and numerous new opportunities are now available. For example, Allard (2004, updated through 2011) continually updates an online statewide list of bryophytes of Vermont. This atlas includes global rankings and synonyms, with information at the level of the township, rather than state or county. Ability to update rapidly and to obtain feedback increases the utility of the atlas. Internet technology allows expanded opportunities for understanding species distributions, habitat requirements, and gaps in knowledge. Eventually, overlays with forest cover type, natural community classification, soils, bedrock, drainage, and land use could enable prioritization of habitat protection or at least recognition of conditions that are conducive to certain rare species.

At the same time, a push toward standardization of floras (Palmer et al. 1995) should help assure that the best possible data are reported in a manner that allows comparison across regions, continents, or the world. Palmer and associates have developed the Floras of North America project (Palmer 2013) with explorations of ways in which floristic inventories can be used across regions. We do not know all the uses that future researchers will find for the plant lists we prepare today, but those who work on checklists and atlases are alert to how easily errors might be perpetuated. These errors may occur because of (1) misidentifications, (2) duplicate entries that result when a species is identified and its genus (typically with "sp." for an undetermined species) is also included, or (3) failure to represent nomenclatural changes. Despite the many challenges, the preparation of a flora is worthwhile for its many uses, not the least of which are serving as a hypothesis to test, and assigning research priorities.

The purpose of this report is to establish a baseline list of vascular plants for the PEF in the form of a checklist. Though lichens and bryophytes have not yet been comprehensively surveyed in the PEF, these two groups are included as provisional lists. A secondary objective is to set the checklist in the context of what is known about plant species diversity in Maine. In this paper the PEF checklist is related to an ongoing effort to standardize floras, and the discussion includes a projection of uses for the checklist under several scenarios.

METHODS

All data reported here were collected at the PEF (44°49.8' to 44°52.1' N, 68°39.5' to 68°36.2' W) in Bradley, Penobscot County, Maine. Since 1994, the property has been owned by the University of Maine Foundation, Orono, Maine, with its flagship campus only 1.6 km away as the crow flies. About 500 ha of adjacent properties in the Dwight Demeritt Forest are owned by the University of Maine system but are not part of the PEF.

The PEF is in the Penobscot River watershed with a primary stream, Blackman Stream, as the major drainage. This is a glaciated low-elevation (< 75 m) landscape with mostly flat topography, ranging from 29-77 m, without significant bedrock outcrops and containing only a few large glacial erratics. The soils are diverse, with an average depth of organic matter at <16 cm, over about 50-100 cm of glacial till. Safford et al. (1969) summarized the B-horizon as having a soil texture that ranges from silt-loam to sandy-loam, and drainage characteristics that range from good to poor. A cool, humid climate prevails, with mean annual temperature of 6.7 ±0.3 °C (±SD, 1971-2000). About half the annual precipitation of 1,066 ±137 mm falls between May and October, with average annual snowfall of 289 ±78 cm (Larouche et al. 2010). The growing season is 183 ±15 days (Brissette 1996).

Dominant vegetation consists of mixed northern conifers, and has been described as representative of the Acadian Forest (Sendak et al. 2003), an ecotone between the conifer-dominated boreal forest and the hardwoods prevalent southward. The type is characterized especially by red spruce (*Picea rubens*), an economically valuable conifer with low genetic variability (Hawley and DeHayes 1994) that is common in parts of Maine, New Brunswick, and Nova Scotia, with smaller populations in New Hampshire, eastern New York, Vermont, high elevations of the Appalachians farther to the south, and Quebec, and an outlying population in Ontario. With it grow balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), and northern white-cedar (*Thuja occidentalis*). Also present but rarely dominant are white spruce (*Picea glauca*), black spruce (*P. mariana*), tamarack (*Larix laricina*), and red pine (*Pinus resinosa*). Hardwoods include especially red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), gray birch (*B. populifolia*), quaking aspen (*Populus tremuloides*), and bigtooth aspen (*P. grandidentata*). Additional hardwoods are American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), white ash (*Fraxinus americana*), and sugar maple (*Acer saccharum*).

In the Acadian Forest, natural disturbances tend to be in the form of small gaps rather than stand-replacing events. Fire-return interval and catastrophic windthrow events are thought to occur on a cycle of no less than 800 years, though human disturbance can alter this frequency (Seymour et al. 2002). Longevity of red spruce, eastern hemlock, and northern white-cedar contribute to a stable shade environment unless stands are influenced by timber harvest, insect outbreak, or similar canopy disturbances.

Land use at the PEF has consisted of some timber harvest since the 1790s, especially near Blackman Stream, but not much clearing for agriculture except at the west end of the property. The PEF has been the site of continuous, ongoing silvicultural treatments and monitoring conducted by the U.S. Forest Service, Northern Research Station since the 1950s. Repeated harvests have been conducted in 10 replicated treatments that include even-age and uneven-age prescriptions with entries from 5-20 years (Kenefic et al. 2006, Safford et al. 1969, Sendak et al. 2003). Approximately 580 CFI plots are arranged within the treatment compartments on a more-or-less evenly distributed pattern that typically avoids the road system and wetter areas. Data have been collected especially on more productive sites and uplands, whereas the wetlands contain fewer plots and have not been thoroughly inventoried.

Valuable knowledge about sustainable forest management has been derived from the data collected in these experiments, with focus on timber management, spruce budworm, coarse woody material, economics, biodiversity, growth and yield modeling, avian habitats, invasive plants in relation to soil properties and silvicultural treatment, and much more. Few stands at the PEF are unharvested old growth; at one time or another, most or all of the forest has been cut. Numerous stump sprout hardwoods and cut stumps are in evidence in most stands. In some areas, entry might have been more than 100 years ago. A reference compartment, which lacks any recent harvest, represents baseline conditions, and features a hiking trail enjoyed by visitors to the Maine Forest and Logging Museum at Leonard's Mills Historic Settlement, which is adjacent to the PEF. A general overview of the PEF as managed by the Northern Research Station and additional details can be found on the U.S. Forest Service's Web page for the PEF (U.S. Forest Service 2012).

For this report, a list of vascular plant, lichen, and bryophyte taxa on the PEF was derived from any relevant PEF publications and from some additional collecting in 2011. Most plant specimens were identified to the nearest species, though for 14 taxa a particular subspecies is the one known for this region; thus the list includes subspecific taxa. This aspect of plant identification was inconsistent between studies, and in some cases a taxon is represented at the genus level only. Nomenclature for vascular plants follows the USDA Natural Resources Conservation Service (NRCS) database, an atlas of all vascular plants and some bryophytes in the United States, which is online. The NRCS database is used by the U.S. Forest Service's Forest Inventory and Analysis Program and has gained acceptance for many uses, though its practicality as a sole nomenclatural source for a flora is questionable. Resources such as Haines (2011) that have gained popular usage among Maine botanists make a nationwide treatment less relevant unless the NRCS database reflects recent name changes.

The papers consulted include, in chronological order: Safford et al. 1969, Rinaldi 1970, Dibble et al. 1999 (including unpublished data for PEF vascular plant species that had not occurred with sufficient frequency to be included in analyses for the study), Schofield 2003, Miller et al. 2007, Miller et al. 2008, and Bryce 2009. Effort was made to consult every written document that contains a plant list, including unpublished masters theses that are not in peer-reviewed journals. For observations of ferns, graminoids, shrubs, subshrubs, vines, and forbs, only growing-season data were used. For trees, data collected during other times of year were also used.

Because study objectives and sampling methods differed between studies, plant lists are not directly comparable. For example, in some studies percentage cover of every vascular plant species was included (Bryce 2009, Dibble et al. 1999); in another, percentage cover of grasses, sedges, and rushes was not to the species level (Schofield 2003). The list was evaluated for plausibility as some identifications could be incorrect. Voucher specimens for questionable entries were examined if they were available. Nomenclature for species and family names, and native status (i.e., plants thought to be native to Maine rather than introduced or adventives) follow the NRCS database. Each taxon was assigned a growth form, e.g., fern (or fern ally), herb, graminoid, shrub, subshrub, tree, and vine. No abundance metric was assigned.

In addition to published reports, the checklist includes data from an informal list of lichens that were observed by James W. Hinds and Patricia Hinds during a field meeting of the Josselyn Botanical Society at the PEF in 1994. Nomenclature follows Hinds and Hinds (2007). Bryophyte species information came from several sources. Some bryophytes were included in plot data by Dibble et al. (1999) and Bryce (2009) but most of those were at the genus level. Miller et al. (2007, 2008) found certain epiphytic bryophytes and lichens to be important to invertebrate diversity. Otherwise bryophyte and lichen observations have been incidental in just a few studies at the PEF. Some common species to be expected in such a large conifer-dominated area were not yet listed. To increase the utility of this paper, I made additional observations in 2010-11 in three locations: (1) a mature red spruce-dominated stand at the Field Demonstration Trail, (2) a riparian mature northern white-cedar swamp called Dismal Swamp, and (3) low-lying mixed conifer forest near the freshwater marsh at Blackman Stream. Bryophyte nomenclature follows Allen (2005) through the Timmiaceae, and Crosby et al. (1999) for additional moss genera. For liverworts, nomenclature follows Stotler and Crandall-Stotler (1977).

Additional records, not published, that were considered for the plant list include (1) Orono sedge, *Carex oronensis*, which I documented at four locations in the PEF; (2) slippery elm, *Ulmus rubra*, determined by field crew during data collection for the Forest Inventory and Analysis Program in the 1990s, but not vouchered or confirmed, and otherwise undocumented in Maine since 1935; and (3) purple clematis, *Clematis occidentalis*, which is State Special Concern (Maine Department of Agriculture, Conservation, and Forestry 2010).

To understand whether species richness is high or low, species richness at the PEF (minus 34 questionable taxa) was compared to that for several other areas in Maine that are of a relevant size and occupied almost entirely by forest and wetlands. The other sites were: Massabesic Experimental Forest in Alfred and Lyman, York County (Dibble et al. 2004); Great Pond Mountain Wildlands in Orland, Hancock County; and Coastal Mountains Land Trust properties at Bald and Ragged Mountains, Camden, Knox County. A very well documented land holding, Acadia National Park with headquarters in Bar Harbor, Maine, was used as a far outlier in this comparison because the flora has been recently updated (Mittelhauser et al. 2010), and because bryophytes and lichens are especially well documented there. All these other areas are not necessarily similar to the PEF in terms of elevation; topography; soils; proximity to major water bodies, including the Atlantic Ocean; or forest management. Plant lists for two of the sites[1] are contained in in-house natural resource inventory reports prepared for land trusts, and are used in development of management plans.

As part of the effort to standardize checklists worldwide, this report was contrasted with Palmer et al. (1995) and with a list of desired components for floras, which is under development (M. Palmer, Oklahoma State University, pers. communication). The PEF checklist of vascular plants reported here is in compliance with Palmer's working list of features so that it could be referred to as an example in the standardization of florae and to assure best utility in the future.

[1] Dibble, A.C.; Rees, C.A. 2006. Great Pond Mountain Wildlands Natural Resource Inventory. Proprietary document held by the Great Pond Mountain Wildlands Trust.

Dibble, A.C. 2005. Ecological inventory of Bald Mountain Preserve, Camden, ME. Addendum 2008, in cooperation with C.A. Rees. Proprietary document held by the Coastal Mountains Land Trust.

Dibble, A.C. 2007. Ecological inventory of Ragged Mountain Preserve, Camden, ME. Addendum 2008, in cooperation with C.A. Rees. Proprietary document held by the Coastal Mountains Land Trust.

RESULTS

More than 300 vascular plant taxa in 71 families and 186 genera were considered appropriate for the PEF checklist (Appendix I), of which 45 species (about 15 percent) are not native to Maine. The list contains five genera for which "sp." is given, meaning that a species was not determined but, in my opinion, is likely to be other than those listed. Ideally the list would be fully resolved to infraspecific taxa; it includes 14 subspecific taxa but for some species it was not possible to resolve further. Vouchers are available for many of these taxa, but not all; collections by Olson et al. (2011), which were examined for this report, are especially useful in documenting the flora. Most are deposited at the Hart Building on the PEF, and unusual species were deposited at the University of Maine Herbarium in Orono. Families that are especially well-represented are the Asteraceae, Rosaceae, Cyperaceae, and Caprifoliaceae (Appendix II, based on NRCS designations). Perennials consisting of forbs, graminoids, shrubs, and trees were the majority of growth forms, with fewer ferns and fern allies, subshrubs, and only a few vines. Two rare plants, *Carex oronensis* (Fig. 1) and *Clematis occidentalis*, have been documented. Ten of the 45 nonnative plants are considered invasive or potentially so according to an unpublished list kept by the Maine Natural Areas Program: *Berberis thunbergii*, *Celastrus orbiculatus*, *Euonymus alata*, *Frangula alnifolia* (Fig. 2), *Lonicera morrowii*, *Lonicera xylosteum*, *Lythrum salicaria*, *Poa nemoralis*, *Rosa multiflora*, and *Rhamnus cathartica*. Several other nonnative species appear to persist and spread at the PEF under closed canopies or in openings, and might be considered invasive where they outcompete native vegetation, e.g., *Epipactis helleborine*, *Hylotelephium telephium*, *Solanum dulcamara*, *Valeriana officinalis*, and *Veronica officinalis*. Omitted taxa and unresolved genera are shown in Appendix III. They either are unlikely in southern Penobscot County and are thought to be misidentifications (e.g., *Krigia virginiana*, *Rosa*

Figure 1.—*Carex oronensis*, Orono sedge. It is known from several small populations in the PEF and at Leonard's Mills. (Photo courtesy of A.C. Dibble.)

Figure 2.—*Frangula alnifolia*, glossy buckthorn. This shade-tolerant tall shrub is spreading in the PEF in part because birds eat the fruits in autumn and spread them ever deeper into the forest. (Photo courtesy of A.C. Dibble.)

johannensis) or are believed to overlap known species (e.g., "*Salix* sp."); voucher specimens could not be found to check these.

Plant name changes make preparation of a checklist more complicated. Of the taxa in Appendix I, revisions in Haines (2011) have led to 34 changes in family designation, compared to the NRCS database. For 32 taxa, species became recognized at the subspecific level because that subspecies is the only one known in Maine. For 16 taxa, genus has changed, and these are likely to present particular challenge as some are common and likely in many parts of the PEF, such as northern starflower, *Trientalis borealis* (now *Lysimachia borealis*), and bunchberry, *Cornus canadensis* (now *Chamaepericlymenum canadense*). Five taxa had a change in specific epithet, and there were numerous changes in naming authority, though some are slight.

Most species on the list are common and widespread in Maine and elsewhere in northeastern North America. Some are shade-associated, and are not usually abundant in forest openings; examples are *Goodyera repens* (Fig. 3), *Mitchella repens*, *Monotropa uniflora*, *Moneses uniflora*, *Oxalis montana*, and *Trillium undulatum* (Fig. 4). Their presence in the silvicultural treatment at the PEF suggests their resilience to canopy disturbance.

Plants listed as rare in Maine are not frequent or abundant in the PEF, but I documented one, *Carex oronensis* (Orono sedge) (Dibble and Campbell 2001), state threatened, at two widely separated sites on the forest (at Leonard's Mills and on a roadside at

Figure 3.—*Goodyera repens*, lesser rattlesnake plantain. This native terrestrial orchid is shade adapted and with potential as an indicator of closed-canopy conifer stands. (Photo courtesy of A.C. Dibble.)

Figure 4.—*Trillium undulatum*, painted trillium. It can tolerate the low shade under balsam fir and other conifers, where few other vascular plants thrive. (Photo courtesy of A.C. Dibble.)

Compartment 10) in 1991. In 2011, I found another subpopulation along a woods road. Another listed rare plant is *Clematis occidentalis* (western virginsbower), State Special Concern, documented by Molly Schauffler near the beaver dam at Compartment 26.

Some plants are unusual in Maine, though not yet on a state rare plant list. An example is ditch stonecrop (*Penthorum sedoides*), which occurs in sandy oxbows along small rivers. Its presence at the PEF is noteworthy because habitat was not typical, perhaps reflecting a general lack of knowledge about this undercollected plant, and not necessarily a status as rare. There was no reference specimen at the University of Maine Herbarium until recently when the gap was noticed, an omission that might indicate the plant is infrequent and local.

Sixty-two lichens (macrolichens and crustose lichens) have been documented in the PEF (Appendix IV) from published lists; in-house lists; recent, brief surveys at three sites in the PEF; and other sources. None of the lichens is rare or highly unusual. Nine liverworts species and 40 mosses were found (Appendix V). Again, none is considered rare.

DISCUSSION

Vascular plant species richness is not particularly high for this size area of forested land in Maine, and is at least 13.5 percent lower than for the other areas compared in Appendix VI. Only 16.5 percent of the total number of 2,103 vascular plant taxa recorded in Maine (Campbell et al. 1995) are documented on the PEF. Characteristic of the shady understory in spruce-fir forest types, low species richness is due in part to thin, acid soils; acidifying needle litter; and “low shade,” in which the conifer lower canopy excludes direct sunlight except for brief exposure to sun flecks. The proportion of the light spectrum in red : far red light is important for seed germination of forest plants (Jankowska-Blaszczuk and Daws 2007). Because this proportion differs between coniferous and deciduous canopies, growing conditions might be poor under spruce-fir and hemlock for otherwise common understory herbs and shrubs.

The percentage of the PEF flora comprising nonnative plants is lower than the overall percentage in Maine, which has 634 naturalized vascular plant species. At the PEF, 42 naturalized species have been found, representing 12.1 percent of the flora, whereas in the entire state, 30.1 percent are nonnative. The percentage at the PEF is not particularly low for small florae (Palmer, pers. communication).

The changes in focus over time for observations at the PEF are reflected in the checklist. Earliest studies focused on the trees valuable for timber; then shrubs were included in the list of Safford et al. (1969). Rinaldi (1970) quantified trees, shrubs and herbs and the latter were in broad groups, not to species. In the early 1990s, I included percentage cover estimates for all vascular plant species and some bryophytes and lichens in a study of red spruce regeneration habitat that included plots in the PEF, but species with low frequency were dropped for analyses, and a complete list for the PEF was not published. The most comprehensive plant list for the PEF was Bryce (2009), who found 234 plant species on CFI plots. That total includes some entities identified to genus only, with possible overlap for entities identified to species. Abundance data are available on plots and as a frequency of measured plots. Common lichens and bryophytes were included in that study, but were a low priority with 13 genera and only 5 identified to species. I added 43 moss species based on observations at two sites in autumn 2010 and spring 2011. Schofield's (2003) list was for the Acadian Forest Ecosystem Research Program section of the PEF and is not as comparable to the other lists, though it contains many similarities, especially for woody plants.

There are numerous sources of error in the exercise of preparing plant checklists. Selection of taxa for inclusion in the list is somewhat arbitrary. The list reported here could be improved if a group of botanists familiar with the flora of southern Penobscot County and the entire state were to go through the list line by line and reach a consensus about what must be excluded, but in this report, only one botanist made those choices. Standard methods for treating questionable species have not yet been adopted. In the PEF checklist, excluded taxa had a variety of problems that led to their removal. If a genus was already represented in the list by one or more likely species, then it seemed that duplication would result by also listing the genus with no specific epithet (e.g., *Amelanchier* sp.).

Misidentifications were apparent—Safford et al. (1969) identified a plant as wickopee, *Dirca palustris* (Fig. 5), but the voucher specimen housed at the PEF is *Viburnum*. In recent years, Olson spotted *D. palustris* on the forest at the PEF, and verified it through use of a photo; this species is included in Appendix I. A few of Schofield's (2003) determinations were omitted due to extreme rarity in Maine, out of known range, inappropriate habitat, lack of confirmation because no voucher could be located, or a combination of these reasons. Examples are: *Asplenium* sp., *Corylus americana*, *Cystopteris* sp., *Krigia virginiana*, and *Rosa johannensis*.

Another challenge is plant name changes, which can be confusing—some names change and then change back again to the original name. Even more problematic is that name changes in taxon concepts or taxon ranks—such as when a subspecies is elevated to full species status—can generate complications when subspecies and varieties are lumped together (Palmer, pers. communication). Most of these entities

Figure 5.—*Dirca palustris*, wickopee. Known at the PEF from a single small plant, it flowers in early spring. (Photo courtesy of A.C. Dibble.)

can be updated and cross-referenced with powerful and widely available Web tools, but the NRCS plant database lags behind important taxonomic treatments including Haines (2011). There is wide expectation that Haines (2011) will serve as the standard for field botanists in New England, and eventually the NRCS plant database could adopt plant names that are likely to be in common usage. Further, the NRCS plant database contains at least a few subtle errors that could influence a plant checklist project, e.g., an erroneous name for *Carex foenea*, which has become confused with *C. siccata*. The NRCS currently includes only a few lichens and bryophytes, so its full utility for those groups is not realized. Haines (2011) includes only vascular plants. Additional complications in the PEF checklist can arise through published errors; for example, Miller et al. (2008) referred inadvertently to three species prominent in their study of arboreal arthropod diversity as "bryophytes," but those are epiphytic lichens.

The PEF checklist matches Palmer et al. (1995) regarding the recommended standards in most ways. The list is presented by genus, and other components such as elevational range are included. The PEF list departs in that precision of location data is not to standard. If latitude and longitude could be obtained for every population of each taxon, then relative abundance could be derived. This level of information might be prohibitive, even in a well-studied forest area. Bryce (2009) calculated species relative abundance based on frequency of each taxon in her study plots, providing a start toward finding associations between certain plant species and overstory conditions, soils, and other environmental variables.

Ways in Which the PEF Checklist Can Be Improved

Researchers can approach this checklist in several ways to identify gaps in our knowledge, and in doing so, can expand and improve the checklist itself. Not in any particular order by priority, these approaches include:

1. Further document the weedy plants of roadsides and log landings. Disturbed areas should be checked for invasive plants on a regular basis because of the threat such plants place upon the long-term silvicultural experiments if they are not controlled.
2. Survey the recently harvested 1,200 ha that are adjacent to the PEF. The parcel was recently added to ownership by the University of Maine System. Additional plant species are likely for the checklist.
3. Monitor known rare plant populations in the PEF periodically, perhaps every 5 years, in conformity with the New England Wild Flower Society and Maine Natural Areas Program reporting protocols.
4. Seek and document common plants of spruce-fir forests in Maine that are not yet on the checklist, such as: *Dulichium arundinaceum*, *Equisetum sylvaticum*, *Glyceria canadensis*, *Monotropa hypopithys*, *Osmunda regalis*, *Vaccinium vitis-idaea* var. *minus*, and *Viola macloskeyi* ssp. *pallens*.
5. Seek and document common nonnative plants, including *Rumex acetosella*, *Trifolium pratensis*, *Phalaris arundinacea*, and *Festuca filiformis*. These species might be present but were not found on plots. Because plots tended to be on better-drained soils, weedy plants of disturbed ditches might be underrepresented. Or there could be worker bias in that graminoid identification requires training and experience, is time-consuming, and might not be pertinent to project goals in some forest studies.
6. Many fern, graminoid, and other plant species can be resolved to species or subspecies only when their spore-bearing structures, flowers, or fruits are present. For the sake of best-quality data, and mindful of budget constraints, efforts should be made to verify questionable species wherever possible by returning to a plant population later in the season and pressing a voucher specimen.

7. Survey habitats that are underrepresented in Appendix I such as wetter areas that have not been actively managed for timber. Riparian zones, forested wetlands, swales, and boggy areas have not yet been investigated beyond walk-throughs between plots and a few casual visits by botanists and other researchers. Bryophytes are not well-inventoried in any of the habitats and should be sampled as part of a rigorous inventory (see Newmaster et al. 2005).

8. Survey taxonomic groups that are underrepresented in PEF research, including the lichens, bryophytes, and fungi. Of these the crustose lichens and liverworts need particular attention to make the list more representative of the flora and thus more useful. Crustose lichens were a major influence on the lichen checklist for Katahdin in Baxter State Park (Dibble et al. 2009, Hinds et al. 2009). At Acadia National Park, Sullivan (1996) found that more than half of the lichen diversity was in crustose lichens (198 of 379 species, Appendix VI). Although the PEF has hosted mycological field meetings, no list of fungi could be found for this report. I suggest that a requirement for use of the PEF as a field trip site for any botanical organization should be the understanding that species lists will be presented to the University of Maine and U.S. Forest Service.

9. Give particular thought to relative abundance when designing studies. An abundance rank for each species would be possible for many species in Appendix I, especially trees using the PEF plot data, and for many understory plants using Bryce's thesis data (2009), but the actual abundance on the forest might not be accurate based on purposes for which the sampling was designed. Data collected on plots do not always represent actual abundance in the area. Relative abundance is of sufficient importance to warrant a thoughtful approach in other studies.

10. Seek the "lost" species. A few species were reported by Safford et al. (1969) and have not been documented since, including *Acer saccharinum*, *Andromeda glaucophylla*, *Arceuthobium pusillum*, *Aronia melanocarpa*, and *Cephalanthus occidentalis*. For each of these, relocation of a population seems likely. At Acadia National Park, 200 of the total 862 species known for the park have not been seen for more than 20 years, such as numerous orchid species. This apparent loss could reflect change in land use, overcollection, or other factors (Greene et al. 2005, Mittelhauser et al. 2010).

    On the other hand, Safford et al. (1969) featured plants such as *Frangula alnifolia* and *Rosa multiflora*, which are widely recognized now as invasive. They did not mention whether they considered them invasive. They did not list Oriental bittersweet, *Celastrus orbiculatus*, which can now be found in numerous places on the PEF, suggesting that it is a recent arrival. Because Oriental bittersweet spreads rapidly due to bird dispersal of the fruits, this invasive vine should be given priority in management of the PEF. Oriental bittersweet, perhaps more than most of the other invasive plants present, could impact forest regeneration on study plots in the silvicultural treatments.

11. Prepare vegetation maps for the PEF to include recently described natural communities of Gawler and Cutko (2010). Although forest types as categorized by the Society of American Foresters (SAF) and other vegetation classification schemes have been assigned to some of the vegetation in the PEF, especially regarding the silvicultural treatments, there is not yet a complete map of vegetation at the PEF. Broad forest types might not be sufficient to understand habitat requirements of certain plants of interest. Types assigned by timber stocking conditions might be used as a surrogate for canopy closure, which could be helpful in study of the shade-associated understory plants such as *Goodyera repens* (Fig. 3) and *Trillium undulatum* (Fig. 4). Bryce (2009) measured canopy closure on a subset of her plots and

found that species that had been shown in other studies to frequent shady understory conditions did not always do so at the PEF, so other factors could be involved in their distribution.

Plant checklists for land trusts are sometimes prepared by habitat or community type, and such an approach at the PEF would require some careful investigation for many of the plant species, to establish their plant associations and see how the natural community descriptions depart from what is actually found on the property. Natural communities as described by Gawler and Cutko (2010) in coordination with NatureServe have not yet been applied to the vegetation at the PEF, but some stands could be considered for possible classification as the spruce-pine woodland (state rank S4), spruce-northern hardwoods forest (S5), lower elevation spruce-fir forest (S5), hemlock forest (S4), early successional forest (S5), with small patches of black spruce woodland (S2) or black spruce bog (S4), red maple swamp (S4), and northern white-cedar swamp (S4). Such community designations might be at a finer scale than the SAF forest types, and a plant checklist could eventually be prepared to reflect those natural communities. A purpose for such an exercise would be to recognize plant species that occur in only one or a few such communities; then management of the overstory might differ from what is otherwise being done. It should be noted that the northern white-cedar swamp at Dismal Swamp has not had any obvious recent harvest and apparently is outside of the CFI plot system. Cedar regeneration has been studied recently by Larouche et al. (2010) using data from the PEF, but not from Dismal Swamp.

12. To improve data quality in general, all studies in the PEF should include voucher specimens, particularly for any woody species not yet in Appendix I, and for herbs, grasses, sedges, and rushes; and lichens, mosses, and liverworts. If a plant is present in sufficient abundance, two specimens should be collected, one for the University of Maine Herbarium, where specimens can be examined if any questions arise, or for further study, and the other specimen for retention at the Hart Building on the PEF for handy access by field crews. This procedure would increase the utility of the specimens, but might involve administrative prioritization because a curation of vouchers takes up space, requires some preparation, and needs some maintenance over time. A maintenance schedule and curation protocols should be implemented at the PEF because even though the number of specimens is small compared to the Herbarium's collection, the voucher specimens are of untold importance for future studies, and are vulnerable to insect attack, mold, and other damage.

Future of the PEF Checklist

The usefulness of a plant checklist is only partly known. The PEF checklist might become incorporated into a larger study with many other checklists from other areas (see Palmer et al. 1995). There could be vast changes to the PEF that would make this checklist a vital record by which to compare to future conditions. For instance, climate change could bring about disruption to the canopy due to increased intensity and frequency of storms, and spread of nonnative insect pests (e.g., balsam woolly adelgid, *Adelges piceae*) as minimum temperatures in winter are elevated. With increased canopy opening—apart from harvest activities related to ongoing experiments at the PEF—climate change could be accompanied by the accelerated spread of invasive plants and native ruderal plant species. Some of these plants might interfere with regeneration of desirable tree species. Increased shrub and graminoid cover might alter fuel characteristics in the PEF (Dibble and Rees 2005); in turn, these changes in fuel could affect fire-return interval and intensity of burns (Dibble et al. 2008). Presence of invasive plants might also alter fuels; plant species of northeastern North America differ in their combustion properties and some invasive plants are more flammable than their native counterparts (Dibble et al. 2007). By comparing the number of more flammable species in a checklist to those thought to be relatively unflammable, differences in the fuels might be assessed.

Many changes are likely to be made to the PEF checklist in coming years. Like any snapshot of data, a presence-absence checklist is not a true reflection of the vegetation so much as a tool by which workers can know whether they are within the realm of possibility as they identify plants they have found on the forest. Toward that end, this checklist will be especially useful.

ACKNOWLEDGMENTS

Thank you to John Brissette and Laura Kenefic for inviting me to write this paper and for helpful comments on earlier versions. Elizabeth Bryce Olson provided the plant list resulting from her thesis and made available voucher specimens for verification. Her publications are shown below under Bryce and also under Olson. Arthur Haines identified some specimens for E. Olson's thesis. L. Kenefic and J. Brissette, with assistance from John Misener, helped in assuring that no studies were missed. Jim Hinds verified several lichen specimens, and Marnie Reeve refined identification of *Sphagnum* species. Reviews of an earlier version by Michael Palmer and Dorothy Allard led to substantive improvements in the paper. The Josselyn Botanical Society, especially Jim and Patricia Hinds, were helpful with lichen lists. Rick Dionne made available maps and records that contributed to this paper. Thank you to Robert Frank and Robert Seymour for introducing me to the PEF in 1993.

LITERATURE CITED

Allard, D. 2004. **Vermont bryophytes, with global and state ranks and synonyms.** Last updated April 2, 2011. Available at http://sites.google.com/site/dorothyallard/vtbryolist. (Accessed March 2012).

Allen, B. 2005. **Maine mosses: Sphagnaceae–Timmiaceae.** Memoirs of the New York Botanical Garden 93. Bronx, NY: The New York Botanical Garden Press. 420 p.

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

Bryce, E. 2009. **Influence of silvicultural treatment, site characteristics, and land use history on native and nonnative forest understory plant composition on the Penobscot Experimental Forest in Maine.** Orono, ME: University of Maine. 123 p. M.S. thesis.

Campbell, C.S.; Adams, H.P.; Adams, P.; Dibble, A.C.; Eastman, L.M.; Gawler, S.C.; Gregory, L.L.; Grunden, B.A.; Haines, A.D.; Jonson, K.; Rooney, S.C.; Vining, T.F.; Weber, J.E.; Wright, W.A . 1995. **Checklist of the vascular plants of Maine.** 3rd revision. Orono, ME: Josselyn Botanical Society of Maine, Bull. 13. University of Maine, Maine Agricultural and Experiment Station, Bull. 844. 100 p.

Crosby, M.R.; Magill, R.E. 2005. **Index of bryophytes 2001-2004.** St. Louis, MO: Missouri Botanical Garden. 31 p.

Crosby, M.R.; Magill, R.E. 2006. **Index of bryophytes 2005.** St. Louis, MO: Missouri Botanical Garden. 12 p.

Crosby, M.R.; Magill, R.E.; Allen, B.; He, S. 1999. **A checklist of the mosses.** St. Louis, MO: Missouri Botanical Garden. Available with updates at http://www.mobot.org/MOBOT/tropicos/most/checklist.shtml. (Accessed May 2013).

Dibble, A.C.; Brissette, J.C.; Hunter, M.L., Jr. 1999. **Putting community data to work: Some understory plants indicate red spruce regeneration habitat.** Forest Ecology and Management. 114(2-3): 275-291.

Dibble, A.C.; Campbell, C.S. 2001. **Conservation status of *Carex oronensis* (Cyperaceae), a Maine endemic.** Rhodora. 103: 351-379.

Dibble, A.C.; Rees, C.A. 2005. **Does the lack of reference ecosystems limit our science? A case study in nonnative invasive plants as forest fuels.** Journal of Forestry. Oct/Nov: 1-10.

Dibble, A.C.; Rees, C.A.; Sendak, P.E.; Brissette, J.C. 2004. **Vegetation of forested uplands in the Massabesic Experimental Forest.** Gen. Tech. Rep. NE-320. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 71 p.

Dibble, A.C.; White, R.H.; Lebow, P.K. 2007. **Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants.** International Journal of Wildland Fire. 16(4): 1-20.

Dibble, A.C.; Zouhar, K.; Kapler-Smith, J. 2008. **Northeastern bioregion.** In: Zouhar, K.; Smith, J.K.; Brooks, M.L.; Sutherland, S. Wildland fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 61-90. Vol. 6.

Dibble, A.C.; Miller, N.G.; Hinds, J.W.; Fryday, A.M. 2009. **Lichens and bryophytes of the alpine and subalpine zones on Katahdin, Maine, I: overview, ecology, climate and conservation aspects.** The Bryologist. 112(4): 651-672.

Ellison, A.M.; Bank, M.S.; Clinton, B.D.; Colburn, E.A.; Elliott, K.; Ford, C.R.; Foster, D.R.; Kloeepel, B.D.; Knoepp, J.D.; Lovett, G.M.; Mohan, J.; Orwig, D.A.; Rodenhouse, N.L.; Sobczak, W.V.; Stinson, K.A.; Stone, J.K.; Swan, C.M.; Thompson, J.; Von Holle, B.; Webster, J.R. 2005. **Loss of foundation species: consequences for the structure and dynamics of forested ecosystems.** Frontiers in Ecology and Environment. 3(9): 479-486.

Esslinger, T.L. 2011. **A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada.** (First posted December 1,1997; most recent version [#18] Dec 13, 2012). Fargo, N.D.: North Dakota State University. Available at http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm. (Accessed May 2013).

Gawler, S.C.; Cutko, A. 2010. **Natural landscapes of Maine: a classification of vegetated natural communities and ecosystems.** Augusta, ME: Maine Department of Agriculture, Conservation, and Forestry—Bureau of Geology, Natural Areas, and Coastal Resources: Maine Natural Areas Program.

Greene, C.W.; Gregory, L.L.; Mittelhauser, G.H.; Rooney, S.C.; Weber, J.E. 2005. **Vascular flora of the Acadia National Park region, Maine.** Rhodora. 107: 117-185.

Haines, A. 2011. **New England Wild Flower Society's Flora Novae Angliae: a manual for the identification of native and naturalized higher vascular plants of New England.** New Haven, CT: Yale University Press. 973 p.

Hawley, G.J.; DeHayes, D.H. 1994. **Genetic diversity and population structure of red spruce (*Picea rubens*).** Canadian Journal of Botany. 72 (12): 1778-1786.

Hinds, J.W.; Fryday, A.M.; Dibble, A.C. 2009. **Lichens of the alpine and subalpine zones on Katahdin, Maine, II. The Bryologist.** 112(4): 673-703.

Hinds, J.W.; Hinds, P.L. 2007. **Macrolichens of New England.** Memoirs of the New York Botanical Garden 96. Bronx, NY: The New York Botanical Garden Press.

Jankowska-Blaszczuk, M.; Daws, M.I. 2007. **Impact of red : far red ratios on germination of temperate forest herbs in relation to shade tolerance, seed mass and persistence in the soil.** Functional Ecology. 21(6): 1055-1062.

Kenefic, L.S.; Sendak, P.E.; Brissette, J.C. 2006. **Turning data into knowledge for over 50 years: USDA Forest Service research on the Penobscot Experimental Forest.** In: Irland, L.C.; Camp, A.E.; Brissette, J.C.; Donohew, Z.R., eds. Long-term silvicultural and ecological studies - results for science and management. Global Institute of Sustainable Forestry Research Paper 005. New Haven, CT: Yale University Press: 26-33.

Larouche, C.; Kenefic, L.S.; Ruel, J-C. 2010. **Northern white-cedar regeneration dynamics on the Penobscot Experimental Forest in Maine: 40-year results.** Northern Journal of Applied Forestry. 27(1): 5-12.

Maine Department of Agriculture, Conservation, and Forestry. 2010. **Maine Natural Areas Program rare plant fact sheet for *Clematis occidentalis*.** Available at http://www.maine.gov/doc/nrimc/mnap/features/cleocc.htm. (Accessed May 20, 2013).

Miller, K.M.; Wagner, R.G.; Woods, S.A. 2007. **Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine.** Canadian Journal of Forest Research. 37: 2175-2187.

Miller, K.M.; Wagner, R.G.; Woods, S.A. 2008. **Arboreal arthropod associations with epiphytes following gap harvesting in the Acadian forest of Maine.** The Bryologist. 111(3): 424-434.

Mittelhauser, G.H.; Gregory, L.L.; Rooney, S.C.; Weber, J.E. 2010. **The plants of Acadia National Park.** Orono, ME: University of Maine Press. 530 p.

Natural Resources Conservation Service. 2013. **Plants database.** Available at www.plants.usda.gov. (Accessed April 15, 2013).

Newmaster, S.G.; Belland, R.J.; Arsenault, A.; Vitt, D.H.; Stephens, T.R. 2005. **The ones we left behind: comparing plot sampling and floristic habitat sampling for estimating bryophyte diversity.** Diversity and Distributions. 11(1): 57-72.

Olson, E.; Kenefic, L.S.; Dibble, A.C.; Brissette, J.C. 2011. **Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: influence of site, silviculture, and land use history.** Journal of the Torrey Botanical Society. 138(4): 453-464.

Palmer, M. 2013. **The Floras of North America project.** Available at http://botany.okstate.edu/floras/index.html. (Accessed April 15, 2013).

Palmer, M.W.; Wade, G.L.; Neal, P. 1995. **Standards for the writing of floras.** BioScience. 45 (5): 339-345.

Rinaldi, A.M. 1970. **Deer and hare forage following strip clearcutting and slash disposal on the Penobscot Experimental Forest, Maine.** Orono, ME: University of Maine. 83 p. M.S. thesis.

Safford, L.O.; Frank, R.M.; Little, E.L., Jr. 1969. **Trees and shrubs of the Penobscot Experimental Forest Penobscot County, Maine.** Res. Pap. NE-128. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 27 p.

Schofield, D.A. 2003. **Vegetation dynamics and tree radial growth response in harvest gaps, natural gaps, and closed canopy conditions in Maine's Acadian forest.** Orono, ME: University of Maine. 163 p. M.S. thesis.

Sendak, P.E.; Brissette, J.C.; Frank, R.M. 2003. **Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** Canadian Journal of Forest Research. 33: 2116-2128.

Seymour, R.S.; White, A.S.; deMaynadier, P.G. 2002. **Natural disturbance regimes in northeastern North America – evaluating and formulating silvicultural systems using natural scales and frequencies.** Forest Ecology and Management. 155: 357-367.

Stotler, R.E.; Crandall-Stotler, B.J. 1977. **A checklist of the liverworts and hornworts of North America.** The Bryologist. 80: 405-428.

U.S. Forest Service. 2012. **Penobscot Experimental Forest.** Available at http://www.nrs.fs.fed.us/ef/locations/me/penobscot/. (Accessed May 2013).

APPENDIX I.

Checklist of the vascular plants of the Penobscot Experimental Forest, Bradley, Maine, at the level of species, with family name, growth form, status as nonnative (= *) or nonnative invasive (= **). Nomenclature follows that used in the NRCS database (NRCS 2013). Changes in family ("→"), genus, species, or subspecies in Haines (2011) are shown.

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Alismataceae	*Sagittaria latifolia* Willd.		forb	1
Anacardiaceae	*Rhus typhina* L.	*Rhus hirta* (L.) Sudworth	shrub	1
Anacardiaceae	*Toxicodendron radicans* (L.) Kuntze		subshrub	1
Apiaceae	*Hydrocotyle americana* L.		forb	1
Apiaceae	*Sium suave* Walter		forb	1
Aquifoliaceae	*Ilex mucronata* (L.) Powell, Savolainen & Andrews		shrub	1
Aquifoliaceae	*Ilex verticillata* (L.) A. Gray		shrub	1
Araceae	*Arisaema triphyllum* (L.) Schott		forb	1
Araceae	*Calla palustris* L.		forb	1
Araliaceae	*Aralia hispida* Vent.	(→ Apiaceae)	subshrub	1
Araliaceae	*Aralia nudicaulis* L.	(→ Apiaceae)	subshrub	1
Araliaceae	*Aralia racemosa* L.	*Aralia racemosa* L. ssp. *racemosa* (→ Apiaceae)	shrub	1
Araliaceae	*Aralia spinosa* L.	(→ Apiaceae)	shrub	1
Asteraceae	*Achillea millefolium* L.*	*Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper	forb	
Asteraceae	*Anaphalis margaritacea* (L.) Benth. & Hook.*		forb	
Asteraceae	*Doellingeria umbellata* (Mill.) Nees		forb	1
Asteraceae	*Erechtites hieraciifolia* (L.) Raf. ex DC.	*Erechtites hieraciifolius* (L.) Raf. ex DC. var. *hieraciifolius*	forb	1
Asteraceae	*Eurybia macrophylla* L.		forb	1
Asteraceae	*Eurybia radula* (Aiton) G.L. Nesom		forb	1
Asteraceae	*Euthamia graminifolia* (L.) Nutt.		forb	1
Asteraceae	*Hieracium aurantiacum* L.*		forb	
Asteraceae	*Hieracium caespitosum* Dumort.*		forb	
Asteraceae	*Hieracium lachenalii* C. C. Gmel.*		forb	

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Asteraceae	*Hieracium pilosella* L.*		forb	
Asteraceae	*Hieracium piloselloides* Vill.*		forb	
Asteraceae	*Lactua canadensis* L.		forb	1
Asteraceae	*Lapsana communis* L.*		forb	
Asteraceae	*Leontodon autumnalis* L.*	*Scorzoneroides autumnalis* (L.) Moench	forb	
Asteraceae	*Oclemena acuminata* (Michx.) Greene		forb	1
Asteraceae	*Petasites frigidus* (L.) Fr.	*Petasites frigidus* (L.) Fries var. *palmatus* (Ait.) Cronq.	forb	1
Asteraceae	*Solidago altissima* L.	*Solidago altissima* L. ssp. *altissima*	forb	1
Asteraceae	*Solidago canadensis* L.		forb	1
Asteraceae	*Solidago gigantea* Ait.		forb	1
Asteraceae	*Solidago hispida* Mulh. ex Willd.	*Solidago hispida* Mulh. ex Willd. var. *hispida*	forb	1
Asteraceae	*Solidago juncea* Ait.		forb	1
Asteraceae	*Solidago nemoralis* Ait.	*Solidago nemoralis* Ait. var. *nemoralis*	forb	1
Asteraceae	*Solidago puberula* Nutt.	*Solidago puberula* Nutt. var. *puberula*	forb	1
Asteraceae	*Solidago rugosa* Mill.		forb	1
Asteraceae	*Symphyotrichum ciliolatum* (Lindl.) A. Löve & D. Löve		forb	1
Asteraceae	*Symphyotrichum lateriflorum* (L.) A. Löve & D. Löve		forb	1
Asteraceae	*Symphyotrichum novi-belgii* (L.) G.L. Nesom		forb	1
Asteraceae	*Symphyotrichum puniceum* (L.) A. Löve & D. Löve		forb	1
Asteraceae	*Symphyotrichum racemosum* (Eliott) G.L. Nesom		forb	1
Asteraceae	*Taraxacum officinale* F.H. Wigg.*	*Taraxacum officinale* G.H. Weber ex Wiggers*	forb	
Balsaminaceae	*Impatiens capensis* Meerb.		forb	1
Berberidaceae	*Berberis thunbergii* DC.**		shrub	
Betulaceae	*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen		shrub	1
Betulaceae	*Betula alleghaniensis* Briton		tree	1
Betulaceae	*Betula papyrifera* Marsh.		tree	1
Betulaceae	*Betula populifolia* Marsh.		tree	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Betulaceae	*Corylus americana* Walter		shrub	1
Betulaceae	*Corylus cornuta* Marsh.	*Corylus cornuta* Marsh. ssp. *cornuta*	shrub	1
Betulaceae	*Ostrya virginiana* (Mill.) K. Koch		tree	1
Brassicaceae	*Erysimum cheiranthoides* L.*		forb	
Callitrichaceae	*Callitriche palustris* L.	(→ Plantaginaceae)	forb	1
Campanulaceae	*Lobelia inflata* L.		forb	1
Caprifoliaceae	*Diervilla lonicera* Mill.		shrub	1
Caprifoliaceae	*Linnaea borealis* ssp. *longiflora* (Torr.) Hulten	*Linnaea borealis* L. ssp. *americana* (Forbes) Hultén ex Clausen	subshrub	1
Caprifoliaceae	*Lonicera* × *bella* Zabel [*morrowii* × *tatarica*]**		shrub	
Caprifoliaceae	*Lonicera canadensis* Bartram ex Marsh.		shrub	1
Caprifoliaceae	*Lonicera morrowii* A. Gray**		shrub	
Caprifoliaceae	*Lonicera villosa* (Michx.) Schult.		shrub	1
Caprifoliaceae	*Lonicera xylosteum* L.**		shrub	
Caprifoliaceae	*Sambucus nigra* L. ssp. *canadensis* (L.) R. Bolli	(→ Adoxaceae)	shrub	1
Caprifoliaceae	*Sambucus racemosa* L. var. *racemosa*	*Sambucus racemosa* L. (→ Adoxaceae)	shrub	1
Caprifoliaceae	*Viburnum acerifolium* L.	(→ Adoxaceae)	shrub	1
Caprifoliaceae	*Viburnum dentatum* L.	(→ Adoxaceae)	shrub	1
Caprifoliaceae	*Viburnum lentago* L.	(→ Adoxaceae)	shrub	1
Caprifoliaceae	*Viburnum nudum* var. *cassinoides* (L.) Torr. & A. Gray	(→ Adoxaceae)	shrub	1
Caprifoliaceae	*Viburnum opulus* var. *opulus* L.*	*Viburnum opulus* ssp. *opulus* L.* (→ Adoxaceae)	shrub	
Caryophyllaceae	*Moehringia lateriflora* (L.) Fenzl		forb	1
Celastraceae	*Celastrus orbiculatus* Thunb.**		vine	
Celastraceae	*Euonymus alata* (Thunb.) Siebold**	*Euonymus alatus* (Thunb.) Siebold**	shrub	
Convolvulaceae	*Calystegia sepium* L.		forb	1
Cornaceae	*Cornus alternifolia* L. f.	*Swida alternifolia* (L. f.) Small	shrub	1
Cornaceae	*Cornus amomum* P. Mill. ssp. *amomum*	*Swida amomum* (P. Mill.) Small	shrub	1
Cornaceae	*Cornus canadensis* L.	*Chamaepericlymenum canadense* (L.) Aschers. & Graebn.	subshrub	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Cornaceae	*Cornus rugosa* Lam.	*Swida rugosa* (Lam.) Rydb.	shrub	1
Cornaceae	*Cornus sericea* L.	*Swida sericea* (L.) Holub	shrub	1
Crassulaceae	*Hylotelephium telephium* (L.) H. Ohba ssp. *telephium**		forb	
Crassulaceae	*Penthorum sedoides* L.	(→ Penthoraceae)	forb	1
Cucurbitaceae	*Echinocystis lobata* (Michx.) Torr. & A. Gray		vine	1
Cupressaceae	*Juniperus communis* L. var.*depressa* Pursh		shrub	1
Cupressaceae	*Thuja occidentalis* L.		tree	1
Cyperaceae	*Carex arctata* Boott ex Hook.		gramin	1
Cyperaceae	*Carex bromoides* Schkuhr ex Willd.	*Carex bromoides* Schkuhr ex Willd. ssp. *bromoides*	gramin	1
Cyperaceae	*Carex brunnescens* (Pers.) Poir.		gramin	1
Cyperaceae	*Carex communis* L.H. Bailey	*Carex communis* Bailey var. *communis*	gramin	1
Cyperaceae	*Carex debilis* Michx.		gramin	1
Cyperaceae	*Carex deflexa* Horem.	*Carex deflexa* Hornem. var. *deflexa*	gramin	1
Cyperaceae	*Carex deweyana* Schwein.	*Carex deweyana* Schwein. var. *deweyana*	gramin	1
Cyperaceae	*Carex disperma* Dewey		gramin	1
Cyperaceae	*Carex gracillima* Schwein.		gramin	1
Cyperaceae	*Carex gynandra* Schwein.		gramin	1
Cyperaceae	*Carex intumescens* Rudge		gramin	1
Cyperaceae	*Carex lacustris* Willd.		gramin	1
Cyperaceae	*Carex leptalea* Wahlenb.	*Carex leptalea* Wahlenb. ssp. *leptalea*	gramin	1
Cyperaceae	*Carex leptonervia* (Fernald) Fernald		gramin	1
Cyperaceae	*Carex lucorum* Willd. ex Link	*Carex lucorum* Willd. ex Link ssp. *lucorum*	gramin	1
Cyperaceae	*Carex lurida* Wahlenb.		gramin	1
Cyperaceae	*Carex normalis* Mack.		gramin	1
Cyperaceae	*Carex oronensis* Fernald		gramin	1
Cyperaceae	*Carex projecta* Mackenzie		gramin	1
Cyperaceae	*Carex scoparia* Schkuhr ex Willd.		gramin	1
Cyperaceae	*Carex stipata* Muhl. ex Willd.	*Carex stipata* Muhl. ex Willd. var. *stipata*	gramin	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Cyperaceae	*Carex tenera* Dewey		gramin	1
Cyperaceae	*Carex tribuloides* Wahlenb.	*Carex tribuloides* Wahlenb. var. *tribuloides*	gramin	1
Cyperaceae	*Carex trisperma* Dewey		gramin	1
Cyperaceae	*Scirpus cyperinus* (L.) Kunth		gramin	1
Cyperaceae	*Scirpus hattorianus* Makino		gramin	1
Dennstaedtiaceae	*Dennstaedtia punctilobula* (Michx.) T. Moore		fern	1
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. ex A. Heller	*Pteridium aquilinum* (L.) Kuhn ssp. *latiusculum* (Desv.) Hultén	fern	1
Dryopteridaceae	*Athyrium filix-femina* (L.) Roth.	*Athyrium angustum* (Willd.) C. Presl. (→ Woodsiaceae)	fern	1
Dryopteridaceae	*Dryopteris campyloptera* Clarkson	*Dryopteris campyloptera* (Kunze) Clarkson	fern	1
Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H. P. Fuchs		fern	1
Dryopteridaceae	*Dryopteris clintoniana* (D.C. Eaton) Dowell		fern	1
Dryopteridaceae	*Dryopteris cristata* (L.) A. Gray		fern	1
Dryopteridaceae	*Dryopteris intermedia* (Mulh. ex Willd.) Gray		fern	1
Dryopteridaceae	*Dryopteris marginalis* (L.) A. Gray		fern	1
Dryopteridaceae	*Gymnocarpium dryopteris* (L.) Newman	(→ Woodsiaceae)	fern	1
Dryopteridaceae	*Onoclea sensibilis* L.	(→ Onocleaceae)	fern	1
Dryopteridaceae	*Polystichum acrostichoides* (Michx.) Schott		fern	1
Equisetaceae	*Equisetum arvense* L.		fern	1
Equisetaceae	*Equisetum pratense* Ehrh.		fern	1
Ericaceae	*Andromeda polifolia* L. var. *glaucophylla* (Link) DC.		shrub	1
Ericaceae	*Chamaedaphne calyculata* (L.) Moench		shrub	1
Ericaceae	*Epigaea repens* L.		subshrub	1
Ericaceae	*Gaultheria hispidula* (L.) Muhl. ex Bigelow		subshrub	1
Ericaceae	*Gaultheria procumbens* L.		subshrub	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Ericaceae	*Gaylussacia baccata* (Wangenh.) L. Koch	*Gaylussacia baccata* (Wangenh.) K. Koch	shrub	1
Ericaceae	*Kalmia angustifolia* L.	*Kalmia angustifolia* L. ssp. *angustifolia*	shrub	1
Ericaceae	*Ledum groenlandicum* Oeder.	*Rhododendron groenlandicum* (Oeder) Kron & Judd	shrub	1
Ericaceae	*Rhododendron canadense* (L.) Torr.		shrub	1
Ericaceae	*Vaccinium angustifolium* Ait.		shrub	1
Ericaceae	*Vaccinium corymbosum* L.		shrub	1
Ericaceae	*Vaccinium macrocarpon* Ait.		shrub	1
Ericaceae	*Vaccinium myrtilloides* Michx.		shrub	1
Ericaceae	*Vaccinium oxycoccos* L.		shrub	1
Euphorbiaceae	*Euphorbia* sp.*		forb	
Fabaceae	*Lotus corniculatus* L.*		forb	
Fabaceae	*Trifolium hybridum* L.*		forb	
Fabaceae	*Trifolium repens* L.*		forb	
Fabaceae	*Vicia cracca* L.*	*Vicia cracca* L. ssp. *cracca*	forb	
Fabaceae	*Vicia tetrasperma* (L.) Schreb.*		forb	
Fagaceae	*Fagus grandifolia* Ehrh.		tree	1
Fagaceae	*Quercus rubra* L.		tree	1
Geraniaceae	*Geranium* sp.		forb	1
Grossulariaceae	*Ribes hirtellum* Michx.		shrub	1
Grossulariaceae	*Ribes lacustre* (Pers.) Poir.		shrub	1
Hamamelidaceae	*Hamamelis virginiana* L.		shrub	1
Iridaceae	*Iris versicolor* L.		forb	1
Juncaceae	*Juncus effusus* L.		gramin	1
Juncaceae	*Juncus* sp.		gramin	1
Juncaceae	*Juncus tenuis* Willd.		gramin	1
Juncaceae	*Luzula acuminata* Raf.		gramin	1
Juncaceae	*Luzula multiflora* (Ehrh.) Lej.		gramin	1
Lamiaceae	*Galeopsis tetrahit* L.*		forb	
Lamiaceae	*Lycopus americanus* Muhl. ex W. Bartram		forb	1
Lamiaceae	*Lycopus uniflorus* Michx.		forb	1
Lamiaceae	*Prunella vulgaris* L.*		forb	

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Lamiaceae	*Scutellaria galericulata* L.		forb	1
Lamiaceae	*Scutellaria lateriflora* L.		forb	1
Liliaceae	*Clintonia borealis* (Aiton) Raf.		forb	1
Liliaceae	*Maianthemum canadense* Desf.	(→ Ruscaceae)	forb	1
Liliaceae	*Maianthemum racemosa* (L.) Link	*Maianthemum racemosum* (L.) Link ssp. *racemosum* (→ Ruscaceae)	forb	1
Liliaceae	*Medeola virginiana* L.		forb	1
Liliaceae	*Polygonatum pubescens* (Willd.) Pursh	(→ Ruscaceae)	forb	1
Liliaceae	*Streptopus lanceolatus* (Aiton) Reveal		forb	1
Liliaceae	*Trillium erectum* L.	(→ Melanthiaceae)	forb	1
Liliaceae	*Trillium undulatum* Willd.	(→ Melanthiaceae)	forb	1
Liliaceae	*Uvularia sessilifolia* L.	(→ Colchicaceae)	forb	1
Lycopodiaceae	*Lycopodium annotinum* L.	*Spinulum annotinum* (L.) A. Haines	fern	1
Lycopodiaceae	*Lycopodium clavatum* L.		fern	1
Lycopodiaceae	*Lycopodium hickeyi* W.H. Wagner, Beitel & Moran	*Dendrolycopodium hickeyi* (W.H. Wagner, Beitel & Moran) A. Haines	fern	1
Lycopodiaceae	*Lycopodium obscurum* L.	*Dendrolycopodium obscurum* (L.) A. Haines	fern	1
Lythraceae	*Lythrum salicaria* L.**		forb	
Monotropaceae	*Monotropa uniflora* L.	(→ Ericaceae)	forb	1
Myricaceae	*Comptonia peregrina* (L.) J. M. Coult.		shrub	1
Myricaceae	*Myrica gale* L.		shrub	1
Oleaceae	*Fraxinus americana* L.		tree	1
Oleaceae	*Fraxinus nigra* Marsh.		tree	1
Oleaceae	*Fraxinus pennsylvanica* Marsh.		tree	1
Onagraceae	*Chamerion angustifolium* (L.) Holub ssp. *angustifolium*	*Chamerion angustifolium* (L.) Holub ssp. *circumvagum* (Mosq.) Kartesz	forb	1
Onagraceae	*Circaea alpina* L.	*Circaea alpina* L. ssp. *alpina*	forb	1
Onagraceae	*Circaea lutetiana* L. ssp. *canadensis* (L.) Aschers. & Magnus	*Circaea canadensis* (L.) Hill ssp. *canadensis*	forb	1
Onagraceae	*Epilobium ciliatum* Raf.		forb	1
Onagraceae	*Epilobium coloratum* Biehler		forb	1
Onagraceae	*Epilobium leptophyllum* Raf.		forb	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Onagraceae	*Ludwigia palustris* (L.) Elliott		forb	1
Onagraceae	*Oenothera perennis* L.		forb	1
Orchidaceae	*Cypripedium acaule* Aiton		forb	1
Orchidaceae	*Epipactis helleborine* (L.) Crantz*		forb	
Orchidaceae	*Goodyera repens* (L.) R. Br.	*Goodyera repens* (L.) R. Br. in Ait. & Ait. f.	forb	1
Orchidaceae	*Goodyera tessellata* Lodd		forb	1
Osmundaceae	*Osmunda cinnamomea* L.	*Osmundastrum cinnamomeum* (L.) C. Presl	fern	1
Osmundaceae	*Osmunda claytoniana* L.		fern	1
Osmundaceae	*Osmunda* sp.		fern	1
Oxalidaceae	*Oxalis corniculata* L.		forb	1
Oxalidaceae	*Oxalis montana* Raf.		forb	1
Oxalidaceae	*Oxalis stricta* L.		forb	1
Pinaceae	*Abies balsamea* (L.) Mill.		tree	1
Pinaceae	*Larix laricina* (Du Roi) K. Koch		tree	1
Pinaceae	*Picea abies* (L.) Karst*		tree	
Pinaceae	*Picea glauca* (Moench) Voss		tree	1
Pinaceae	*Picea mariana* (Mill.) Britton, Sterns & Poggenb.		tree	1
Pinaceae	*Picea rubens* Sarg.		tree	1
Pinaceae	*Pinus resinosa* Aiton		tree	1
Pinaceae	*Pinus strobus* L.		tree	1
Pinaceae	*Tsuga canadensis* (L.) Carriere		tree	1
Poaceae	*Agrostis perennans* (Walter) Tuck.		gramin	1
Poaceae	*Agrostis scabra* Willd.		gramin	1
Poaceae	*Anthoxanthum odoratum* L.*		gramin	
Poaceae	*Brachyelytrum aristosum* (Michx.) Trel.	*Brachyelytrum aristosum* (Michx.) Trel. in Branner & Coville	gramin	1
Poaceae	*Calamagrostis canadensis* (Michx.) P. Beauv.		gramin	1
Poaceae	*Cinna latifolia* (Trevis ex Goepp.) Griseb.		gramin	1
Poaceae	*Danthonia compressa* Austin	*Danthonia compressa* Austin ex Peck	gramin	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Poaceae	*Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult.		gramin	1
Poaceae	*Dichanthelium acuminatum* (Sw.) Gould & C.A. Clark		gramin	1
Poaceae	*Glyceria striata* (Lam.) A. S. Hitchcock		gramin	1
Poaceae	*Muhlenbergia uniflora* L.	*Muhlenbergia uniflora* (Muhl.) Fern.	gramin	1
Poaceae	*Oryzopsis asperifolia* Michx.		gramin	1
Poaceae	*Poa nemoralis* L.**		gramin	
Polygalaceae	*Polygala paucifolia* Willd.		forb	1
Polygalaceae	*Polygala sanguinea* L.		forb	1
Polygonaceae	*Fallopia scandens* (L.) Holub.		forb	1
Polygonaceae	*Polygonum convolvulus* L. var. *convolvulus*	*Fallopia convolvulus* (L.) A. Löve	forb	1
Polygonaceae	*Polygonum sagittatum* L.	*Persicaria sagittata* (L.) H. Gross	vine	1
Polygonaceae	*Polygonum* sp.		forb	1
Polygonaceae	*Rumex orbiculatus* A. Gray	*Rumex britannica* L.	forb	1
Primulaceae	*Lysimachia quadrifolia* L.	*Lysimachia quadrifolia* Sims (→ Myrsinaceae)	forb	1
Primulaceae	*Lysimachia terrestris* (L.) B.S.P.	(→ Myrsinaceae)	forb	1
Primulaceae	*Trientalis borealis* Raf.	*Lysimachia borealis* (Raf.) U Manns & A. Anderb. (→ Myrsinaceae)	forb	1
Pyrolaceae	*Moneses uniflora* (L.) A. Gray	(→ Ericaceae)	forb	1
Pyrolaceae	*Orthilia secunda* (L.) House	(→ Ericaceae)	forb	1
Pyrolaceae	*Pyrola americana* Sweet	(→ Ericaceae)	forb	1
Pyrolaceae	*Pyrola elliptica* Nutt.	(→ Ericaceae)	forb	1
Ranunculaceae	*Actaea rubra* (Aiton) Willd.		forb	1
Ranunculaceae	*Anemone quinquefolia* L.	*Anemone quinquefolia* L. var. *quinquefolia*	forb	1
Ranunculaceae	*Clematis occidentalis* (Hornem.) DC.	*Clematis occidentalis* (Hornem.) DC. ssp. *occidentalis*	vine	1
Ranunculaceae	*Coptis trifolia* (L.) Salisb.		forb	1
Ranunculaceae	*Ranunculus abortivus* L.		forb	1
Ranunculaceae	*Ranunculus acris* L.*		forb	
Ranunculaceae	*Ranunculus hispidus* L.	*Ranunculus hispidus* Michx.	forb	1
Ranunculaceae	*Ranunculus recurvatus* Poir.	*Ranunculus recurvatus* Poir. var. *recurvatus*	forb	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Ranunculaceae	*Thalictrum pubescens* Pursh		forb	1
Rhamnaceae	*Frangula alnus* Mill.**		shrub	
Rhamnaceae	*Rhamnus alnifolia* L. Her.		shrub	1
Rhamnaceae	*Rhamnus cathartica* L.**		shrub	
Rosaceae	*Amelanchier arborea* (Michx. f.) Fernald		tree	1
Rosaceae	*Amelanchier bartramiana* (Tausch) M. Roemer		shrub	1
Rosaceae	*Amelanchier canadensis* (L.) Medik.		shrub	1
Rosaceae	*Amelanchier laevis* Wiegand		shrub	1
Rosaceae	*Crataegus macrosperma* Ashe		tree	1
Rosaceae	*Dalibarda repens* L.	*Rubus dalibarda* L.	forb	1
Rosaceae	*Fragaria vesca* L.*		forb	
Rosaceae	*Fragaria virginiana* Duchesne		forb	1
Rosaceae	*Geum laciniatum* Murray		forb	1
Rosaceae	*Malus pumila* Mill.*		tree	
Rosaceae	*Malus sylvestris* (L.) Mill.*		tree	
Rosaceae	*Photinia melanocarpa* (Michx.) K.R. Robertson & Phipps	*Aronia melanocarpa* (Michx.) Ell.	shrub	1
Rosaceae	*Potentilla norvegica* L.		forb	1
Rosaceae	*Potentilla simplex* Michx.		forb	1
Rosaceae	*Prunus pensylvanica* L. f.	*Prunus pensylvanica* L. f. var. *pensylvanica*	tree	1
Rosaceae	*Prunus serotina* Ehrh.	*Prunus serotina* Ehrh. var. *serotina*	tree	1
Rosaceae	*Prunus virginiana* L.	*Prunus virginiana* L. var. *virginiana*	tree	1
Rosaceae	*Rosa multiflora* Thunb.**	*Rosa multiflora* Thunb. ex Murr.	shrub	
Rosaceae	*Rosa palustris* Marsh.		shrub	1
Rosaceae	*Rosa virginiana* Mill.		shrub	1
Rosaceae	*Rubus allegheniensis* Porter		shrub	1
Rosaceae	*Rubus* cf. *vermontanus* Blanch.		shrub	1
Rosaceae	*Rubus flagellaris* Willd.		shrub	1
Rosaceae	*Rubus hispidus* L.		subshrub	1
Rosaceae	*Rubus idaeus* ssp. *strigosus* (Michx.) Focke		forb	1
Rosaceae	*Rubus occidentalis* L.		shrub	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Rosaceae	*Rubus pensilvanicus* Poir.		shrub	1
Rosaceae	*Rubus pubescens* Raf.		subshrub	1
Rosaceae	*Sorbus americana* Marsh.		tree	1
Rosaceae	*Spiraea alba* Du Roi var. *latifolia*		shrub	1
Rosaceae	*Spiraea tomentosa* L.		shrub	1
Rubiaceae	*Cephalanthus occidentalis* L.		shrub	1
Rubiaceae	*Galium asprellum* Michx.		forb	1
Rubiaceae	*Galium palustre* L.		forb	1
Rubiaceae	*Galium trifidum* L.		forb	1
Rubiaceae	*Galium triflorum* Michx.		forb	1
Rubiaceae	*Houstonia caerulea* L.		forb	1
Rubiaceae	*Mitchella repens* L.		subshrub	1
Salicaceae	*Populus balsamifera* L.	*Populus balsamifera* L. ssp. *balsamifera*	tree	1
Salicaceae	*Populus grandidentata* Michx.		tree	1
Salicaceae	*Populus tremuloides* Michx.		tree	1
Salicaceae	*Salix bebbiana* Sarg.		shrub	1
Salicaceae	*Salix discolor* Muhl.		shrub	1
Salicaceae	*Salix eriocephala* Michx.	*Salix eriocephala* Michx. ssp. *eriocephala* var. *eriocephala*	shrub	1
Salicaceae	*Salix lucida* Muhl.	*Salix lucida* Muhl. ssp. *lucida*	shrub	1
Salicaceae	*Salix pedicellaris* Pursh		shrub	1
Salicaceae	*Salix sericea* Marsh.		shrub	1
Sapindaceae	*Acer pensylvanicum* L.		tree	1
Sapindaceae	*Acer platanoides* L.**		tree	
Sapindaceae	*Acer rubrum* L.		tree	1
Sapindaceae	*Acer saccharinum* L.		tree	1
Sapindaceae	*Acer saccharum* Marsh.	*Acer saccharum* Marsh. var. *saccharum*	tree	1
Sapindaceae	*Acer spicatum* Lam.		tree	1
Saxifragaceae	*Mitella nuda* L.		forb	1
Saxifragaceae	*Tiarella cordifolia* L.	*Tiarella cordifolia* L. var. *cordifolia*	forb	1
Scrophulariaceae	*Chelone glabra* L.	(→ Plantaginaceae)	forb	1
Scrophulariaceae	*Gratiola neglecta* Torr.	(→ Plantaginaceae)	forb	1
Scrophulariaceae	*Linaria vulgaris* Mill.**	(→ Plantaginaceae)	forb	
Scrophulariaceae	*Melampyrum lineare* Desr.	(→ Orobanchaceae)	forb	1

(Appendix I continued on next page)

Appendix I (continued)

Family	NRCS species with naming authority	Haines (2011), new name and change in family if applicable	Growth form	Native
Scrophulariaceae	*Veronica officinalis* L.*	(→ Plantaginaceae)	forb	
Scrophulariaceae	*Veronica serpyllifolia* L.*	(→ Plantaginaceae)	forb	
Solanaceae	*Solanum dulcamara* L.**		vine	
Sparganiaceae	*Sparganium*		herb	1
Taxaceae	*Taxus canadensis* Marsh.		shrub	1
Thelypteridaceae	*Phegopteris connectilis* (Michx.) Watt		fern	1
Thelypteridaceae	*Thelypteris noveboracensis* (L.) Nieuwl.	*Parathelypteris noveboracensis* (L.) Ching	fern	1
Thelypteridaceae	*Thelypteris palustris* Schott var. *pubescens* (Lawson) Fern.	*Thelypteris palustris* Schott var. *pubescens* (G. Lawson) Fern.	fern	1
Thelypteridaceae	*Thelypteris simulata* (Davenport) Nieuwl.	*Parathelypteris simulata* (Davenport) Holttum	fern	1
Thymelaeaceae	*Dirca palustris* L.		shrub	1
Tiliaceae	*Tilia americana* L.	(→ Malvaceae)	tree	1
Ulmaceae	*Ulmus americana* L.		tree	1
Valerianaceae	*Valeriana officinalis* L.**	(→ Caprifoliaceae)	forb	
Violaceae	*Viola blanda* Willd.		forb	1
Violaceae	*Viola cucullata* Ait.		forb	1
Violaceae	*Viola pubescens* Aiton		forb	1
Violaceae	*Viola renifolia* A. Gray		forb	1
Viscaceae	*Arceuthobium pusillum* Peck		forb	1
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.		vine	1

APPENDIX II.

Number of species per plant family, and growth form of vascular plants of the Penobscot Experimental Forest, Bradley, Maine. This summary follows the NRCS database, not Haines (2011) (see Appendix I), and includes some of the unresolved genera.

	Growth form							
Family	fern	graminoid	herb	shrub	subshrub	tree	vine	Total
Alismataceae			1					1
Anacardiaceae				1	1			2
Apiaceae			2					2
Aquifoliaceae				2				2
Araceae			2					2
Araliaceae				2	2			4
Asteraceae			31					31
Balsaminaceae			1					1
Berberidaceae				1				1
Betulaceae				3		4		7
Brassicaceae			1					1
Callitrichaceae			1					1
Campanulaceae			1					1
Caprifoliaceae				13	1			14
Caryophyllaceae			1					1
Celastraceae				1			1	2
Clusiaceae			1					1
Convolvulaceae			1					1
Cornaceae				4	1			5
Crassulaceae			2					2
Cucurbitaceae							1	1
Cupressaceae				1		1		2
Cyperaceae		26						26
Dennstaedtiaceae	2							2
Dryopteridaceae	10							10
Equisetaceae	2							2
Ericaceae				11	3			14
Euphorbiaceae			1					1
Fabaceae			5					5
Fagaceae						2		2

(Appendix II continued on next page)

Appendix II (continued)

Family	Growth form							Total
	fern	graminoid	herb	shrub	subshrub	tree	vine	
Geraniaceae			1					1
Grossulariaceae				2				2
Hamamelidaceae				1				1
Iridaceae			1					1
Juncaceae		5						5
Lamiaceae			6					6
Liliaceae			9					9
Lycopodiaceae	4							4
Lythraceae			1					1
Monotropaceae			1					1
Myricaceae				2				2
Oleaceae						3		3
Onagraceae			8					8
Orchidaceae			4					4
Osmundaceae	3							3
Oxalidaceae			3					3
Pinaceae						9		9
Poaceae		13						13
Polygalaceae			2					2
Polygonaceae			4				1	5
Primulaceae			3					3
Pyrolaceae			4					4
Ranunculaceae			8				1	9
Rhamnaceae				3				3
Rosaceae			6	15	2	8		31
Rubiaceae			5	1	1			7
Salicaceae				6		3		9
Sapindaceae						6		6
Saxifragaceae			2					2
Scrophulariaceae			6					6
Solanaceae							1	1
Sparganiaceae			1					1
Taxaceae				1				1

(Appendix II continued on next page)

Appendix II (continued)

Family	Growth form							Total
	fern	graminoid	herb	shrub	subshrub	tree	vine	
Thelypteridaceae	4							4
Thymeliaceae				1				1
Tiliaceae						1		1
Ulmaceae						1		1
Valerianaceae			1					1
Violaceae			4					4
Viscaceae			1					1
Vitaceae							1	1
Grand total	25	44	132	71	11	38	6	327

APPENDIX III.

(a) Some vascular plant taxa that have been proposed for inclusion by various researchers, but are omitted from the list. These taxa may lack appropriate habitat at the PEF or be out of known range. Unavailability of voucher specimens prevents their listing.

Asplenium sp.

Cystopteris sp.

Krigia virginica

Lactuca sativa

Pyrola chlorantha

Rosa johannensis

(b) Unresolved genera, some of which probably duplicate species already listed in Appendix I. During field work, plant material might have lacked flowers or fruits and could not be resolved below genus level, yet the genus is represented already by known species or subspecies in Appendix I.

Agrostis sp.

Amelanchier sp.

Aster sp.

Betula sp.

Bidens sp.

Carex sp.

Circaea sp.

Cornus sp.

Crataegus sp.

Danthonia sp.

Dryopteris sp.

Epilobium sp.

Equisetum sp.

Fraxinus sp.

Galium sp.

Geum sp.

Hieracium sp.

Hypericum sp.

Ilex sp.

Lonicera sp.

Luzula sp.

Lycopodium sp.

Oxalis sp.

Picea sp.

Poa sp.

Polygala sp.

Populus sp.

Potentilla sp.

Prenanthes sp.

Prunus sp.

Pyrola sp.

Ranunculus sp.

Ribes sp.

Rosa sp.

Rubus sp.

Salix sp.

Silene sp.

Solidago sp.

Sorbus sp.

Sparganium sp.

Thelypteris sp.

Trifolium sp.

Trillium sp.

Vaccinium sp.

Viola sp.

APPENDIX IV.

Provisional list of lichens of the Penobscot Experimental Forest, Bradley, Maine. Nomenclature follows Esslinger (2011).

Lichens	Macrolichen	Crustose lichen
Bryoria furcellata (Fr.) Brodo & D. Hawksw.	1	
Bryoria nadvornikiana (Gyelnik) Brodo & D. Hawksw.	1	
Caloplaca sp.		1
Candelariella sp.	1	
Cetrelia olivetorum (Nyl.) W.L. Culb. & C.F. Culb.	1	
Cladina sp.	1	
Cladonia chlorophaea group	1	
Cladonia coniocraea (Flörke) Sprengel	1	
Cladonia fimbriata (L.) Fr.	1	
Cladonia furcata (Hudson) Schrader	1	
Cladonia squamosa Hoffm.	1	
Cladonia sp.	1	
Cladonia spp. (*squamulose*)	1	
Collema subflaccidum Degel.	1	
Evernia mesomorpha Nyl.	1	
Flavoparmelia caperata (L.) Ach.	1	
Hypogymnia physodes (L.) Nyl.	1	
Lecanora sp.		1
Lepraria sp.		1
Leptogium corticola (Taylor) Tuck.	1	
Leptogium cyanescens (Rabenh.) Körber	1	
Leptogium saturninum (Dickson) Nyl.	1	
Lobaria pulmonaria (L.) Hoffm.	1	
Lobaria quercizans Michaux	1	
Melanelia halei (Ahti) Essl.	1	
Melanelia subaurifera (Nyl.) Essl.	1	
Myelochroa galbina (Ach.) Elix & Hale	1	
Nephroma parile (Ach.) Ach.	1	
Parmelia squarrosa Hale	1	
Parmelia sulcata Taylor	1	
Parmeliopsis ambigua (Wulfen) Nyl.	1	
Parmeliopsis hyperopta (Ach.) Arnold	1	
Peltigera canina (L.) Willd.	1	
Peltigera horizontalis (Hudson) Baumg.	1	
Peltigera polydactylon (Necker) Hoffm.	1	
Peltigera praetextata (Flörke ex Sommerf.) Zopf	1	
Peltigera rufescens (Weiss) Humb.	1	
Peltigera cf. *membranacea* (Ach.) Nyl.	1	

(Appendix IV continued on next page)

Appendix IV (continued)

Lichens	Macrolichen	Crustose lichen
Peltigera aphthosa (L.) Willd. or *leucophlebia* (Nyl.) Gyelnik	1	
Phaeophyscia pusilloides (Zahlbr.) Essl.	1	
Phaeophyscia rubropulchra (Degel.) Essl.	1	
Physcia millegrana Degel.	1	
Physconia detersa (Nyl.) Poelt	1	
Platismatia glauca (L.) W.L. Culb. & C.F. Culb.	1	
Platismatia tuckermanii (Oakes) W.L. Culb. & C.F. Culb.	1	
Punctelia rudecta (Ach.) Krog	1	
Pyxine sorediata (Ach.) Mont.	1	
Ramalina americana Hale	1	
Ramalina dilacerata (Hoffm.) Hoffm.	1	
Ramalina intermedia (Delise ex Nyl.) Nyl.	1	
Tuckermannopsis ciliaris (Ach.) Gyelnik grp.	1	
Usnea filipendula Stirton	1	
Usnea lapponica Vainio	1	
Usnea merrillii Motyka	1	
Usnea mutabilis Stirt.	1	
Usnea strigosa subsp. *strigosa*	1	
Usnea subfloridana Stirton	1	
Usnocetraria oakesiana (Tuck.) M.J. Lai & C.J. Wei	1	
Verrucaria sp.	1	
Vulpicida pinastri (Scop.) J.-E. Mattsson & M.J. Lai	1	
Xanthoparmelia conspersa (Ehrh. ex Ach.) Hale	1	
Xanthoparmelia tasmanica (Hooker f. & Taylor) Hale/*angustiphylla* (Gyelnik) Hale	1	
Total	59	3

APPENDIX V.

Provisional list of bryophytes at the Penobscot Experimental Forest, including 9 liverworts and 40 mosses. Nomenclature for liverworts follows Crosby and Magill (2005, 2006) and Stotler and Crandall-Stotler (1977). Nomenclature for mosses follows Allen (2005), except for pleurocarpous mosses (Crosby et al. 1999).

Bryophytes
Liverworts
Bazzania trilobata (L.) S. Gray var. *trilobata*
Frullania bolanderi Austin
Frullania tamarisci (L.) Dum. subsp. *asagrayana* (Mont.) Hatt.
Nowellia curvifolia (Dicks.) Mitt.
Pellia epiphylla (L.) Corda
Ptilidium ciliare (L.) Hampe
Ptilidium pulcherrimum (G. Web.) Hampe
Radula complanata (L.) Dum.
Scapania nemorosa (L.) Dum.
Mosses
Anomodon attenuatus (Hedwig) Hübener
Atrichum oerstedianum (C. Müller) Mitten
Atrichum sp.
Brachythecium cf. *laetum* (Brid.) B.S.G.
Brachythecium erythrorhizon W.P. Schimper in B.S.G.
Bryhnia novae-angliae (Sullivant & Lesquereux) Grout
Climacium dendroides (Hedwig) Weber & D. Mohr
Dicranum spp.
Dicranum montanum Hedwig
Dicranum polysetum Swartz
Dicranum scoparium Hedwig
Drepanocladus aduncus (Hedwig) Warnstorf
Hedwigia ciliata (Hedwig) Palisot de Beauvois
Homalia trichomanoides (Hedwig) W.P. Schimper in B.S.G.
Hylocomium splendens (Hedwig) W.P. Schimper in B.S.G.
Hypnum imponens Hedwig
Isopterygiopsis muelleriana (W.P. Schimper) Iwatsuki
Leucobryum glaucum (Hedwig) Ångström in Fries
Leucodon andrewsianus (H. Crum & L.E. Anderson) W.D. Reese & L.E. Anderson
Mnium hornum Hedwig
Neckera pennata Hedwig
Othodicranum flagellare (Hedw.) Loeske
Pleurozium schreberi (Willdenow ex Bridel) Mitten
Polytrichum sp.
Polytrichum commune Hedwig
Polytrichum ohioense Ren. & Card.

(Appendix V continued on next page)

Bryophytes
Mosses (continued)
Ptilium crista-castrensis (Hedwig) De Notaris
Rhizomnium appalachianum
Rhytidiadelphus triquetrus (Hedwig) Warnstorf
Sphagnum affine Renauld & Cardot
Sphagnum capillifolium (Ehrhart) Hedwig
Sphagnum fimbriatum Wils.
Sphagnum girgensohnii Russ.
Sphagnum palustre L.
Sphagnum squarrosum Crome
Sphagnum wulfianum Girg.
Tetraphis pellucida Milde.
Thuidium delicatulum (Hedw.) Schimp.
Ulota crispa (Hedw.) Brid.
Warnstorfia fluitans (Hedw.) Loeske

APPENDIX VI.

Comparison of species richness in the checklist of taxa for Penobscot Experimental Forest, Bradley, Maine, with that of some other land bases in Maine. Numbers are approximate and do not reflect some recent additions and name changes.

Land base	Number of hectares	Number of vascular plant taxa	Number of nonnative taxa (percentage of total known)	Number of lichen species reported	Number of liverwort species reported	Number of moss species reported
Maine, entire state	9,164,673	2,103	634 (30%)	(ca. 700)	147	(ca. 430)
Penobscot Experimental Forest, Bradley	1,618	344	45 (15%)	59	9	40
Massabesic Experimental Forest, Alfred and Lyman, York County	1,497	464	43 (9%)	Not reported	Not reported	Not reported
Great Pond Mountain Wildlands, Orland, Hancock County	1,700	400+	40 (10%)	12	5	14
Acadia National Park, Bar Harbor, Hancock County	14,648	1,135	284 (25%)	379, of which 198 are crustose	11+	51+

UNDERSTANDING PATTERNS AND REGULATORY PATHWAYS IN CONIFER ONTOGENY: THE ROLE OF THE PENOBSCOT EXPERIMENTAL FOREST

Michael E. Day, Michael S. Greenwood, Katherine Spencer, and Stephanie L. Adams

Abstract.—Multi-cohort stands maintained by the U.S. Department of Agriculture, Forest Service on the Penobscot Experimental Forest (PEF) have played a central role in research into the mechanisms that regulate ontogenetic trends in forest conifers as they control effects due to population, climatic, and edaphic factors. These long-term silvicultural studies have permitted direct comparisons of trends in morphology and physiology across life-stages, and experimental reciprocal grafting research among juvenile, mid-aged and old-growth individuals has proved an important approach to discriminating between trends due to tree size and those related to life-stage. The results of this research have provided valuable insight into the physiological mechanisms that underlie age-related trends in growth and development. Two decades of study on the PEF have identified a surprising paradox of high photosynthetic rates and declining stemwood production that characterizes the transition from mid-aged to old-growth life-stages in spruce. Ultimately, this research has led to a novel explanation for that paradox in the ecologically stable strategy hypothesis, which integrates environment, intrinsic regulation of development, and life-stage specific challenges.

INTRODUCTION

For the past two decades the Penobscot Experimental Forest (PEF) has been a key asset for the University of Maine's research program in tree physiology and physiological ecology in the School of Forest Resources. A major focus of research by the school's plant physiology and physiological ecology group is how external factors, such as climate, and internal factors, such as life-stage (ontogeny), control tree productivity and how they relate to tree form (anatomy and structure) and function (physiology). In turn, we seek to understand how the influence of these factors relates to species' competitive abilities, range-limits, and response to changing climates. While working on the gas exchange physiology of red spruce (*Picea rubens* Sarg.) in the early 1990s, we were struck by substantial differences in morphological and physiological attributes between various tree age classes. The older age classes in multi-cohort stands differed from younger trees not only in overall form, but also in branching patterns, needle morphology, and physiological properties such as stomatal sensitivity to atmospheric humidity and, potentially, in photosynthetic rates. It had been well established that stemwood production declines in forest trees after they reach roughly the midpoint of their normal lifespan (Assmann 1970). However, a physiological explanation for this and other observed age- and size-related trends was lacking.

The PEF stands that the U.S. Department of Agriculture (USDA), Forest Service has maintained under long-term selection silvicultural systems provided an ideal field laboratory to experimentally study age- and size-related phenomena in search of a physiological explanation for these trends. Stands in the Forest Service compartments on the PEF, managed for more than 50 years with an emphasis on red spruce, contain individuals from a common population ranging from germinants to old-growth trees, over a century and a half in age, all growing on similar soil types. Moreover, by using adjacent stands managed under selection and shelterwood systems, individuals of both free-to-grow and shaded crown status of all age classes could be selected to control for the effects of light environment on form and function.

The decline in stemwood growth efficiency (production per unit foliage) from mid-age to old age is of particular importance to forest management and silvicultural decisions. The paradigm of decreasing productivity with tree age forms the basis for silvicultural decisions on harvesting by defining expected returns on tree growth. This model is particularly important when considering the value of old trees in uneven-aged silviculture, carbon sequestration, and biomaterials production, and can result in a tension between short- and long-rotation silvicultural approaches.

EARLY STUDIES

Our initial assessments showed that red spruce on the PEF did indeed decrease stemwood production efficiency approximately 50 percent between the mid-aged time of maximum production (60 yr) and the oldest individuals (Fig. 1) (Day et al. 2001). This trend was subsequently confirmed by Seymour and Kenefic (2002). In needle morphology, older trees produce foliage that is more massive (lower specific leaf area, SLA) irrespective of sun-foliage or shade-foliage status (Fig. 2), demonstrating the interplay of heteroblasty and heterophylly in foliar development (Greenwood et al. 2009). In addition, old conifers deviate from the pyramidal crown form of younger individuals and develop a characteristic flat-topped form with low rates of stem and branch elongation and increased rates of lateral branch initiation (Fig. 3).

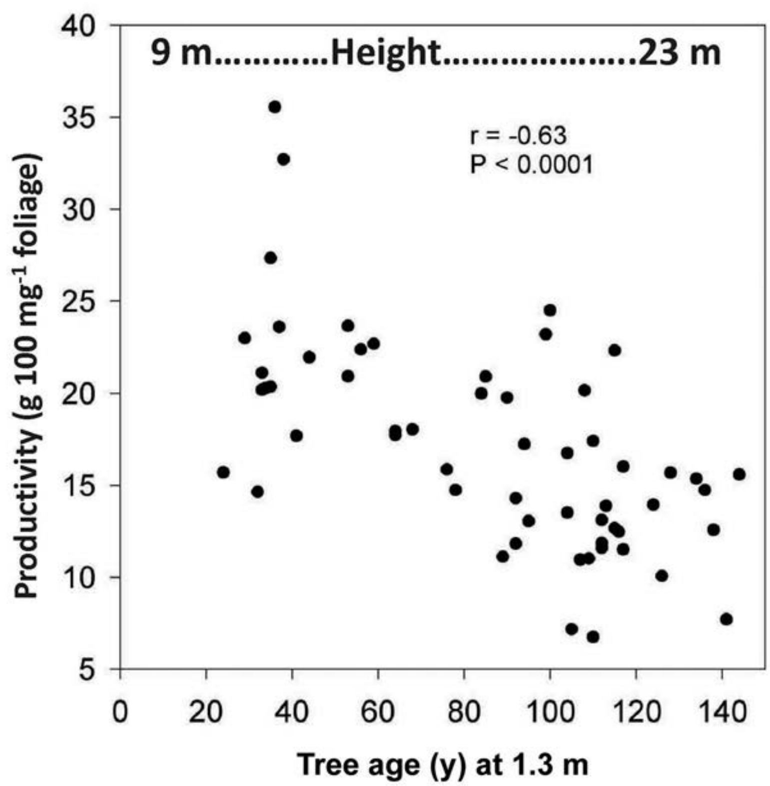


Figure 1.—Foliar efficiency in wood production for reproductively mature red spruce in the PEF (after Day et al. 2001).

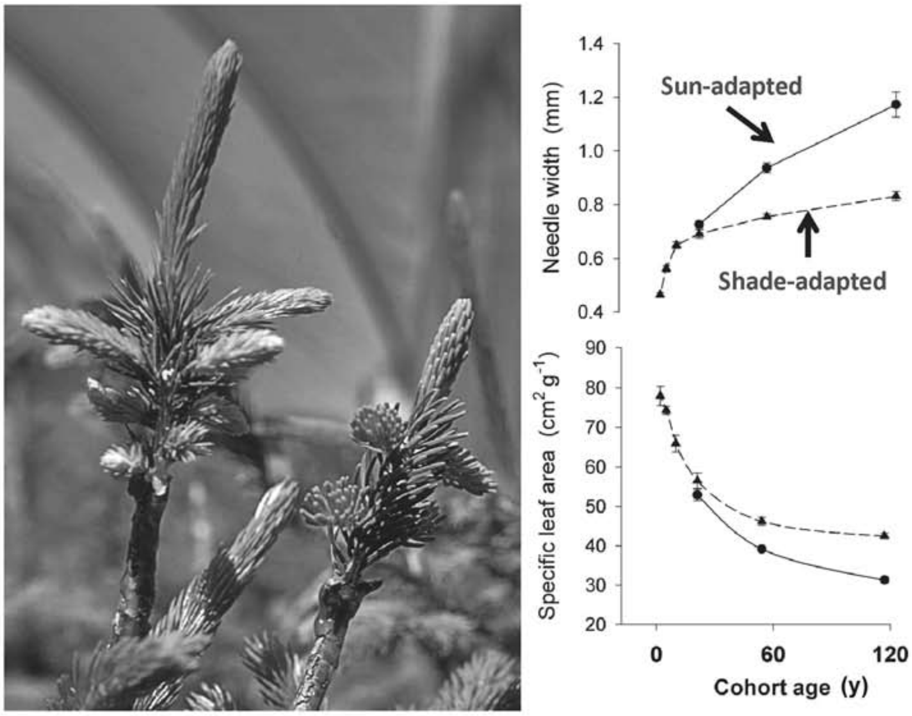


Figure 2.—Trends with tree age in specific leaf area for red spruce foliage from the PEF. Left, juvenile and old-growth foliage after grafting to common juvenile rootstock showing differences in overall needle morphology and robustness; right, independent trends associated with ontological heteroblasty and sun-shade heterophylly. (Means ± standard error.) (Data from Day et al. 2001). Photo courtesy of University of Maine.

Figure 3.—Typical age- and size-related changes in crown structure, branch elongation, and branches per stem length for red spruce in the PEF with a mid-aged (60 yr) tree on the left and old-growth (150 yr) on the right. Insets detail upper crown lateral branches. Photos courtesy of University of Maine.

Studies in western North America during the 1990s suggested that observed trends in productivity and perhaps morphology were due to decreased photosynthetic rates and/or enhanced midday depression of photosynthesis in old trees because of the increased hydraulic stress associated with longer water transport pathways (Ryan and Yoder 1997, Yoder et al. 1994). Others suggested restricted availability of nutrients, as more became incorporated in living biomass and coarse woody material (e.g., Binkley et al. 1995). Research on redwoods (*Sequoia sempervirens*) (Koch et al. 2004) and Douglas-fir (*Pseudotsuga menziesii*) (Woodruff et al. 2008) further suggested that height gradients in needle SLA are correlated with increasing water stress with tree height through limitations on cell number and/or expansion growth of developing tissues. Because most studies on the issue of age- and size-related declines in productivity, foliar morphology, and crown form were based on very tall (60-100+ m) trees in the Pacific Northwest, a major thrust of our research has been the applicability of "tall tree" hypotheses to the 20- to 30-m-high species typical of the Acadian Forest of northeastern North America. In some of the tallest trees, the biophysical mechanisms that transport water from soil to foliage may reach their upper bounds (Koch et al. 2004). The influences of gravity and resistance of long transport pathways on water potential (approximately -0.02 MPa m^{-1}) are likely to play various roles such as limiting CO_2 uptake for photosynthesis, and limiting the turgor pressure within developing cells required for their expansion. But it also seems likely that biophysical restrictions on water transport and their effects on physiology and morphology are much diminished in species of shorter stature growing in mesic forests.

RESEARCH ON GRAFTING

Although age-related trends in productivity and outward morphology of forest trees and their organs are manifest, understanding the bases for these phenomena is complicated by the confounding effects of size, chronological age, and external environment on long-lived organisms that progress in biomass through many orders of magnitude during their lifespan. One approach to addressing these potentially confounding factors is through grafting experiments in which scions from donors of various ages or sizes are grafted onto rootstock of a common age. A more comprehensive approach is reciprocally grafting scions from different ages onto rootstock representing the ages of the scion donors (Day et al. 2002). Earlier experiments using the former approach, where scions from older age classes are grafted onto juvenile rootstock, suggested that specific foliar traits, such as needle width, and growth habits such as plagiotropy are maintained in the genetic "memory" of scions from older donors (Day et al. 2001, Rebbeck et al. 1992).

In 2002 we initiated a reciprocal grafting study on the PEF between juvenile (< 10 yr, 1 m in height), mid-aged (60 yr, 10 m), and old (120+ yr, 20 m) red spruce, using multiple grafts in the crowns of eight trees in each of the two mature age-classes, and single grafts on juvenile rootstock. Three years into the study we made extensive in situ physiological and morphological measurements, and we completed a second series of measurements including destructive sampling when scions were harvested 7 years after grafting. Using this approach, we were able to separate the intrinsic and extrinsic mechanisms that regulate numerous morphological and physiological traits (Day and Greenwood 2011, Greenwood et al. 2010). In this regulatory scheme, intrinsic traits are those that are mainly influenced by mechanisms originating in shoot apical meristems (SAMs), the growth points for production of new cells that elongate shoots and branches. Intrinsic changes in SAM behavior in red spruce include age-related trends in rooting ability, decreased apical control of lateral buds, wider and more massive foliage, and increased reproductive competency. In contrast, extrinsic regulation results from influences outside of the SAM, and includes gas exchange behavior and resource allocation patterns. Other age- and size-related trends were explained by a complex interaction of intrinsic and extrinsic regulatory pathways (Fig. 4) (Day and Greenwood 2011). The influence of intrinsic and extrinsic factors

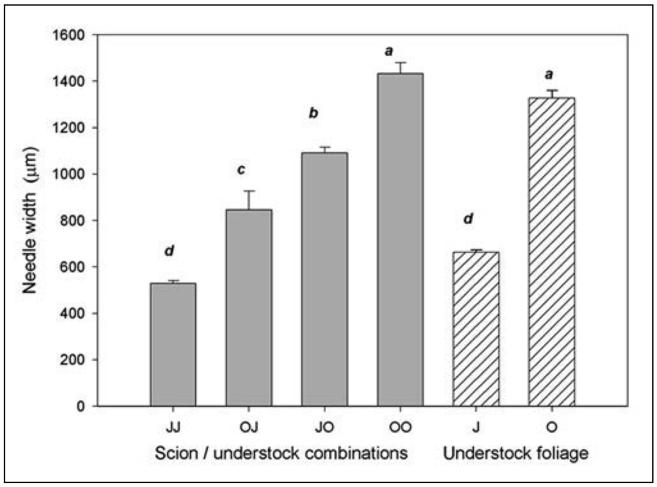


Figure 4.—Reciprocal grafting results showing complex intrinsic-extrinsic (relative to meristem) regulation of foliar morphology. Grafting combinations (left) are compared to understock foliage on the right. Scions from old donors maintained greater width than scions from juvenile donors on juvenile rootstock from intrinsic regulation, but were narrower than would be expected without extrinsic influence. Scions from juvenile donors grafted onto old rootstock maintained a narrower width of juvenile foliage, but were wider than "normal" juvenile needles. Dissimilar letters indicate significant differences ($\alpha = 0.05$; Tukey's honestly significant difference).

in regulating branching patterns proved of particular significance in understanding age-related trends in crown form (Greenwood et al. 2010).

STUDIES ON RESOURCE SUPPLY LIMITATIONS

During the past decade our lab also tested the relevance of resource supply restrictions on the question of age- and size-related decreases in stemwood increment beyond mid-age in red spruce. Again, the PEF multicohort populations proved invaluable by providing trees that were free to grow on common soil types and with documented harvest histories extending over five decades. In addition, the PEF road and landing system allowed the use of a self-propelled hydraulic lift to reach upper crowns for nondestructive measurements. Our research has demonstrated that neither xylem conductivity, nutrient availability, photosynthetic capacity, nor diurnal trends in stomatal conductance and photosynthesis differ between mid-aged and old red spruce (Fig. 5) (Adams 2006, Day and Greenwood 2011, Greenwood et al. 2008). In addition, a preliminary study of non-structural carbohydrates (NSC) in red spruce foliage suggested that net assimilation, the availability of photosynthetic products beyond the respiratory need of foliage, was not limiting in old trees (Fig. 6) (Day and Greenwood 2011). Subsequently, Spencer (2010) found no differences in soluble sugar concentrations between mid-aged and old trees across seasons and between two successive years. Similar trends in NSC concentrations have recently been reported for lodgepole pine (*Pinus contorta* Douglas ex Loudon) and redwoods in western North America and Australian eucalypts (*Eucalyptus* spp.) (Sala and Hoch 2009, Sillet et al. 2010).

Taken as a whole, the lack of evidence for resource limitations to observed age- and size-related decreases in tree productivity suggests that these trends may be regulated by demand-side (allocation and growth) pathways (Day et al. 2002). Further, Sillet et al. (2010) have suggested that the conventional use of stemwood production as a measure of tree productivity may suffer from a conceptual flaw stemming from a view of trees as wood production systems, as age- and size-related shifts in resource allocation patterns are not recognized. The results of our reciprocal grafting study supported continued high potential productivity in old red spruce (Greenwood et al. 2010). Despite less extension growth and greater branching of all age classes of scions grafted into the tops of old trees, all scions showed the same growth in total biomass after 7 years. Additionally, there were no differences in 7-year biomass increment between scions grafted on old rootstock and those on mid-aged rootstock, suggesting that growth potential was not influenced by age or size of rootstock.

STUDIES EXPLORING THE ECOLOGICALLY SUSTAINABLE STRATEGIES HYPOTHESIS

To address the adaptive significance of these ontological differences in growth habit, we have recently advanced the ecologically sustainable strategies (ESS) hypothesis (Day and Greenwood

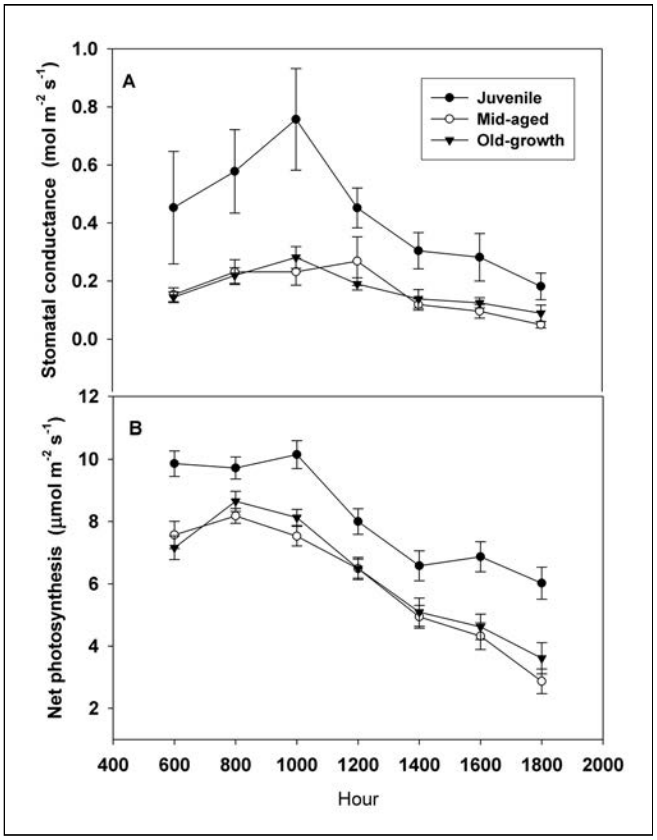


Figure 5.—Diurnal tracking of (A) stomatal conductance and (B) photosynthesis in the sun-adapted foliage of juvenile (10 yr, 1 m), mid-aged (60 yr, 10 m), and old (125+ yr, 20+ m) red spruce trees in the PEF. Juvenile trees exhibited higher net rates. Mid-aged and old trees showed the same rates and pattern of midday decrease in gas exchange. (Means ± standard error, n=24.) This pattern corresponds to those of electron transport rates (J_{max}) and carboxylation capacity (Vc_{max}) in the same trees (Greenwood et al. 2007).

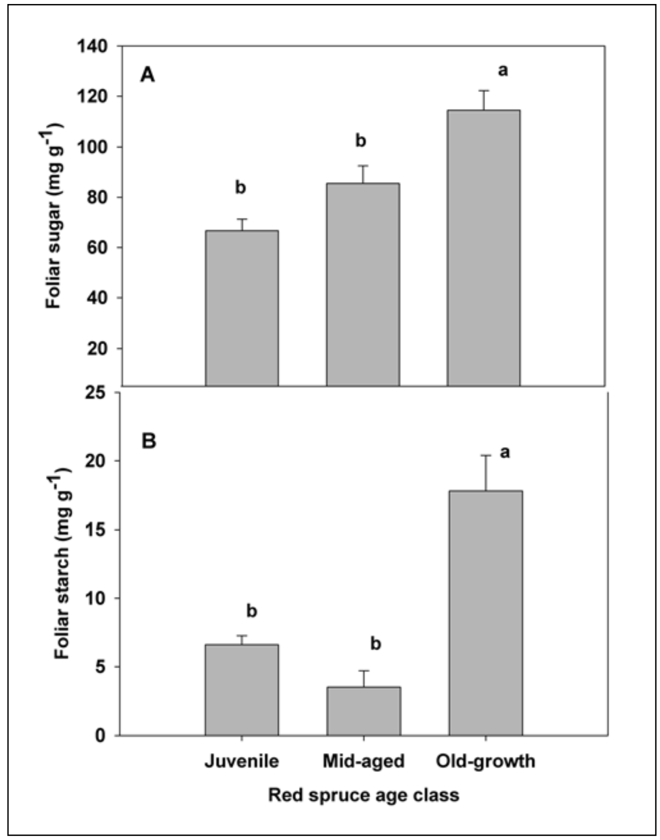


Figure 6.—Midday concentrations of the non-structural carbohydrates (A) sugar and (B) carbohydrates in red spruce foliage for juvenile (12 yr), mid-aged (60 yr), and old (120+ yr) red spruce in the PEF. The concentration of both soluble sugars and starch was greatest in the most rapidly growing age classes.

2011). This hypothesis is built on the evolutionarily sustainable strategy concept from game theory (Vincent et al. 1996), where an individual (or, in our case, a tree species) evolves a life-strategy that permits it to indefinitely occupy a niche regardless of competition from other species. In long-lived tree species such a life-strategy not only requires a degree of plasticity, but will vary through ontogeny in a pattern adapted to confront the highly variable challenges faced by the tree as it progresses through its life-stages. In its overarching concept, the ESS hypothesis predicts that trees growing in regions with high seasonal variability in climate such as the Acadian Region and in stochastic disturbance events, such as downburst cells and extra-tropical or tropical cyclones, will co-evolve a strategically uniform canopy. In these systems, emergent tree species would be evolutionarily penalized by increased risks from disturbance agents, a requirement for greater allocation of resources to stem diameter to counter dynamic loads, and increased likelihood of a shorter residence time in the upper canopy where reproductive effort has the greatest influence on population size. In contrast, maximum height growth resulting from positive-feedback "runaway" competition would be most likely in regions where relatively uniform climates and lower-intensity disturbances reduce the evolutionary costs of maximizing height growth and even provide an advantage to species that grow to their biophysical height limits.

Our continuing research based on the PEF provides support for the ESS hypothesis. We have shown that allocation patterns in conifer germinants are largely under the control of intrinsic mechanisms (Greenwood et al. 2008, Zazzaro 2009). At this life-stage, individuals have very limited capacity to assess their environment beyond a few centimeters' distance and any delay or resource/energy cost associated with sensing and responding to environmental cues decreases the individual's fitness to establish its roots in a water source and move towards a positive carbon balance. Therefore, intrinsically regulated allocation patterns that have been evolutionarily established as effective in previous generations are favored. Once established in the understory, seedlings tend to develop highly branched, flattened crowns and allocate minimal resources to extension growth of the main stem. When the seedling/sapling detects the presence of an overstory gap from changes in incident light quality and quantity, it begins its extension growth. During this phase of increasing stemwood productivity, allocation to the stem, apical down-regulation of lateral branching, and extension growth are maximized. Research on other conifer species suggests a role for a phytochrome-mediated response to altered red:far-red light wavelength composition resulting from gap formation or the presence of competitors in this ontogenetic stage (Hoddinott and Scott 1996). For PEF red spruce, Day and Greenwood (2011) provide evidence for a strong extrinsic control pathway in mid-aged individuals mediated by the external environment. Finally, once the tree reaches a position in the upper canopy, height growth is again decreased in favor of less apical control, increased branching, and more robust foliage, ultimately developing the spreading crown that characterizes the old life-stage. We believe this old-growth strategy minimizes risk and sustains long-term reproductive effort.

The ontogenetic pattern of growth allocation described above is supported by our long-term reciprocal grafting study. Scions from both old and juvenile donors showed the greatest tendency for branch production per centimeter of stem length and those from mid-aged donors showed the greatest tendency for elongation growth on rootstock of all ages (Greenwood et al. 2010). Our research to date suggests that the reversion to higher branchiness in old trees is under a complex mix of extrinsic and intrinsic regulatory mechanisms, but we have yet to identify potential pathways that alter this and other old-tree allocation patterns.

Having established that the foliage of old trees is equal in photosynthetic assimilation to that of mid-aged individuals that show maximum accumulation of stemwood, our current research on the PEF red spruce population seeks to identify the old-tree sinks for the "missing" photosynthate. The more massive needles on old trees also have a 28 percent decrease in internal air space, resulting in a greater specific gravity (Greenwood et al. 2008), and may support thicker cuticles and increased lignin content, all of which may add to both resource cost and foliar longevity. Our preliminary data also suggest that the more conservative strategy in this ontogenetic stage includes substantially increased allocation of carbon to starch reserves in the stem. When reserves are standardized on a unit-foliage basis, old trees are holding more than 4.5 times as much carbon in stem reserves as are mid-aged spruce (Fig. 7), greatly enhancing their resiliency to external stresses.

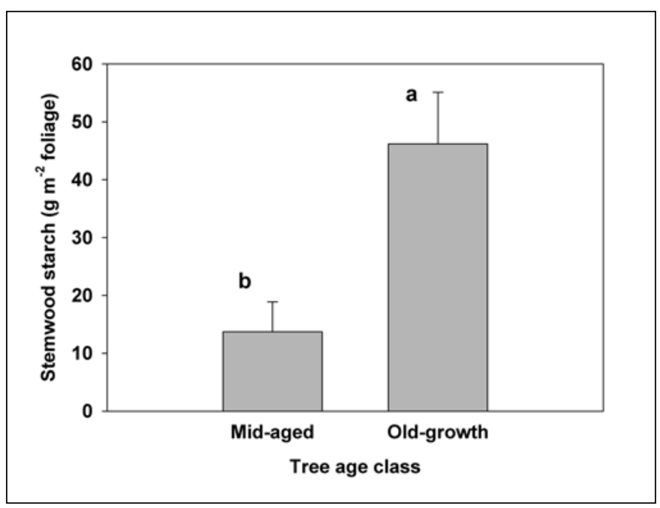


Figure 7.—Starch in stemwood reserves per unit foliage for mid-aged (65 yr) and old (120+ yr) red spruce age classes in the PEF. (Means ± standard errors, P < 0.001, n=16.)

CONCLUSIONS

The Forest Service long-term silvicultural experiment on the PEF has proven a critical resource in advancing our understanding of the complex and recalcitrant questions associated with age- and size-related trends in forest tree physiology and morphology. The answers to these questions will have substantial influence not only within the scientific understanding of tree ontogeny, but also practical application in defining paradigms for multicohort silviculture and the carbon economy of old trees. Our research group is continuing the study of age-related changes in temperate conifers with red spruce as our model species. Current projects include quantifying carbon dynamics and phenological cycles, variation in cell wall and foliar cuticular allocation, and the role of apical dominance in stage-specific crown attributes. The multicohort red spruce populations on the PEF continue to play a key role in our research.

ACKNOWLEDGMENTS

This material is based on work supported by the National Science Foundation under Grant No. IBN-0110142. (Any opinions, findings, conclusions, or recommendations expressed here are those of the authors and do not necessarily reflect the views of the National Science Foundation.) Additionally, the authors' research on age-related trends has been supported by the USDA Forest Service, Northern Research Station; Northeastern States Research Cooperative; and the Maine Agricultural and Forest Experiment Station. We are indebted to the USDA Forest Service for permitting research in its long-term silvicultural studies, and to the many graduate and undergraduate students who have made these studies possible. This is Maine Agricultural and Forest Experiment Station Publication Number 3314.

LITERATURE CITED

Adams, S.L. 2006. **A physiological examination of the age-related decline in photosynthesis in *Picea rubens*.** Orono, ME: University of Maine. 75 p. M.S. thesis.

Assman, E. 1970. **Principles of forest yield study.** Oxford, UK: Pergamon Press Ltd. 506 p.

Binkley, D.; Smith, F.W.; Son, Y. 1995. **Nutrient supply and declines in leaf area and production in lodgepole pine.** Canadian Journal of Forest Research. 25: 621-628.

Day, M.E.; Greenwood, M.S. 2011. **Regulation of ontogeny in temperate conifers.** In: Meinzer, F.C.; Lachenbruch, B.; Dawson, T.E., eds. Size- and age-related changes in tree structure and function. New York: Springer: 91-120.

Day, M.E.; Greenwood, M.S.; White, A.S. 2001. **Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age.** Tree Physiology. 21: 1195-1204.

Day, M.E.; Greenwood, M.S.; Diaz-Sala, C. 2002. **Age- and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control.** Tree Physiology. 22: 507-513.

Greenwood, M.S.; Ward, M.H.; Day, M.E.; Adams, S.A.; Bond, B.J. 2008. **Age-related trends in red spruce foliar plasticity in relation to declining productivity.** Tree Physiology. 28: 255-232.

Greenwood, M.S.; Day, M.E.; Berlyn, G.P. 2009. **Regulation of foliar plasticity in conifers: developmental and environmental factors.** Journal of Sustainable Forestry. 28: 48-62.

Greenwood, M.S.; Day, M.E.; Schatz, J. 2010. **Separating the effects of tree size and meristem maturation on shoot development of grafted scions of red spruce (*Picea rubens* Sarg.).** Tree Physiology. 30: 459-468.

Hoddinott, J.; Scott, R. 1996. **The influence of light quality and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species. I. Growth responses.** Canadian Journal of Botany. 74: 383-390.

Koch, G.E.; Sillet, S.C.; Jennings, G.M.; Davis, S.D. 2004. **The limits of tree height.** Nature. 428: 851-854.

Rebbeck, J.; Jesen, K.F.; Greenwood, M.S. 1992. **Ozone effects on grafted mature and juvenile red spruce: photosynthesis, stomatal conductance, and chlorophyll concentration.** Canadian Journal of Forest Research. 23: 450-456.

Ryan, M.G.; Yoder, B.L. 1997. **Hydraulic limits to tree height and tree growth.** Bioscience. 47(4): 235-242.

Sala, A.; Hoch, G. 2009. **Height-related growth declines in ponderosa pine are not due to carbon limitation.** Plant Cell and Environment. 32: 22-30.

Seymour, R.S.; Kenefic, L.S. 2002. **Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multi-aged northern conifer stands.** Canadian Journal of Forest Research. 32: 2032-2042.

Sillet, S.C.; Van Pelt, R.; Koch, G.W.; Ambrose, A.R.; Carroll, A.L.; Antoine, M.E.; Mifsud, B.M. 2010. **Increasing wood production through old age in tall trees.** Forest Ecology Management. 259: 976-994.

Spencer, K.J. 2010. **Addressing the age-related growth decline in red spruce productivity: integrating physiological and genomic approaches.** Orono, ME: University of Maine. 71 p. M.S. thesis.

Vincent, T.L.; Van, M.V.; Geh, B.S. 1996. **Ecological stability, evolutionary stability and the EES maximum principle.** Functional Ecology. 10: 567-591.

Woodruff, D.R.; Meinzer, F.C.; Lachenbruch, B.; Johnson, D.M. 2008. **Coordination of leaf structure and gas exchange along a height gradient in a tall conifer.** Tree Physiology. 29: 261-272.

Yoder, B.J.; Ryan, M.G.; Waring, R.H.; Schoettle, A.W.; Kaufmann, M.R. 1994. **Evidence of reduced photosynthetic rates in old trees.** Forest Science. 40: 513-527.

Zazzaro, S. 2009. **Plasticity in response to changing light environment for red spruce and balsam fir.** Orono, ME: University of Maine. 74 p. M.S. thesis.

STUDYING THE ROLE OF WOOD-DECAY FUNGI IN CALCIUM CYCLING ON THE PENOBSCOT EXPERIMENTAL FOREST: A PROGRESS REPORT

Walter C. Shortle, Jody Jellison, Kevin T. Smith, and Jonathan S. Schilling

Abstract.—Depletion of essential mineral nutrients from the rooting zone of trees in northern forests may reduce health and productivity. Long-term field investigations coupled with detailed laboratory studies enhance understanding of the biological processes and suggest means to address potential threats. One such investigation by the U.S. Department of Agriculture, Forest Service, in cooperation with the University of Maine, involves the role of wood-decay. fungi in cycling calcium (Ca) and other essential mineral nutrients. The investigation was established on the Penobscot Experimental Forest (Maine) in 1996 and 1997 and replicated in part on the Bartlett Experimental Forest (New Hampshire) in 1995. Some initial findings were: (1) A significant gain in Ca concentration in decaying wood occurred by 6 yr and that gain was sustained through 10 yr; (2) a significant gain in wood potassium was observed at 2 yr, but the gain was not sustained; and (3) observed changes in magnesium concentration in decaying wood were variable. Plans to continue this unique and important long-term study are described in this report.

INTRODUCTION

Calcium (Ca) is the fifth most abundant element in the Earth's crust. Other than nitrogen (N), Ca is considered the most important essential mineral for managing plant diseases (Rahman and Punja 2007). It is also the fifth most abundant element in trees after hydrogen (H), carbon (C), oxygen (O), and N (Shortle et al. 2008). Calcium is a structural link for wood components and regulates acidity, signals changes in various biological functions, and is needed to form protective layers in wood and bark (McLaughlin and Wimmer 1999). Therefore, living trees require a steady supply of Ca for wood formation and protection.

The depletion of root-available Ca from northern forest soils can occur over time by the processes of podzolization (Ponomareva 1969) and can be accelerated by acid deposition, the input of non-biological acidity resulting from regional emissions of sulfur (S) and N oxides (Shortle and Bondietti 1992). Declines in stem growth and mortality due to Ca depletion followed by aluminum (Al) mobilization have been documented in spruce (*Picea* spp.) (Lawrence et al. 1995, 2005; Shortle and Smith 1988; Shortle et al. 1997) and maple (*Acer* spp.) (Johnson et al. 2008, Lawrence et al. 1999, Long et al. 2009, St.Clair et al. 2008, Zaccherio and Finzi 2007).

As trees die and woody parts are shed or broken, wood is added to the forest floor. Root-available Ca is replaced in depleted sites by the action of wood-decay fungi that both release the solar energy stored in cellulose and lignin, the two most abundant organic substances in nature, and enrich the decayed wood residue with Ca from external sources. Microcosm tests demonstrate movement of Ca into decaying wood of conifers (Connolly et al. 1999, Ostrofsky et al. 1997) and hardwoods (Clinton et al. 2009). Many of the fungi that decompose wood are large, long-lived organisms that produce extensive mycelial networks, including cords and rhizomorphs, which move essential elements for many meters through the forest floor in and out of decaying wood (Boddy and Watkinson 1995, Connolly and Jellison 1997, Lindahl et al. 2001). Although commonly regarded as microorganisms, the dominant wood-decay fungi are anything but "micro-".

The purposes of the studies established on the Penobscot Experimental Forest (PEF) in Maine in 1996 and 1997 and on the Bartlett Experimental Forest (BEF) in New Hampshire in 1995 were (1) to determine changes in Ca and the other two essential base cations, magnesium (Mg) and potassium (K), as well as the acid-mobilized metals manganese (Mn), Al, and iron (Fe) in wood decaying in ground contact for at least 15 yr; (2) to determine changes in these elements in the organic and underlying mineral soil contiguous with the decaying wood; and (3) to archive wood samples in progressive stages of decay that preserve features indicative of biological processes of decay and the incorporation of residues into soil. Some key features being studied are differences in decay type (brown-rot, white-rot), variations in cation solubility and exchange properties, and modifications to cell wall polymers, especially lignin.

METHODS

The tree species selected for study were red spruce (*P. rubens* Sarg.) on the PEF and BEF, red maple (*A. rubrum* L.) at both locations, eastern hemlock (*Tsuga canadensis* [L.] Carr.) on the PEF, and paper birch (*Betula papyrifera* Marsh.) on the PEF. For each combination of location and species, 3 groups of 10 trees in a dominant or co-dominant position and 15- to 45-cm diameter at 1.3 m above ground were selected and tagged to identify the tree and treatment. Treatments were assigned at random. One group was used as an uncut reference for soil samples. Trees in a second group were cut and the felled trees left in place to decay in a gap in the canopy. Trees in the third group were cut and sections of the felled trees were hauled and placed under the forest canopy to decay while the gap was left with only stumps to decay (all tops and branches were removed).

Time-zero reference disks, 5 cm thick, were cut from all felled stems at 3 m and 7 m above the stumps. Decaying wood was subsequently collected at 2-yr intervals from the intervening 4-m bolt. Small soil pits dug next to the bolt provided samples of the O-horizon and the underlying 10 cm of mineral soil. Soil pits in the reference group and the stump-only area were taken at approximately where the 4-m bolt would have been if trees were felled. The position of each decaying bolt was mapped for future reference. Decaying wood was collected for chemical analysis by removing and discarding a 10-cm length from the lower end of each bolt followed by the removal and retention of a 5-cm-thick sample disk. Small soil pits were used to sample soil contiguous with the decaying stem at 10 and 15 yr, taking care to avoid the location of the initial sampling pits.

For chemical analysis, wood disks were air-dried at room temperature and then oven-dried at 90 °C. Rectangular prism blocks were split from the sapwood of dried disks from a position 90° around the stem from the point of soil contact. The volume of each block was calculated from the mean of four measurements of each dimension (longitudinal, radial, and tangential) and weighed (± 1 mg). Density (g cm^{-3}) was calculated as the mass to volume ratio. After density was measured, blocks were chiseled into small pieces and ground in a benchtop Wiley mill (Thomas Scientific, Swedesboro, NJ) to pass a 1-mm mesh. One-gram portions of milled wood powder were ashed for 6 h at 550 °C, cooled, dissolved in 3 mL of 6 M HCl, and brought to a volume of 50 mL with deionized water. Concentrations of Ca, Mg, K, Mn, Al, and Fe in ash solutions, analytical standards, and blanks were measured by inductively coupled plasma optical emission spectroscopy (ICP-OES) (Model 750, Thermo Jarrell Ash Corp., Franklin, MA).

Element concentrations determined by ICP-OES were converted from parts per million (ppm) to mmol kg^{-1} by dividing ppm by the atomic weight. Concentrations for comparison on a constant volume basis, mol m^{-3}, were obtained as the product of the mass-based concentration, mmol kg^{-1}, and the wood density, g cm^{-3}. For each set of wood samples taken at 2-yr intervals the mean and 95-percent confidence intervals of replicate samples were determined. Statistical analysis is presented in the initial publication of results through 6-8 yr (Smith et al. 2007).

Soil samples taken at 0 yr for each location and species and at 10 yr for spruce on the PEF, maple on the BEF and PEF, and birch on the PEF were analyzed using a suite of protocols approved by the U.S. Environmental Protection Agency (EPA) for forest soil analysis (loss on ignition, pH, acidity, cation exchange capacity, total Kjeldahl nitrogen, P, Na, Ca, K, Mg, Fe, Al, Zn) in the EPA-certified analytical laboratory at the University of Maine, Orono. Soil sampling was planned for 15 yr for each location and species. Decaying wood samples taken at 10, 12, and 15 yr are being analyzed by the same forest soil protocols applied to the O-horizon samples, in addition to the plant tissue protocol previously described, so that the nutrient status of the forest floor and wood decaying on the floor can be compared after the first decade of ground contact.

PRELIMINARY RESULTS

Preliminary results through the first 6-8 yr (Smith et al. 2007) indicated a significant accumulation of Ca in decaying wood in all tree species at both locations (30-90 percent increase after 6-8 yr). As the wood decayed and Ca was accumulated, Mg concentrations were sustained at approximately the initial concentration or had a small decrease of about 20 percent in some cases. More-detailed results for changes taking place at 2-yr intervals in decaying wood for the first 12 yr will soon be available, along with comparisons of decaying wood and organic soil at 10 and 12 yr.

Sampling decaying wood and soil at 15 yr on the BEF has been completed and chemical analyses are being performed. Sampling decaying wood of spruce and maple on the PEF was completed at 15 yr in 2011, but soil sampling was delayed until 2012 due to standing water on the plots. Soil samples were taken at the maple plots on the PEF in 2012, but standing water again delayed soil sampling at spruce plots until 2013. Sampling decaying wood and soil of hemlock and birch on the PEF has been suspended until work on spruce and maple has been completed. Subsets of archived decaying wood samples previously maintained at the University of Maine have been moved to other locations and are available to those interested in studying wood decay processes.

OUTLOOK

With our work on the Penobscot and Bartlett Experimental Forests, we have demonstrated an important dynamic of the biogeochemistry of northern forests, the translocation of essential Ca by wood-decay fungi. This work on the long-term effects of wood decay complements the existing understanding of the effects of forest management on Ca cycling. This process is driven by large, long-lived fungi in these forests and is far more dynamic than decomposition of a carbon stock—it is a unique connection between the forest floor and the atmosphere.

LITERATURE CITED

Boddy, L.; Watkinson, S.C. 1995. **Wood decomposition, higher fungi, and their role in nutrient redistribution.** Canadian Journal of Botany. 73(Suppl. 1): S1377-S1383.

Clinton, P.W.; Buchanan, P.K.; Wilke, J.P.; Small, S.J.; Kimberley, M.O. 2009. **Decomposition of *Nothofagus* wood in vitro and nutrient mobilization by fungi.** Canadian Journal of Forest Research. 39: 2193-2202.

Connolly, J.H.; Jellison, J. 1997. **Two-way translocation of cations by the brown rot fungus, *Gloeophyllum trabeum*.** International Biodeterioration and Biodegradation. 39: 181-188.

Connolly, J.H.; Shortle, W.C.; Jellison, J. 1999. **Weathering of mineral matter by a non-mychorrhizal fungus.** Canadian Journal of Botany. 77: 179-187.

Johnson, A.H.; Moyer, A.; Bedison, J.E.; Richter, S.L.; Willig, S.A. 2008. **Seven decades of calcium depletion in organic horizons of Adirondack forest soils.** Soil Science Society of America Journal. 72: 1824-1830.

Lawrence, G.B.; David, M.B.; Shortle, W.C. 1995. **A new mechanism for calcium loss in forest-floor soils.** Nature. 378: 162-165.

Lawrence, G.B.; David, M.B.; Shortle, W.C.; Bailey, S.W.; Lovett, G.M. 1999. **Mechanisms of base-cation depletion by acid deposition in forest soils of the northeastern U.S.** Gen. Tech. Rep. NE-261. Radnor, PA: U.S. Department of Agriculture, Forest Service: 75-97.

Lawrence, G.B.; Lapenis, A.G.; Berggren, D.; Aparin, B.F.; Smith, K.T.; Shortle, W.C.; Bailey, S.W.; Varlyguin, D.; Babakov, B. 2005. **Climate dependency of tree growth suppressed by acid deposition effects on soils in northwest Russia.** Environmental Science and Technology. 39: 2004-2010.

Lindahl, B.; Finlay, R.; Olsson, S. 2001. **Simultaneous, bidirectional translocation of ^{32}P and ^{33}P between wood blocks connected by mycelia cords of *Hypholoma fasciculare*.** New Phytologist. 150: 189-194.

Long, R.P.; Horsley, S.B.; Hallet, R.A.; Bailey, S.B. 2009. **Sugar maple growth in relation to nutrition and stress in the northeastern United States.** Ecological Applications. 19: 1454-1466.

McLaughlin, S.B.; Wimmer, R. 1999. **Tansley Review No. 104: calcium physiology and terrestrial ecosystem processes.** New Phytology. 142: 373-417.

Ostrofsky, A.; Jellison, J.; Smith, K.T.; Shortle, W.C. 1997. **Changes in cation concentrations in red spruce wood decayed by brown rot and white rot fungi.** Canadian Journal of Forest Research. 27: 567-571.

Ponomareva, V.V. 1969. **Theory of podzolization.** Gourevitch, A., transl. Israel Program for Scientific Translation, TT 68-50442. Springfield, VA: National Technical Information Service. 309 p.

Rahman, M.; Punja, Z.K. 2007. **Calcium and plant disease.** In: Datnoff, L.E.; Elmer, W.H.; Huber, D.M., eds. **Mineral nutrition and plant disease.** St. Paul, MN: APS Press: 79-93.

Shortle, W.C.; Bondietti, E.A. 1992. **Timing, magnitude, and impact of acidic deposition on sensitive forest sites.** Water, Air, and Soil Pollution. 61: 253-267.

Shortle, W.C.; Murdoch, P.S.; Smith, K.T.; Minocha, R.; Lawrence, G.B. 2008. **Monitoring recovery from calcium depletion and nitrogen saturation.** In: Murdoch, P.S.; Jenkins, J.; Birdsey, R.A., eds. The Delaware River Basin Collaborative Environmental Monitoring and Research Initiative: foundation. Gen. Tech. Rep. NRS-25. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 52-62.

Shortle, W.C.; Smith, K.T. 1988. **Aluminum-induced calcium deficiency syndrome in declining red spruce.** Science. 240: 1017-1018.

Shortle, W.C.; Smith, K.T.; Minocha, R.; Lawrence, G.B.; David, M.B. 1997. **Acidic deposition, cation mobilization, and biochemical indicators of stress in healthy red spruce.** Journal of Environmental Quality. 26: 871-876.

Smith, K.T.; Shortle, W.C.; Jellison, J.; Connolly, J.; Schilling, J. 2007. **Concentrations of Ca and Mg in early stages of sapwood decay in red spruce, eastern hemlock, red maple, and paper birch.** Canadian Journal of Forest Research. 37: 957-965. Available at http://nrs.fs.fed.us/pubs/2888. (Accessed 2 March 2011).

St.Clair, S.B.; Sharpe, W.E.; Lynch, J.P. 2008. **Key interactions between nutrient limitations and climatic factors in temperate forests: a synthesis of the sugar maple literature.** Canadian Journal of Forest Research. 38: 401-414.

Zaccherio, M.T.; Finzi, A.C. 2007. **Atmospheric deposition may affect northern hardwood forest composition by altering soil nutrient supply.** Ecological Applications. 17: 1929-1941.

BOB FRANK'S RECOLLECTIONS MADE ON THE OCCASION OF THE PENOBSCOT EXPERIMENTAL FOREST'S 60TH ANNIVERSARY

Robert M. Frank, Jr., and Laura S. Kenefic

Abstract.—Robert M. (Bob) Frank, Jr., spent his career with the U.S. Forest Service and oversaw the long-term silvicultural research on the Penobscot Experimental Forest in Maine for nearly 30 years. His reflections here span more than four decades, from his first days with the Forest Service until his retirement in 1996. He touches upon the agency's relations with members of the forest industry and the public, changes in the agency's culture and funding over time, and his role in establishing and sustaining long-term studies that continue to this day.

INTRODUCTION

Robert M. (Bob) Frank, Jr., (Fig. 1) began his career with the U.S. Department of Agriculture, Forest Service as a permanent employee in 1957 on a Forest Survey (now Forest Inventory and Analysis) crew at Shin Pond, Maine. He later worked in the Anthracite Region of Pennsylvania before being transferred to the research office in Orono, Maine. Frank was a research forester (silviculturist) at the Penobscot Experimental Forest (PEF) from 1963 until his retirement in 1996. He had primary responsibility for the Forest Service's long-term silvicultural experiments on the PEF from the late 1960s until the end of his career.

Figure 1.—Research forester Robert M. (Bob) Frank, Jr., in his U.S. Forest Service office in Orono, Maine (1993). Photo by U.S. Forest Service.

The following text represents the highlights of a 2-hour conversation Frank had with Laura Kenefic on February 15, 2011. This conversation took the form of an interview in which Frank answered questions posed by Kenefic and John Brissette about his career. The text was transcribed by Matsuye Mairs, excerpted and edited by Kenefic, and reviewed and revised by Frank. Frank's perspective is important not only because of his long tenure at the PEF, but because he is credited with sustaining the long-term research through years of waning organizational interest and investment. Frank is regarded by many of his peers as largely responsible for the existence of the more than 60-year-old Forest Service silvicultural study on the PEF today. He received the David M. Smith Award in Silviculture from the New England Society of American Foresters in 2012 in honor of his contributions to his profession.

EARLY INFLUENCES

I was always interested in wood, even in grammar school and high school. I lived in Newark, New Jersey. There were not many trees in Newark. My uncle had a camp in northern New Jersey and we would go there quite frequently. I just fell in love with being away from the Ironbound section of Newark. When I was 10 years old, in 1942, I saw a movie called "The Forest Rangers," starring Rod Cameron, Susan Hayward, and Fred MacMurray. It was about a forest fire and had some Hollywood romance. I said "Boy, it would be great to be a forest ranger!" I was only 10 years old, and that was the start of it. Fortunately, the pieces came together and I am where I am today.

START OF CAREER WITH THE FOREST SERVICE

My first job with the U.S. Forest Service was in 1953 in the state of Washington on the Gifford Pinchot National Forest, at the Randle Ranger District. Back in the 1950s and 1960s, it was highly recommended by the deans and directors of forestry schools that students spend one summer with the Forest Service. A lot of Forest Service jobs were available back then. In my training it was suggested that we get experience in different timber types. Coming from Penn State in central Pennsylvania, it was nice going out west and seeing the different ecosystems there. I was hired as a fire guard, but 1953 was not a season of fire threats. I spent most of my time hammering wooden shakes on warehouse building roofs. But I got to know some Forest Service personnel and we remained friends for a long time. I just felt comfortable perhaps pursuing a Forest Service job.

When I finished my Master's degree I moved to Boston to sell wholesale lumber. After a few months, I said to myself, "What am I doing in downtown Boston with over 6 years of education in forestry?" So I wrote to my advisor at Penn State. I told him I wasn't happy, and asked if there was anything else he might suggest. He sent me a list of six possibilities around the country. That was in 1957 and there were a lot of jobs for foresters back then. I saw one possibility: a temporary job in northern Maine on Forest Inventory, called Forest Survey back then. So I applied for it and was granted that position.

That was the start of what led to my permanent Forest Service career. I reported for work at Shin Pond, Maine—population 16—on June 17, 1957. Research folks had a good policy at that time; Station Director Ralph Marquis thought it wise for budding researchers to get their feet wet by spending some time on Forest Inventory. Many of us came from suburban or city environments and this got us out in the woods. I would still recommend that this be done today, but of course things have changed. I stayed with Inventory for almost 4 years.

A vacancy occurred in Maine where a temporary office was established in what became the Orono Unit. I was ready to move to Maine when another chance came up. A pastor in Mount Carmel, Pennsylvania, was upset about strip mining in the anthracite coal fields of Pennsylvania. He had contacted a Congressional person, who contacted the Chief of the Forest Service, and—to make a long story short—the Station was asked to conduct a survey of the lands disturbed by strip mining and coal processing plants throughout the entire anthracite area. This was before remote sensing, in the early 1960s. They asked me if I would be interested in doing this project, which would take a year or two. I asked, "Well, what about the offer to go to Maine?" The Director shook my hand and said, "It's a deal. When you finish this job, we'll ship you to Maine." Without any written documentation or bureaucratic bumbling, the Director arranged that I should go to Maine.

After I completed my assignment in Pennsylvania, I reported to duty in Maine on April Fools' Day in 1963. As I remember, the temporary office was on the third floor of the library on campus at the University of Maine in Orono. The building which would contain the USDA office was being constructed at that time. I remember visiting there during February of that year to see the new building. I asked the foreman to let me walk the steel girders, and he showed me where my room was going to be. That was kind of neat.

We only stayed a short time in the library and then the building was ready to be occupied. We moved to our new building sometime in the spring of 1963. We stayed in the USDA building until near the end of my career, when the university needed the space and we were asked to vacate. We moved to a new building off campus, on Godfrey Drive in Orono.

FIRST IMPRESSIONS OF THE PEF

The roads on the Experimental Forest were narrower than they are now, and we did not have the signage that we later developed. I had some experience with the timber type because I spent the better part of two growing seasons in northern Maine. One of the big differences was the amount of hemlock we had in our stands here on the Experimental Forest. Also, there was less spruce than you would see in the so-called spruce-fir part of Maine. We had more hardwoods in some of our sites. They were managed even at that point in time; they were eliminating red maple, as I recall. The plantation of pine was very young; it was planted in the late 1950s. Also, the pine trees at the museum[1] site are certainly a lot bigger now than they were 50 years ago.

FRANK'S ROLE AT THE PEF

I was told before I left Upper Darby [Pennsylvania] that the main reason I would be going to Maine was to address the problems of spruce-fir regeneration in the Compartment Study[2]. The Station wanted to establish a system of inventory for regeneration. Regeneration was not being studied on the Experimental Forest. That was a top-down decision from Station headquarters, but you have to remember, the Station was much smaller then.

So that was my first job: to establish a measurement system for very small trees [Fig. 2]. Up to that point, very little was known about the effect of the various treatments on regeneration. We researched the measurement problem and had statisticians help us and suggest what we should do. The methodology of putting in the plots, we actually got that from reviewing the literature. We developed a system that I guess to some degree is still in operation. You really get to know the different areas on the Experimental Forest when you get on your hands and knees and spend many, many hours looking at regeneration.

I want to mention Orman Carroll [Fig. 3], who was our first technician. Orman was in the logging crew that helped establish our long-term study, which started in 1952. But somewhere near the end—it took several years to install the study; I believe until 1957—they asked Orman if he would be willing to become an employee of the Forest Service. This happened before I was stationed in Maine. The Forest Service wanted him to take over from the logging crews, because they knew there were going to be periodic reentries.

[1] Maine Forest and Logging Museum at Leonard's Mills.

[2] The long-term, large-scale silvicultural experiment on the PEF, consisting of even- and uneven-aged silvicultural treatments and exploitative cuttings, replicated at the stand level.

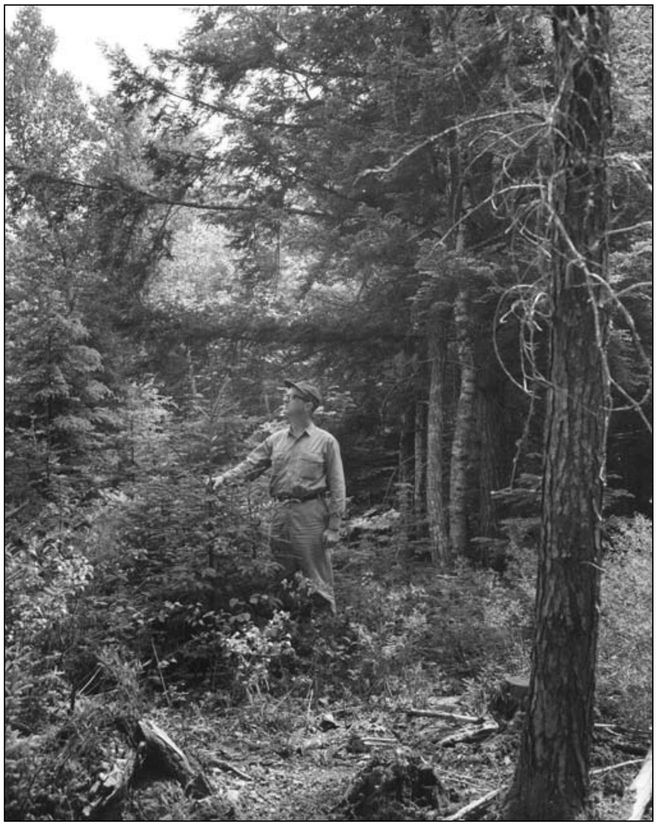


Figure 2.—Bob Frank inspecting red spruce sapling growth on the Penobscot Experimental Forest (ca. 1965). Photo by U.S. Forest Service.

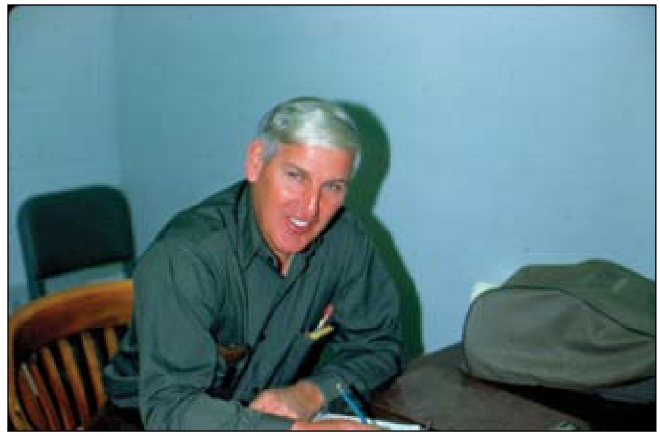


Figure 3.—Penobscot Experimental Forest technician Orman Carroll (1976). Photo by U.S. Forest Service.

Orman accepted and stayed with us until 1979, when he retired. But he was a Cracker Jack technician. He was a hands-on person and could repair equipment. He knew his trees, he knew how to get around in the woods, and he was dedicated. Hours did not mean anything to him; rain did not mean anything to him. He was just the all-around technician that an experimental forest needs. And a great guy to work with, too.

Arthur Hart [Fig. 4] was Project Leader; he had taken over from Frank Longwood about that time. Arthur Hart was a marvelous person. He not only became my advisor, but he was my friend and, most of all, my mentor. Unfortunately, he became ill with cancer early in 1968 and passed away in 1969. That changed things on the Experimental Forest. I was still relatively new. Much of the responsibility fell on me to continue many PEF activities. The Compartment Study was a large study. There were 28 compartments at the time.

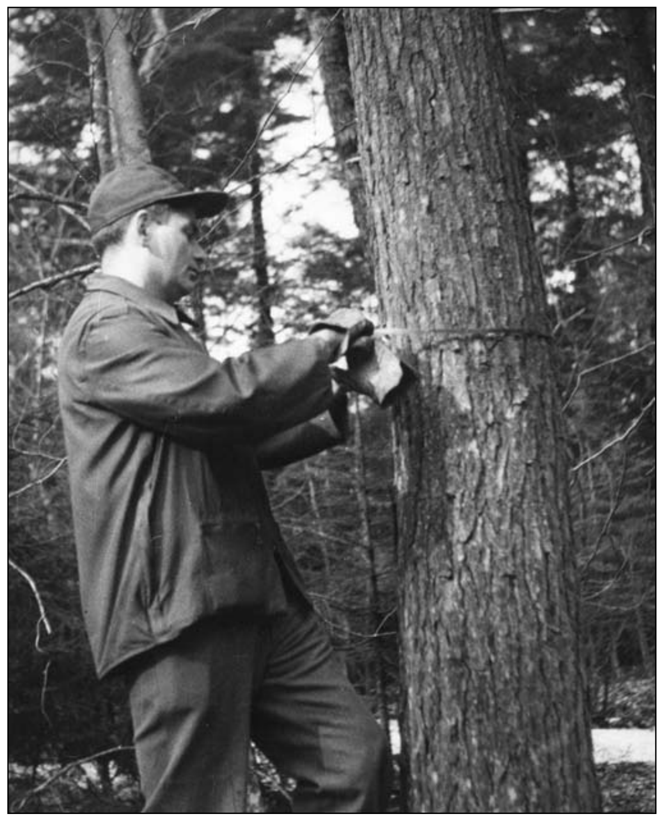


Figure 4.—Arthur Hart measuring tree diameter on the Penobscot Experimental Forest (ca. 1960). Photo by U.S. Forest Service.

THE PEF OPERATING COMMITTEE

The PEF Operating Committee was a small group of industry people—representatives of the landowners—that kept tabs on what we were doing. They were there when we needed help from them. What was nice about that was we always had a little cash from the sale of timber from our experiments. This money was used for research, mainly to hire students for the summer when our Forest Service budgets wouldn't allow for it. At that time there was a lot of comradeship amongst the forestry fraternity and that does not exist as strongly today. It was a time when we had the great companies that no longer exist. These were the folks that wanted the Forest Service to establish a research unit in Maine. It happened and we should be thankful that it is still progressing after 60 years.

MEETING THE NEEDS OF FOREST INDUSTRY

Of course the long-term experiment—the Compartment Study—did not occupy all my time. In the late 1960s forest industry was facing a labor shortage. It was difficult to get people to work in the woods. When I started at the PEF, some of the logging was done with horses. At the same time that we had horse logging, we would occasionally get operators who had "jitterbugs" or small cleat tractors. I remember in early 1969, one of the last operations that Mr. Hart was involved with, we had our first skidder come on site. He was apprehensive and said, "My gosh, this might be the end of some of our regeneration." Well, that proved not to be the case, because we could detect very little difference between operations done with horses, jitterbugs, or small skidders. There was a need for some other means of getting trees from the stump to roadside, and mechanization came into play.

Clearcutting was drawing the attention of some segments of society at that time, and generating controversy. Many clearcuts were commercial clearcuts, even on company lands—by no means true clearcuts. There was little market for low-grade hardwoods and the smaller softwoods, so they were left on site. I remember the PEF Operating Committee stating, "We need studies to show what will happen to advance regeneration when we use larger equipment and when we clearcut." And that was the reason for the strip cutting study[3] here on the Experimental Forest—perhaps one of the first times this harvesting method was tried in Maine [Fig. 5].

About that same time, work was being done in Fish River country in Aroostook County where the first mechanical harvester—a Beloit tree harvester—was brought onto land owned by Seven Islands Land Company, I believe Prentiss and Carlisle, and Great Northern Paper Company. This was a big machine with tracks. The plan was to harvest by clearing strips of different widths and different orientations. Many people were invited; there were probably 30 to 40 forestry-oriented people watching this machine operate [Fig. 6]. You could hear comments like "This will be the end of the Maine forest" and "The Maine forest will not survive this machine." The machine had a 60-foot boom. It drove up to one tree at a time,

[3] Compartment 33; see Bjorkbom and Frank (1968), Czapowskyj et al. (1977), and Frank and Safford (1970).

Figure 5.—Bob Frank explaining the experimental design for the strip cutting experiment (Compartment 33) on the Penobscot Experimental Forest (1969). Photo by U.S. Forest Service.

Figure 6.—Foresters on a field trip to see the Beloit tree harvester in operation in northern Maine (1967). Photo by U.S. Forest Service.

delimbed it, topped it, and laid entire stems down in small bunches. Then a rubber-tired grapple skidder moved out bunches of these long stems to a landing.

I saw this as an opportunity to conduct research. It was one of the most miserable jobs I worked on. The resulting tangle of slash and other debris was almost overwhelming. The crew and I were putting in temporary regeneration plots on industry land to try and assess the effects on advance regeneration. I worked with a forester from Great Northern and we published some of the results.[4] We found that the machine itself did not cause problems because it rode on its own brush, but where the grapple skidder repeatedly traveled, that was the problem. I believe those cleared strips have since been logged again.

That was the beginning of mechanization and clearcutting, and of course the clearcutting debate continued. That forced us here on the Experimental Forest to look more at machines. What is unique about this property is that we would use logging systems that were in vogue at the time as much as possible. I think that has served us well.

MANAGEMENT INTENSITY DEMONSTRATION AREAS

In the late 1960s, Arthur Hart was notified, I think by the Washington Office, that we were an experimental forest, not a demonstration forest. Therefore, we had to eliminate our demonstration areas. At that time we had a 40-acre block as a demonstration area. These MIDs, or management intensity demonstration

[4] Frank and Putnam (1972).

areas, existed on many Forest Service experimental forests[5]. We decided that if we eliminated this 40-acre area, it would be difficult to take many of the groups we had then, like schoolchildren or high school or college students, on silvicultural tours. In a short period of time in the woods, this demonstration area gave many individuals their initial exposure to forest management procedures; perhaps their appetites for additional forestry knowledge would start on this area! We decided to modify and streamline our procedures in order to reduce the work required to maintain the demonstration.

The MIDs were small in area for statistical analysis. We pretty much had to do 100-percent inventories. People back then didn't have the finesse we have now in statistics. So we originally measured every tree, which was too much. But we could really measure those trees! We had technicians who would run through those trees, and we got results.

We modified the treatments through time; I am happy to hear that they are being kept up.

FOREST SERVICE CULTURE

I was first exposed to Forest Service culture in Washington State at the Ranger District in Randle. I liked it. I saw cohesiveness amongst the workers, from the District Rangers to the mule packers. It was great. Being a student at the time, I was invited to loggers' homes for dinner and so forth, and we got to know people quite well. When I came to Orono, because we were a small unit at the time, we were surrounded by non-Forest Service personnel, mainly industrial. You always stood out in the crowd. You were the only federal person, or maybe one other with you. But because of our exposure to various groups, we got to know these people not only professionally but socially.

Back in the 1960s and 1970s, I remember being invited to my project leader's home for dinner. I will never forget the first visit. God bless Min Hart, Arthur Hart's widow. She is still alive and lives next door to us; she is 93. The first time my wife Dorothy and I visited them was in 1964. I know Min wanted to meet my wife and that was one of the reasons we were invited. We had a delightful evening. When we left, she said—this was in the summertime—"Now, we go to bed early, so please don't contact us after 8:30 because we get up at 3 in the morning. We do all our chores and tend to our garden before we go to work at 8 o'clock." And I respect that time to this day and never call her after 8:30.

Even earlier, in the 1950s, we had Christmas parties in Upper Darby. Everyone at Station Headquarters would be invited to a restaurant and you got to talk to the Division Chiefs, Directors, etc. After I was transferred to the Orono Unit, something they did—that I believe is not done today—when someone from Headquarters or from another unit visited, you invited them over for dinner. We would be invited to one of the scientists' homes. When Director Marquis, or Assistant Director Warren Doolittle, or others including the Station Editor or Station Statistician visited, we would always entertain in someone's home. I remember once the Station Editor came to talk about the preparation of publications. My wife Dorothy and I invited him over for dinner. It was an awful, icy winter night; we had to walk about 400 feet down to the house. Everything went well, we had a nice dinner, it was a good visit, and I drove him back to his motel. We did a lot of that and even went on picnics in the summertime. We do less of that in the Forest Service now. Society has changed.

TECHNOLOGY TRANSFER

Throughout my career there was a pull and tug. I knew I had to produce manuscripts in order to stay in the good graces of the organization. On the other hand, I dealt with so many people in forestry who were potential users of our results who I knew would not spend much time reading publications. I tried to make the publications I did write as practical as I could. I wanted them to be guides for people to use in their work.

[5] Also called Cutting Practice Level plots.

I did not solicit people for tours on the Experimental Forest. I did not suggest that when they go home, they tell others to come. They just came. And it increased year after year. Most of them were industrial foresters and government foresters. We also had many organizational groups including The World Forestry Center from Portland, Oregon [Fig. 7]. We had foreigners and I believe that continues to this day. We had many visitors from academia, from the local colleges and other places including Canadian provinces from Ontario to Newfoundland. It was always a treat when you could spend some time, have all your ducks in a row, have nice signs that impress people, have literature to hand them, and even publications. It was the entire package I tried to present. I was always willing to answer questions while they were here. I think it worked well with industrial people, with graduate students and so forth. And I might add, since I retired, the ownership has gone to the University [of Maine] and the use of the Experimental Forest—based on the base that was built here—has increased many, many fold.

REPLICATION IN THE COMPARTMENT STUDY

If there was one mistake I made—though I was never the final decisionmaker—it had to do with replication in the Compartment Study. The study plan was revised in 1974. We decided to reduce the work load without impacting the overall results. Unfortunately, we only had two replicates of our treatments. At the time, we eliminated some compartments. Most of these were eliminated based on the soil-site conditions; we eliminated those that seemed to have variation from the norm. Those became what we called units. We kept them in the state of readiness for future research. Had we created another replicate from them, we might have bolstered the strength of the experiment.

We did not have much additional suitable land within the Experimental Forest, but we might have found some areas where we could have started new compartments. That was about 20 years into the experiment; now we are 60 years in and we would

Figure 7.—Visitors from the World Forestry Center in Portland, Oregon, view Bob Frank's model of tree growth response by species and treatment following precommercial thinning in Study 58 on the Penobscot Experimental Forest (1987). Photo by U.S. Forest Service.

have had 40 years more experience. But we didn't do that. Nor did we get together with other experimental forests. Maybe these could be future goals.

MOTIVATION TO CONTINUE THE WORK

I was having fun. I really enjoyed my work. It was satisfactory and I truly felt we were producing results beneficial to many user groups. If I had to do it over again—only a fool would say they wouldn't change anything—but as far as my forestry career was concerned, I would do it again.

I do not know if this is common knowledge or not, but I was offered a position with a company in Maine, to start a research unit. It was Great Northern Paper Company. I had 3 weeks to make a decision. I was mid-career, and I was thinking, "I am established in my home, in my job, and in my church. My kids are in school. Do I want to change that?" I really wanted to work for industry. Now, when I think of that offer, I'm thankful I did not take it.

I had passion to continue this work. I was always hoping it would continue beyond me, and it is in good hands now. One of the things that really made it happen was computer systems. How could we ever acquire information about problem insects, invasive species, you name it, if we did not have a good data set?

COMPUTERS

Managing the data was always a big job before we had computers. My initial and continuing fear with computers is that when the analysis is done manually, you are likely to only make little mistakes, but with computers you are likely to make big mistakes. To minimize mistakes, you need someone familiar with what is happening in the field to look at the data in order to detect grave mistakes.

When computerization was in its infancy, we started numbering individual trees in the field [in the Compartment Study]; I thought that was an interesting improvement. In order to number trees, we had to create a system to minimize the effort and control errors on remeasured plots, because much of the field work was done by temporary people during the summer months. I went out into the field as much as I dared. We usually had good technician coverage, but mistakes were being made. We reviewed the research on how to number trees, and there were several ways of doing it. The student (I always call them students; they were temporary employees) we had at the time was Bruce Birr. It's funny that we are talking about this now; just the other day I got a letter from John Brissette saying Bruce now works at Rhinelander [Wisconsin]. I haven't seen him in 35 years. He was here in the early 1970s and was the one who went to the library to find ways to number trees. We came up with the "wagon wheel" approach. That worked well until we started to put numbers on trees down to the 1-inch class. We struggled. But we kept the trees in order by dividing the circular plots into ten 36° pie-shaped segments. This procedure enhanced the accuracy of the measurements we were taking. I don't know exactly how it's done now.[6]

Our concern was: How many digits will fit on a small tree? If you add just one more digit, that multiplies how much numbering must be done. Do our plots have to be 1/20-acre for the smallest trees? Could we make these plots smaller and maintain statistical accuracy? I'm not sure how that is unraveling now.[7]

I thought when we started numbering trees and accumulating data and were able to measure the growth of individual trees, that somehow we could correlate this growth with soil type; I mean specific soil type, or the soil on which that one tree was growing! I remember talking to soil scientists about this over the years. I looked at available soils maps and knew these were of little help. You actually have to determine what soil each tree is growing in. It would be an interesting project to get the data necessary to

[6] Comment: This system is still in use.

[7] Comment: The measurement plots for saplings are now 1/50-acre instead of 1/20-acre.

correlate individual tree growth with specific soil data. An additional enhancement in an analysis of this type would be to factor in the relation of the subject tree to adjacent trees. Are they free to grow on one side, two sides, three sides? You should be able to get a better handle on the association between the growth of trees and soil.

BUDGET CUTS OF THE 1980s

The budget cuts were large. Here's how we survived. In a sense, it was a tense time. We all knew how budgets were shrinking. I believe a portion of one budget got cut 85 percent! I remember employing work-study students and volunteers to accomplish our field work. Once, we were able to enlist one or two elderly folks. I think it was a service group. That didn't work out. We struggled. We also asked for and received some money from the companies from the PEF stumpage account.

But here's another part of the budget story. It didn't happen all at once; it took some time to unravel. Orono was on the list for possible closure as budgets were being reduced. Now, this is my interpretation. We heard from different sources, above the Project Leader level, perhaps above the Director level, that research done on the experimental forests was essentially for the National Forests. So what you guys are doing up there in Maine just didn't fit the mold.

These were hard times. Morale was down, people were transferred, and I was going to be transferred to New Hampshire. As I recall, the plan was that I would come back in the summertime and continue to work on the Experimental Forest. Of course you had to accept that possibility. I was not at the higher echelons of any decisionmaking, but a white paper was produced by the Director at the time, and it was suggested that it be distributed to our consumers.

We could not lobby for increased funding. That was illegal; we couldn't do that. So Project Leader Bart Blum and I put together lists of people we were going to visit. I took the northern part of the state and he took the southern part. We went to different people explaining, "You've been consumers of our work in the past, this is what we've done, and these are our publications." We showed them the budgets, but we didn't say anything like "Please, please, will you help us get more financing?" I do not know if that's a blind elephant or not, but it might have appeared desperate at the time.

Many, many letters were written to the Director supporting this unit. He later said, "I was impressed with the response and the support you had from all the difference agencies, companies, and organizations. I was really impressed with what you got from the Maine potato growers. What was that all about?" I said, "Potato fields are just a small percentage of the land they own. They own a lot of spruce-fir country." That was the only way I knew how to answer.

I think the letters had a significant influence; there was another influence also. I received a telephone call from a very influential person wanting to know if I would be willing to talk to Senator George Mitchell about our budget problems. He was scheduled to talk at Husson College [in Bangor, Maine] at a Businessman's Breakfast. I attended those meetings. Many forestry people and business leaders in the community attended, also. Senator Mitchell was giving a talk. I was told that I had his time from when he left the lectern where he was giving his speech until he reached his automobile and I would walk with him. I was thinking, "What can I say to the Senator without violating what I'm not supposed to ask?"

Here's the interesting part. At this time there were two forces working against each other in Congress. George Mitchell was pushing the Clean Air Act and Robert Byrd did not like it. Senator Byrd was from West Virginia and he was concerned about the effect the Clean Air Act would have on the coal industry. So, somehow I had to weave this together. At that time I think we still had eight scientists in the Orono unit. I looked up how many scientists were in West Virginia. I thought, "Well, I can mention that."

As I walked Senator Mitchell down to his automobile, I walked as slowly as I could. He was being very cordial and asked me questions about the work I was doing, who we were, and who we were doing the work for, and so forth. Trying to be as encompassing as I could, I said, "We have eight scientists here in Maine, they have X numbers here and there, and in West Virginia they have 52 scientists." He stopped and looked at me. And he said, "I didn't know that." That was the only time he stopped. Shortly after that walk with Senator Mitchell, I believe the Director received a communication from him. And, as I was told—I'm getting this down through the levels—Senator Mitchell said, "If there is going to be research done for Maine, it is going to be done in Maine." And that was the end of the unit moving from Orono, at least at that time. That's the way I understood it.

TRANSFER OF THE PROPERTY TO THE UNIVERSITY OF MAINE FOUNDATION

What precipitated this was the perception of the PEF owners—and I got this right from the horse's mouth—that because of reduced budgets and conversations they had with other people that I was unaware of, that the Forest Service was probably going to give up and pull out [of the PEF]. I was in most of the meetings when the owners met. I remember one meeting where the decision had to be made: What were the owners going to do? I was at this meeting—I don't recall anyone else from the Forest Service being there—a dean [from the University of Maine] actually asked me, "Bob, is it something the museum could undertake?" I said, "There is no way the museum could do it, though there may be a part it can play somehow." He was thinking in terms of gearing up for it with an employee or two, or something like that. The university said, "There is no way we can handle the work load, the data collection, and so forth." So it eventually wound up with the agreement we have now. The university owns it and we have a memorandum of understanding. I think that is working out fine.

Would I have liked it to go any other way? I can't say at this point in time. The majority of what might be considered pertinent work or studies with firm results are still being maintained. We now have the university overlaying their own set of studies on other parts of the Forest, plus an increase in graduate student work because of this.

THOUGHTS ON CHANGES SINCE FRANK'S RETIREMENT

I don't know all the work you are involved with, Laura. One of the potential opportunities that bothered me when I was working here is we did so little with northern white-cedar. I love cedar. I've hammered thousands of wooden shingles on my home, my barn, my garage, my camp, and outbuildings. I've even replaced, in one case, a set of shingles. I use a lot of cedar for posts, I use a lot of cedar lumber for paneling, for railings … I just love cedar. It's good to see an increase in cedar research. Much of the initiative with cedar came from you and others. It was a void, no question about it. So that's good.

I am happy that the research is being maintained. I think I was somewhat more fussy about how the Experimental Forest looked when I was here, but that's a natural reaction when someone leaves. If a sign is falling over or you can't read it, you should get it out of there. That sort of thing. Some of the roads could be improved. I realize that there are constraints. As far as the work is concerned, I think that with the staff you have and the means you have to do it, I feel it is being utilized and progress is being made. I know that you are involved in so many things and John is spread so thin. And you have one technician who keeps everything else going here.

ANECDOTES ABOUT THE OLD FOREST SERVICE BUILDING ON THE PEF

When a new study had to be installed, I spent quite a bit of time on the PEF. I tried to pare it down so I could get my work done behind the desk. We would bring our lunches out and meet in the old building [Fig. 8]. I call it the old building; I think it was built in 1952. Naturally I was sad to see it go.[8]

On hot days we would all go into the building and it would be cool. We never had more than one permanent technician assigned to the Experimental Forest. We also had summer students hired as work-study or government employees. We always had a crew. There would usually be a minimum of four of us, maybe more. We even had loggers that would come and chitchat. We renovated that building and installed a bathroom, shower, an oven, and a wood stove. On one occasion we entertained a busload of budworm research people from Vermont for a 2-day visit. The night they were here, we cooked a turkey in the oven for them and served them a complete meal. It was an adequate building for many purposes. It's all gone now.

[8] The building was torn down in 2010.

One of the most humorous stories I remember from the Experimental Forest took place in the old building. Our technician Orman Carroll had three daughters. His wife would line up the lunches on the counter so when they went out the door they could pick a lunch. One day at lunchtime, we opened our lunches. Orman didn't talk too much, but I heard him say "What in the world is this?!" He had, instead of lunch, a daughter's gym suit! We all had a good laugh and shared our lunches with him.

Figure 8.—The Forest Service building on the Penobscot Experimental Forest (1952). Photo by U.S. Forest Service.

FRANK'S FOREST SERVICE LEGACY

I know how eastern spruce-fir research began. I never met the man who began the research in the 1920s—Marinus Westveld—but I worked with someone who knew him and worked with him. That was Arthur Hart, who was Project Leader toward the end of his career. I currently live next door to a lady that met Marinus Westveld—it is Arthur's wife. I have much respect for that early work. We look at it now with so much added knowledge that we think, "My goodness, that was pretty basic." But when you build a pyramid you have to start at the base and eventually you put that top stone in.

So if this experiment—the PEF—continues, and I might add that the Penobscot Experimental Forest is probably as well known now as any time in history, I would like to think that I was an important cog in the wheel that kept it going [Fig. 9].

I think I did the best I could. Fortunately, I think I was able to do it in both a satisfactory and meaningful manner. I had good people to be associated with, below me, above me, and equal to me.

I certainly appreciate the opportunity to talk with you in this way. And it is still fun!

ACKNOWLEDGMENTS

We thank John Brissette for his assistance in crafting the interview questions and Matsuye Mairs for her careful work in transcribing the audio recording. Susan Stout and Peter Stine provided helpful reviews of the manuscript.

Figure 9.—Bob Frank at the entrance to the Penobscot Experimental Forest shortly before his retirement (1995). Photo by U.S. Forest Service.

LITERATURE CITED

Bjorkbom, J.C.; Frank, R.M. 1968. **Slash burning and whole-tree skidding fail to provide mineral-soil seedbeds for spruce-fir.** The Northern Logger and Timber Processor. 16(7): 20, 45.

Czapowskyj, M.M.; Rourke, R.V.; Frank, R.M. 1977. **Strip clearcutting did not degrade the site in a spruce-fir forest in central Maine.** Res. Pap. NE-367. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Research Station. 8 p.

Frank, R.M.; Putnam, E.L. 1972. **Seedling survival in spruce-fir after mechanical tree harvesting in strips.** Res. Pap. NE-224. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Research Station. 16 p.

Frank, R.M.; Safford, L.O. 1970. **Lack of viable seeds in the forest floor after clearcutting.** Journal of Forestry. 68: 776-778.

PUBLICATIONS OF THE PENOBSCOT EXPERIMENTAL FOREST, 1950-2010

Laura S. Kenefic and John C. Brissette

This bibliography includes all journal articles, technical reports, proceedings, U.S. Forest Service publications, and theses published about or using data from the Penobscot Experimental Forest (PEF) during its first 60 years. Abstracts, Web pages, tour handouts, unpublished reports, and articles from newsletters, magazines, and newspapers are not included. This list was compiled using records maintained by the Forest Service, Internet resources, and the literature cited sections of known PEF publications, with input from current and former PEF scientists and cooperators. Each publication was obtained in digital format and the use of PEF data confirmed; if the study site was not named, expert opinion (e.g., type and general location of the research and knowledge of former studies on the experimental forest) was used to determine if the study was conducted on the PEF. Although we are confident that we have not made errors of inclusion, it is possible that we have made errors of omission due to the length of record, large number of cooperators and publication outlets, and abundance of gray literature originating from the PEF. Note that many of the PEF publications with Forest Service authors can be obtained from the online Treesearch database (http://www.treesearch.fs.fed.us/).

Abbott, Herschel G.; Hart, Arthur C. 1961. **Mice and voles prefer spruce seed.** Station Paper 153. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 12 p.

Adams, Stephanie L. 2006. **A physiological examination of the age-related decline in photosynthesis in *Picea rubens*.** Orono, ME: University of Maine. 75 p. M.S. thesis.

Alkon, Philip U. 1961. **Nutritional and acceptability values of hardwood slash as winter deer browse.** Journal of Wildlife Management. 25(1): 77-81.

Bailey, Michael E. 1977. **Production and deer utilization of vegetation on small clearcuts in central Maine.** Orono, ME: University of Maine. 99 p. M.S. thesis.

Bjorkbom, John C. 1967. **Seedbed preparation methods for paper birch.** Research Paper NE-79. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 15 p.

Bjorkbom, John C. 1971. **Production and germination of paper birch seed and its dispersal into a forest opening.** Research Paper NE-209. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 14 p.

Bjorkbom, John C. 1972. **Stand changes in the first 10 years after seedbed preparation for paper birch.** Research Paper NE-238. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 10 p.

Bjorkbom, John C.; Frank, Robert M. 1968. **Slash burning and whole-tree skidding fail to provide mineral-soil seedbeds for spruce-fir.** The Northern Logger and Timber Processor. 16(7): 20, 45.

Blomquist, Sean M. 2008. **Relative fitness and behavioral compensation of amphibians in a managed forest.** Orono, ME: University of Maine. 185 p. Ph.D. dissertation.

Blomquist, Sean M.; Hunter, Malcolm L., Jr. 2007. **Externally attached radio-transmitters have limited effects on the antipredator behavior and vagility of *Rana pipiens* and *Rana sylvatica*.** Journal of Herpetology. 41 (3): 430-438.

Blomquist, Sean M.; Hunter, Malcolm L., Jr. 2009. **A multi-scale assessment of habitat selection and movement patterns by Northern leopard frogs (*Lithobates* [*Rana*] *pipiens*) in a managed forest.** Herpetological Conservation and Biology. 4: 142-160.

Blomquist, Sean M.; Hunter, Malcolm L., Jr. 2010. **A multi-scale assessment of amphibian habitat selection: wood frog response to time of harvesting.** Ecoscience. 17: 251-264.

Blomquist, Sean M.; Zydlewsk, Joseph D.; Hunter, Malcolm L., Jr. 2008. **Efficacy of PIT tags for tracking the terrestrial anurans *Rana pipiens* and *Rana sylvatica*.** Herpetological Review. 39: 174-179.

Blum, Barton M. 1973. **Some observations on age relationships in spruce-fir regeneration.** Research Note NE 169. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Blum, Barton M. 1975. **Regeneration and uneven-aged silviculture—the state of the art.** In: Uneven-aged silviculture and management in the eastern United States; combined proceedings of two in-service workshops; 1975 July 15-17; Morgantown, WV; 1976 October 19-21; Redding, CA. Gen. Tech. Rep. WO-24. Washington, DC: U.S. Department of Agriculture, Forest Service: 63-83.

Blum, Barton M. 1977. **Animal damage to young spruce and fir in Maine.** Research Note NE-231. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Blum, Barton M. 1984a. **Selection system of silviculture in spruce-fir.** Forest Technique: Micro-Journal for Information Transfer. 84(8): 10.

Blum, Barton M. 1984b. **U.S. Forest Service research -- alive and well in Maine.** National Woodlands. 7(4): 8-10.

Blum, Barton M. 1985. **Appropriate silviculture.** In: Spruce-fir management and spruce budworm: Society of American Foresters, Region VI, Technical Conference; 1984 April 24-26; Burlington, VT. Gen. Tech. Rep. NE-99. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 185-191.

Blum, Barton M. 1987. **Forest research, Orono, Maine.** NE-INF-74-87. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Blum, Barton M. 1988. **Variation in the phenology of bud flushing in white and red spruce.** Canadian Journal of Forest Research. 18: 315-319.

Blum, Barton M.; Solomon, Dale S. 1980. **Growth trends in pruned red spruce trees.** Research Note NE-294. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 6 p.

Bondietti, Ernest A.; Momoshima, Noriyuki; Shortle, Walter C.; Smith, Kevin T. 1990. **A historical perspective on divalent cation trends in red spruce stemwood and the hypothetical relationship to acidic deposition.** Canadian Journal of Forest Research. 20: 1850-1858.

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

Brissette, John C.; Ducey, Mark J.; Gove, Jeffrey H. 2003. **A field test of point relascope sampling of down coarse woody material in managed stands in the Acadian Forest.** Journal of the Torrey Botanical Society. 130(2): 79-88.

Brissette, John C.; Frank, Robert M., Jr.; Stone, Timothy L.; Skratt, Thomas A. 1999. **Precommercial thinning in a northern conifer stand: 18-year results.** The Forestry Chronicle. 75(6): 967-972.

Brissette, John C.; Kenefic, Laura S. 2000. **Eastern hemlock response to even- and uneven-age management in the Acadian Forest: results from the Penobscot Experimental Forest long-term silvicultural study.** In: McManus, K.A.; Shields, K.S.; Souto, D.R., eds. Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America; 1999 June 22-24; Durham, NH. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 23-28.

Brissette, John C.; Saunders, Michael R.; Kenefic, Laura S.; Sendak, Paul E. 2006. **Long-term research on classical silvicultural approaches in the Acadian Forest: Penobscot Experimental Forest Part I.** In: Proceedings, Society of American Foresters 2006 national convention; 2006 October 25-29; Pittsburgh, PA. Bethesda, MD: Society of American Foresters. [CD-ROM]. 10 p.

Bryce, Elizabeth K. 2009. **Influence of silvicultural treatment, site characteristics, and land use history on native and nonnative forest understory plant composition on the Penobscot Experimental Forest in Maine.** Orono, ME: University of Maine. 123 p. M.S. thesis.

Bulger, John M.; Durgin, Jerry J.; Giffen, R. Alec; Tyron, Theodore C.; Griffen, Ralph H.; Weiland, George W.; Frank, Robert M. 1974. **Forest practice goals and standards for the improvement, maintenance, and protection of the forest resources of Maine.** The Maine Forest Review. 7: 1-21.

Chalmers, Rebecca J. 2004. **Wetland and nest scale habitat use by the four-toed salamander (*Hemidactylium scutatum*) in Maine, and a comparison of survey methods.** Orono, ME: University of Maine. 109 p. M.S. thesis.

Chalmers, Rebecca J.; Loftin, Cynthia S. 2006. **Wetland and microhabitat use by nesting four-toed salamanders in Maine.** Journal of Herpetology. 40(4): 478-485.

Chapman, Gordon L.; Grove, Edwin R.; McLintock, Thomas F. 1951. **Influence of silvicultural practice and species on the solid wood contents of peeled, stacked pulpwood.** Technical Note No. 9. Orono, ME: University of Maine, Forestry Department. 2 p.

Collins, Judith A.; Jennings, Daniel T. 1987. **Nesting height preferences of eumenid wasps (Hymenoptera: Eumenidae) that prey on spruce budworm (Lepidoptera: Tortricidae).** Annals of the Entomological Society of America. 80: 435-438.

Crawford, Hewlette S. 1982. **Seasonal food selection and digestibility by tame white-tailed deer in central Maine.** Journal of Wildlife Management. 46(4): 974-982.

Crawford, Hewlette S.; Frank, Robert M. 1986. **Is good forestry good wildlife management?--Some examples.** In: Is good forestry good wildlife management? Proceedings of a joint conference of: New England Chapter of the Society of American Foresters, Maine Chapter of the Wildlife Society, Atlantic International Chapter of the American Fisheries Society; 1985 January 6-8; Portland, ME. University of Maine Miscellaneous Publication 689. Orono, ME: Maine Agricultural Experiment Station, University of Maine: 17-22.

Crawford, Hewlette S.; Frank, Robert M. 1987. **Wildlife habitat responses to silvicultural practices in spruce-fir forests.** In: McCabe, Richard E., ed. Transactions of the 52nd North American wildlife and natural resources conference; 1987 March 20-25; Quebec City, Quebec. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 92-100.

Crawford, Hewlette S.; Frank, Robert M. 1988. **Rating spruce-fir silviculture for wildlife and forestry.** Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Information Management Group. 23 p.

Crawford, Hewlette S.; Hankinson, Diane H. 1984. **White-tailed deer vs. bovine inocula for in vitro digestibilities.** Journal of Wildlife Management. 48(2): 649-652.

Crawford, Hewlette S.; Stutzman, Warren L. 1983. **Microwave attenuation as an indicator of sampling weight of herbaceous and woody plants in the field.** Forest Science. 29(4): 726-734.

Cronan, Christopher S.; Lytle, David; Piampiano, Jeffrey. 1998. **Influence of seasonal drought on water-table levels and hydrochemistry in two forested wetlands, Maine.** Northeastern Naturalist. 5(4): 313-322.

Czapowskyj, Miroslaw M. 1977. **Status of fertilization and nutrition research in northern forest types.** In: Proceedings of the symposium of intensive culture of northern forest types; 1976 July 20-22; Orono, ME. Gen. Tech. Rep. NE-29. Upper Darby, Pa: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 185-203.

Czapowskyj, Miroslaw M. 1979. **Foliage nutrient concentration in balsam fir as affected by soil drainage and methods of slash disposal.** Research Note NE-278. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Czapowskyj, Miroslaw M.; Rourke, Robert V.; Frank, Robert M. 1977. **Strip clearcutting did not degrade the site in a spruce-fir forest in central Maine.** Research Paper NE-367. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Research Station. 8 p.

Davis, Grant. 1958. **Growth of white pine and red spruce trees after pruning.** Research Note No. 83. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Davis, Grant; Hart, Arthur C. 1961. **Effect of seedbed preparation on natural reproduction of spruce and hemlock under dense shade.** Station Paper No. 160. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 12 p.

Day, Michael. 2000a. **Factors influencing net primary production in red spruce.** Orono, ME: University of Maine. 172 p. Ph.D. dissertation.

Day, Michael E. 2000b. **Influence of temperature and leaf-to-air vapor pressure deficit on net photosynthesis and stomatal conductance in red spruce (*Picea rubens*).** Tree Physiology. 20: 57-63.

Day, Michael E.; Greenwood, Michael S.; White, Alan S. 2001. **Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age.** Tree Physiology. 21: 1195-1204.

Dean, Thomas J.; Roberts, Scott D.; Gilmore, Daniel W.; Maguire, Douglas A.; Long, James N.; O'Hara, Kevin L.; Seymour, Robert S. 2002. **An evaluation of the uniform stress hypothesis based on stem geometry in select North American conifers.** Trees. 16(8): 559-568.

deMaynadier, Philip G. 1996. **Patterns of movement and habitat use by amphibians in Maine's managed forests.** Orono, ME: University of Maine. 207 p. Ph.D. dissertation.

deMaynadier, Phillip G.; Hunter, Malcolm L., Jr. 1998. **Effects of silvicultural edges on the distribution and abundance of amphibians in Maine.** Conservation Biology. 12: 340-352.

deMaynadier, Phillip G.; Hunter, Malcolm L., Jr. 1999. **Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine.** Journal of Wildlife Management. 63: 441-450.

deMaynadier, Phillip G.; Hunter, Malcolm L., Jr. 2000. **Forest roads and amphibian movements in Maine.** Natural Areas Journal. 20: 56-65.

DeRose, R. Justin. 2004. **Leaf area index - relative density relationships in even-aged *Abies balsamea* - *Picea rubens* stands in Maine.** Orono, ME: University of Maine. 83 p. M.S. thesis.

DeRose, R. Justin; Seymour, Robert S. 2003. **Relationships between leaf area, structure and relative density in even-aged spruce-fir stands in Maine.** In: Cooperative Forestry Research Unit: 2003 annual report. Miscellaneous Report 2684. Orono, ME: Maine Agricultural and Forest Experiment Station: 28-30.

DeRose, R. Justin; Seymour, Robert S. 2009. **The effect of site index on growth efficiency of upper crown class *Picea rubens* and *Abies balsamea* in Maine, USA.** Canadian Journal of Forest Research. 39: 1-8.

DeRose, R. Justin; Seymour, Robert S. 2010. **Patterns of leaf area index during stand development in even-aged balsam fir - red spruce stands.** Canadian Journal of Forest Research. 40: 629-637.

Dibble, Alison C. 2004. **Use of comparison areas rather than controls in a study of fuels in invaded forests of the Northeast and mid-Atlantic states.** In: Proceedings, Society of American Foresters 2003 national convention; 2003 October 25-29; Buffalo, NY. SAF Publication 04-01. Bethesda, MD: Society of American Foresters: 319-324.

Dibble, Alison C.; Brissette, John C.; Hunter, Malcolm L., Jr. 1999. **Putting community data to work: Some understory plants indicate red spruce regeneration habitat.** Forest Ecology and Management. 114(2-3): 275-291.

Dibble, Alison C.; Rees, Catherine A.; Ducey, Mark J.; Patterson, William A., III. 2003. **Fuelbed characteristics of invaded forest stands.** In: 2003 workshop proceedings: using fire to control invasive plants: What's new, what works in the Northeast? 2003 Jan 24; Portsmouth, NH. Durham, NH: University of New Hampshire Cooperative Extension: 26-29.

DiMauro, Danielle. 1998. **Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests.** Orono, ME: University of Maine. 77 p. M.S. thesis.

DiMauro, Danielle; Hunter, Malcolm L., Jr. 2002. **Reproduction of amphibians in natural and anthropogenic temporary pools in managed forests.** Forest Science. 48: 397-406.

Filauro, Anthony. 1973. **Movement of applied nutrients through Plaisted and Howland soils under mixedwood forest cover types.** Orono, ME: University of Maine. 111 p. M.S. thesis.

Frank, Robert M. 1973. **The course of growth response in released white spruce -- 10-year results.** Research Paper NE-258. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 6 p.

Frank, Robert M. 1974. **Options for and probable benefits of timber stand improvement in Maine.** Maine Forest Review. 6: 2-4.

Frank, Robert M. 1977a. **Indications of silvicultural potential from long-term experiments in spruce-fir types.** In: Proceedings of the symposium on intensive culture of northern forest types; 1976 July 20-22; Orono, ME. Gen. Tech. Rep. NE-29. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 159-177.

Frank, Robert M. 1977b. **Silvicultural options for obtaining high yields in spruce-fir.** In: Filip, Stanley M.; Frank, Robert M.; Smith, David M., eds. High-yield forestry in northern hardwoods, spruce-fir and white pine. Concord, NH: Society of the Protection of New Hampshire Forests: 5-9, 16.

Frank, Robert M. 1983. **Balsam fir (*Pinaceae Abies balsamea*) silvics, silviculture, and natural regeneration methods.** In: Proceedings of the silvicultural guides workshop, Chippewa and Superior National Forests; 1983 February 14-18; Grand Rapids, MN. Duluth, MN: U.S. Forest Service, Superior National Forest: 114-136.

Frank, Robert M. 1984. **Shelterwood system of silviculture in spruce-fir forests.** Forest Technique: Micro-Journal for Information Transfer. 84(8): 9.

Frank, Robert M. 1986. **Shelterwood -- an ideal silvicultural strategy for regenerating spruce-fir stands.** In: Integrated pest management symposium for northern forests: the proceedings; 1986 March 24-27; Madison, WI. Madison, WI: University of Wisconsin, Cooperative Extension Service: 139-150.

Frank, Robert M. 1987. **The Penobscot Experimental Forest -- a unique laboratory.** Forest Technique: Micro-Journal for Information Transfer. 85(3): 20.

Frank, Robert M. 1990. ***Abies balsamea* (L.) Mill. balsam fir.** In: Silvics of North America. 1: Conifers. Agricultural Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 26-35.

Frank, Robert M. 1992. **Tree and wildlife diversity responses to silvicultural practices in northern conifers.** In: Proceedings of the seminar on integrated resource management; 1992 April 7-8; Hugh John Flemming Forestry Centre, N.B. Information Report M-X-183E. Fredericton, NB: Forestry Canada-Maritimes Region: 59-76.

Frank, Robert M.; Bjorkbom, John C. 1973. **A silvicultural guide for spruce-fir in the northeast.** Gen. Tech. Rep. NE-6. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 29 p.

Frank, Robert M.; Blum, Barton M. 1978. **The selection system of silviculture in spruce-fir stands -- procedures, early results, and comparisons with unmanaged stands.** Research Paper NE-425. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 15 p.

Frank, Robert M.; OKeefe, Timothy G. 1983. **A transfer system to reach a selected audience: woodlot owners and mill managers.** Proceedings of the Technology Transfer Society International Symposium: 371-378.

Frank, Robert M.; Safford, Lawrence O. 1970. **Lack of viable seeds in the forest floor after clearcutting.** Journal of Forestry. 68: 776-778.

Frank, Robert M.; Stone, Timothy L.; Crawford, Hewlette S. 1996. **Tree/wildlife diversity responses to silvicultural practices in northern conifers.** In: Forests sustaining people: proceedings of the 1995 Society of American Foresters convention; 1995 October 28-November 1; Portland, ME. Bethesda, MD: Society of American Foresters: 413-414.

Fraver, Shawn; Wagner, Robert G.; Day, Michael. 2002. **Dynamics of coarse woody debris following gap harvesting in the Acadian Forest of central Maine, U.S.A.** Canadian Journal of Forest Research. 32: 2094-2105.

Garber, Sean M.; Brown, John P.; Wilson, Duncan S.; Maguire, Douglas A.; Heath, Linda S. 2005. **Snag longevity under alternative silvicultural regimes in mixed species forests of central Maine.** Canadian Journal of Forest Research. 35: 787-796.

Garrett, Peter W.; Schreiner, Ernst J.; Kettlewood, Harry. 1973. **Geographic variation of eastern white pine in the Northeast.** Research Paper NE-274. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 14 p.

Georgitis, Kathryn M. 2001. **Evaluating shade bias in insect trap catch and assessing the short- and long-term impacts of herbicide application in regenerating clearcuts on flowering plant communities.** Orono, ME: University of Maine. 81 p. M.S. thesis.

Gibbs, Carter B.; Carlaw, James B. 1973. **The New England spruce-fir seed orchard program.** In: Joint proceedings of the 10th Lake States forest tree improvement conference and the 7th Central States forest tree improvement conference; 1971 September 22-24; Madison, WI. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 53-56.

Gilmore, Daniel W. 1995. **Crown structure stem form development and foliage-sapwood area relationships for balsam fir in central Maine.** Orono, ME: University of Maine. 137 p. Ph.D. dissertation.

Gilmore, Daniel W.; Seymour, Robert S. 1996. **Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Maine, USA.** Forest Ecology and Management. 84(1-3): 209-218.

Gilmore, Daniel W.; Seymour, Robert S. 1997. **Crown architecture of *Abies balsamea* from four canopy positions.** Tree Physiology. 17: 71-80.

Gilmore, Daniel W.; Seymour, Robert S. 2004. **Foliage-sapwood area equations for balsam fir require local validation.** Forest Science 50(4): 566-570.

Gilmore, Daniel W.; Seymour, Robert S.; Halteman, William A.; Greenwood, Michael S. 1995. **Canopy dynamics and the morphological development of *Abies balsamea*: effects of foliage age on specific leaf area and secondary vascular development.** Tree Physiology. 15(1): 47-55.

Gilmore, Daniel W.; Seymour, Robert S.; Maguire, Douglas A. 1996. **Foliage sapwood area relationships for *Abies balsamea* in central Maine, USA.** Canadian Journal of Forest Research. 26(12): 2071-2079.

Greenwood, Michael S.; Day, Michael E.; Berlyn, Graeme P. 2009. **Regulation of foliar plasticity in conifers: developmental and environmental factors.** Journal of Sustainable Forestry. 28: 48-62.

Greenwood, Michael S.; Day, Michael E.; Schatz, Jason. 2010. **Separating the effects of tree size and meristem maturation on shoot development of grafted scions of red spruce (*Picea rubens* Sarg.).** Tree Physiology. 30: 459-468.

Greenwood, Michael S.; Livingston, William H.; Sokol, Kerry A. 1999. **The legacy of diameter-limit cutting: a case study for red spruce.** In: Cooperative Forestry Research Unit: 1999 annual report. Miscellaneous Report 417. Orono, ME: Maine Agricultural and Forest Experiment Station: 33-35.

Greenwood, Michael S.; McConville, Daniel. 2002. **Factors affecting the regeneration of red spruce and balsam fir.** In: Cooperative Forestry Research Unit: 2002 annual report. Miscellaneous Report 431. Orono, ME: Maine Agricultural and Forest Experiment Station: 37-40.

Greenwood, Michael S.; Ward, Margaret H.; Day, Michael E.; Adams, Stephanie L.; Bond, Barbara J. 2008. **Age-related trends in red spruce foliar plasticity in relation to declining productivity.** Tree Physiology. 28: 225-232.

Grisez, Ted J. 1954a. **1954 hurricane damage of Penobscot Experimental Forest.** Forest Research Note No. 39. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Grisez, Ted J. 1954b. **Results of a mouse census in a spruce-fir-hemlock forest in Maine.** Forest Research Note No. 28. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Hale, Kathy N. 1977. **The genetic improvement of northeastern spruce species.** Orono, ME: University of Maine. 105 p. M.S. thesis.

Hart, Arthur C. 1952. **A wrist guard for pulpwood handlers.** The Northeastern Logger. 1(5): 37.

Hart, Arthur C. 1953. **Small-forest management in the spruce-fir region.** Northeastern Research Note No. 21. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 4 p.

Hart, Arthur C. 1956a. **Logging on the Penobscot Experimental Forest.** The Northeastern Logger. 5(6): 33, 90-91.

Hart, Arthur C. 1956b. **Results of small woodlot cuttings on Penobscot Experimental Forest, 1953 and 1954.** Forest Research Note No. 61. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Hart, Arthur C. 1958. **Penobscot woodlands yield annual cuts.** Forest Research Note No. 84. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 2 p.

Hart, Arthur C. 1959. **Silvical characteristics of balsam fir (*Abies balsamea*).** Station Paper No. 122. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 21 p.

Hart, Arthur C. 1961. **Thinning balsam fir thickets with soil sterilants.** Station Paper No. 152. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

Hart, Arthur C. 1963. **Spruce-fir silviculture in northern New England.** In: Proceedings, Society of American Foresters national convention; Boston, MA. Society of American Foresters: 107-110.

Hart, Arthur C. 1964. **The Penobscot management-intensity demonstration plots.** Research Paper NE-25. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 24 p.

Hart, Arthur C. 1966. **Research programs of the Northeastern Forest Experiment Station.** American Pulpwood. January: 23-25.

Hart, Arthur C.; Abbott, Herschel G.; Ladd, Edward R. 1968. **Do small mammals and birds affect reproduction of spruce and fir?** Research Paper NE-110. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

Hart, Arthur C.; Bissell, Lewis P. 1959. **Farm woodlots: cost and income.** Maine Extension Service Circular 338. [Place of publication unknown]. Agricultural Extension Service, University of Maine and the U.S. Department of Agriculture Cooperating. 12 p.

Hart, Arthur C.; Tuttle, Harold B. 1957. **A new wrinkle in chemical debarking.** The Northeastern Logger. 6(1): 16.

Hartley, Mitschka J. 2003. **Effects of small-gap timber harvests on songbird community composition and site-fidelity.** Orono, ME: University of Maine. 141 p. Ph.D. dissertation.

Hawley, Gary; DeHayes, Donald; Schaberg, Paul; Brissette, John. 2006. **Genetic effects of diameter-limit cutting.** In: Kenefic, Laura S.; Nyland, Ralph D., eds. Proceedings of the conference on diameter-limit cutting in northeastern forests; 2005 May 23-24; Amherst, MA. Gen. Tech. Rep. NE-342. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 41-42.

Hawley, Gary J.; Schaberg, Paul G.; DeHayes, Donald H.; Brissette, John C. 2005. **Silviculture alters the genetic structure of an eastern hemlock forest in Maine, USA.** Canadian Journal of Forest Research. 35: 143-150.

Hoar, Leigh E., Jr.; Young, Harold E. 1965. **Mensuration methods for site classification of shade tolerant tree species.** Technical Bulletin 18. Orono, ME: Maine Agricultural and Forest Experiment Station. 15 p.

Hofton, Michelle; Dubayah, Ralph; Blair, J. Bryan; Rabine, David. 2006. **Validation of SRTM elevations over vegetated and non-vegetated terrain using medium footprint Lidar.** Photogrammetric Engineering & Remote Sensing. 72(3): 279-285.

Horton, Brent. 2007. **Corticosterone and morph-specific variation in the reproductive behavior of the polymorphic white-throated sparrow (*Zonotrichia albicollis*).** Orono, ME: University of Maine. 112 p. Ph.D. dissertation.

Horton, Brent M.; Holberton, Rebecca L. 2009. **Corticosterone manipulations alter morph-specific nestling provisioning behavior in male white-throated sparrows, *Zonotrichia albicollis*.** Hormones and Behavior. 56: 510-518.

Horton, Brent M.; Holberton, Rebecca L. 2010. **Morph-specific variation in baseline corticosterone and the adrenocortical response in breeding white-throated sparrows (*Zonotrichia albicollis*).** The Auk. 127(3): 540-548.

Houseweart, Mark W.; Jennings, Daniel T.; Berkett, Lorraine P.; Brann, Thomas B. 1980. **Parasitic mites (Acari: Erythraeidae) on spruce budworm moths (Lepidoptera: Tortricidae).** The Canadian Entomologist. 112(2): 193-197.

Houseweart, Mark W.; Southard, Susan G.; Jennings, Daniel T. 1982. **Availability and acceptability of spruce budworm eggs to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae).** The Canadian Entomologist. 114: 657-666.

Irvine, Kathryn M.; Woods, Stephen A. 2007. **Evaluating shading bias in Malaise and window-pane traps.** Journal of the Acadian Entomological Society. 3: 38-48.

Jennings, Daniel T.; Crawford, Hewlette S. 1983. **Pine siskin preys on egg masses of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae).** The Canadian Entomologist. 115: 439-440.

Jennings, D.T.; Frank, R.M.; Houseweart, M.W. 1984. **Attraction of male spruce budworm moths, *Choristoneura fumiferana* (Clemens), to pheromone-baited traps in small-tree thinnings.** Journal of Chemical Ecology. 10(1): 125-133.

Jennings, Daniel T.; Houseweart, Mark W. 1983. **Sticky-board trap for measuring dispersal of spruce budworm larvae.** Research Paper NE-526. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Jennings, Daniel T.; Houseweart, Mark W. 1986. **Helicopter propwash dislodges few spruce budworms.** Research Note NE-333. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Jennings, Daniel T.; Houseweart, Mark W. 1989. **Sex-biased predation by web-spinning spiders (Araneae) on spruce budworm moths.** Journal of Arachnology. 17(2): 179-194.

Jennings, Daniel T.; Sferra, Nancy J. 2002. **An arthropod predator-prey-kleptoparasite association.** Northeastern Naturalist. 9(3): 325-330.

Johnston, Jason C. 2007. **The effects of forest management and food availability on the ecophysiology of pre-breeding and breeding hermit thrushes (*Catharus guttatus*).** Orono, ME: University of Maine. 166 p. Ph.D. dissertation.

Johnston, Jason C.; Holberton, Rebecca L. 2009. **Forest management and temporal effects on food abundance for a ground-foraging bird (*Catharus guttatus*).** Forest Ecology and Management. 258(7): 1516-1527.

Jordan, James S.; Rushmore, Francis M. 1969. **Animal damage to birch.** In: Larson, E. vH., ed. The birch symposium; proceedings; 1969 August 19-21; Durham, NH. Research Paper NE-146. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Research Station: 155-163.

Kanoti, Keith-George. 2005. **Factors influencing the germination, emergence, and early survival of boreal, temperate and exotic Acadian Forest tree species in central Maine.** Orono, ME: University of Maine. 127 p. M.S. thesis.

Kendall, David M.; Jennings, Daniel T.; Houseweart, Mark W. 1982. **A large-capacity pheromone trap for spruce budworm moths (Lepidoptera: Tortricidae).** The Canadian Entomologist. 114: 461-463.

Kenefic, Laura S. 1999. **Multi-aged silviculture in the Acadian Forest of Maine.** In: Harrison, Girvan; Whitney, Robert; Swift, Edwin, eds. Proceedings of the tolerant softwood workshop; 1999 April 13-15; Fredericton, N.B. Maritime Forest Ranger School. 11: 1-31.

Kenefic, Laura S. 2000. **Leaf area, stemwood volume growth and stand structure in mixed-species, multi-aged stands.** Orono, ME: University of Maine. 164 p. Ph.D. dissertation.

Kenefic, Laura S.; Brissette, John C. 2001. **Long-term dynamics of structure and composition in uneven-aged northern conifer stands.** In: Forestry at the great divide: proceedings, Society of American Foresters national convention; 2001 September 13-17; Denver, CO. Bethesda, MD: Society of American Foresters: 405-407.

Kenefic, Laura S.; Brissette, John C.; Kanoti, Keith, contributors. 2009. **Penobscot Experimental Forest—leaving something to grow on.** In: Experimental forests and ranges: 100 years of research success stories. Gen. Tech. Rep. FPL-182. Washington, DC: U.S. Department of Agriculture, Forest Service: 4-5.

Kenefic, Laura S.; Brissette, John C.; Sendak, Paul E. 2004. **The effects of alternative diameter-limit cutting treatments: some findings from a long-term northern conifer experiment.** In: Ward, Jeffrey S.; Twery, Mark J., eds. Forestry across borders: proceedings of the New England Society of American Foresters 84th winter meeting; 2004 March 23-26; Quebec City, Canada. Gen. Tech. Rep. NE-314. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 22-24.

Kenefic, Laura S.; Brissette, John C.; Sendak, Paul E. 2006. **Overview of USDA Forest Service research on diameter-limit cutting in northern conifers.** In: Kenefic, Laura S.; Nyland, Ralph D., eds. Proceedings of the conference on diameter-limit cutting in northeastern forests; 2005 May 23-24; Amherst, MA. Gen. Tech. Rep. NE-342. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 24-31.

Kenefic, Laura S.; Nyland, Ralph D. 2005. **Diameter-limit cutting and silviculture in northeastern forests: a primer for landowners, practitioners, and policymakers.** NA-TP-02-05. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Area State and Private Forestry. 18 p.

Kenefic, Laura S.; Sendak, Paul E.; Brissette, John C. 2002. **Fixed diameter-limit versus selection cutting: a long-term assessment in northern conifers.** In: Forestry at the great divide: proceedings, Society of American Foresters national convention; 2001 September 13-17; Denver, CO. Bethesda, MD: Society of American Foresters: 408-409.

Kenefic, Laura S.; Sendak, Paul E.; Brissette, John C. 2005. **Comparison of fixed diameter-limit and selection cutting in northern conifers.** Northern Journal of Applied Forestry. 22(2): 77-84.

Kenefic, Laura S.; Sendak, Paul E.; Brissette, John C. 2006. **Turning data into knowledge for over 50 years: USDA forest service research on the Penobscot Experimental Forest.** In: Irland, Lloyd C.; Camp, Ann E.; Brissette, John C.; Donohew, Zachary R., eds. Long-term silvicultural and ecological studies: results for science and management. Global Institute of Sustainable Forestry Research Paper 005. New Haven, CT: Yale University: 26-33.

Kenefic, Laura S.; Seymour, Robert S. 1999. **Leaf area prediction models for *Tsuga canadensis* in Maine.** Canadian Journal of Forest Research. 29: 1574-1582.

Kenefic, Laura S.; Seymour, Robert S. 2000. **Growth patterns of *Tsuga canadensis* in managed uneven-aged northern conifer stands.** In: McManus, K.A.; Shields, K.S.; Souto, D.R., eds. Proceedings: symposium on the sustainable management of hemlock ecosystems in eastern North America; 1999 June 22-24; Durham, NH. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 29-33.

Kenefic, Laura S.; Seymour, Robert S. 2002. **Leaf area - stemwood volume growth relationships for eastern hemlock, balsam fir, and red spruce in multi-aged stands.** In: Forestry at the great divide: proceedings, Society of American Foresters national convention; 2001 September 13-17; Denver, CO. Bethesda, MD: Society of American Foresters: 410-411.

Kenefic, Laura S.; White, Alan S.; Fraver, Shawn. 2004. **Reference conditions for silviculture field studies in Maine: limitations and opportunities.** In: Proceedings, Society of American Foresters 2003 national convention; 2003 October 25-29; Buffalo, NY. SAF Publication 04-01. Bethesda, MD: Society of American Foresters: 344-349.

Kenefic, Laura S.; White, Alan S.; Cutko, Andrew R.; Fraver, Shawn. 2005. **Reference stands for silvicultural research: a Maine perspective.** Journal of Forestry. 103(7): 363-367.

Kidd, Walter J., Jr. 1952. **A small-tree diameter gauge.** Journal of Forestry. 50: 220.

Larouche, Catherine. 2009. **La régénération du thuya après coupes partielles en peuplement mixtes.** Quebec, QC: Université Laval. 158 p. Ph.D. dissertation.

Larouche, Catherine; Kenefic, Laura S.; Ruel, Jean-Claude. 2010. **Northern white-cedar regeneration dynamics on the Penobscot Experimental Forest in Maine: 40-year results.** Northern Journal of Applied Forestry. 27(1): 5-12.

Larouche, Catherine; Morissette, Sabrina; Ruel, Jean-Claude; Lussier, Jean-Martin; Kenefic, Laura S. 2007. **Regeneration of *Thuja occidentalis* L. in mixedwood stands after partial cutting.** In: Proceedings of the Carrefour de la recherche forestière. 2007 Sept. 19-20, Quebec, QC. 5 p. In French.

Li, Rongxia; Weiskittel, Aaron R. 2010. **Comparison of model forms for estimating stem taper and volume in the primary conifer species of the North American Acadian Region.** Annals of Forest Science. 67: 302(1-16).

Lindemuth, Robert M. 2007. **A field trial comparison of sampling methods for estimating basal area and volume in partially harvested stands in Maine.** Orono, ME: University of Maine. 100 p. M.S. thesis.

Longwood, Franklin R. 1958. **The Penobscot Experimental Forest.** In: 5th northeastern forest tree improvement conference; 1957 August 22-23; Orono, ME. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 28.

Maguire, Douglas A.; Brissette, John C.; Gu, Lianhong. 1998. **Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine.** Canadian Journal of Forest Research. 28: 1233-1240.

Mahoney, Eileen M.; Milgroom, Michael G.; Sinclair, Wayne A.; Houston, David R. 1999. **Origin, genetic diversity, and population structure of *Nectria coccinea* var. *faginata* in North America.** Mycologia. 91(4): 583-592.

McConville, Daniel J.; Wagner, Robert G.; Seymour, Robert S. 2003. **Study site establishment and measurement of the Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2003 annual report. Miscellaneous Report 2684. Orono, ME: Maine Agricultural and Forest Experiment Station: 24-25.

McConville, Daniel J.; Wagner, Robert G.; Seymour, Robert S. 2004. **Commercial Thinning Research Network: maintenance, measurements, and analysis.** In: Cooperative Forestry Research Unit: 2004 annual report. Miscellaneous Report 435. Orono, ME: Maine Agricultural and Forest Experiment Station: 25-29.

McLintock, Thomas F. 1952. **Cost of pruning red spruce in natural stands.** Journal of Forestry. 50: 485-486.

McLintock, Thomas F. 1954. **The Penobscot Experimental Forest.** Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 26 p.

McLintock, Thomas F. 1958. **Hardpans in the spruce-fir forests of Maine.** In: Proceedings, Society of American Foresters meeting; 1957 November 10-13; Syracuse, NY. Washington, DC: Society of American Foresters: 65-66.

McLintock, Thomas F. 1959. **Soil moisture patterns in a northern coniferous forest.** Station Paper 128. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 5 p.

Meyer, Spencer R. 2004. **Leaf area as a growth predictor of *Abies balsamea* and *Picea rubens* in managed stands in Maine.** Orono, ME: University of Maine. 117 p. M.S. thesis.

Meyer, Spencer R.; Wagner, Robert G.; Seymour, Robert S. 2006. **Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2005-2006 annual report. Miscellaneous Report 440. Orono, ME: Maine Agricultural and Forest Experiment Station: 24-27.

Meyer, Spencer R.; Wagner, Robert G.; Seymour, Robert S. 2007. **Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2006-2007 annual report. Miscellaneous Report 444. Orono, ME: Maine Agricultural and Forest Experiment Station: 20-24.

Meyer, Spencer R.; Wagner, Robert G.; Seymour, Robert S.; Russell, Matthew. 2009. **Commercial thinning research network.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2008 annual report. Orono, ME: University of Maine: 25-26.

Meyer, Spencer R.; Wagner, Robert G.; Seymour, Robert S.; Russell, Matthew. 2010. **Commercial thinning research network.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2009 annual report. Orono, ME: University of Maine: 21-22.

Miller, Kathryn M. 2006. **Arboreal arthropod associations with epiphytes and the effects of gap harvesting in the Acadian Forest of central Maine.** Orono, ME: University of Maine. 69 p. Ph.D. dissertation.

Miller, Kathryn M.; Wagner, Robert G.; Woods, Stephen A. 2007. **Effect of gap harvesting on epiphytes and bark-dwelling arthropods in the Acadian forest of central Maine.** Canadian Journal of Forest Research. 37: 2175-2187.

Miller, Kathryn M.; Wagner, Robert G.; Woods, Stephen A. 2008. **Arboreal arthropod associations with epiphytes following gap harvesting in the Acadian forest of Maine.** The Bryologist. 111(3): 424-434.

Minocha, Rakesh; Long, Stephanie; Wagner, Robert G. 2004. **Effects of commercial thinning on physiological stress in balsam fir and red spruce.** In: Cooperative Forestry Research Unit: 2004 annual report. Miscellaneous Report 435. Orono, ME: Maine Agricultural and Forest Experiment Station: 40-42.

Minocha, Rakesh; Long, Stephanie; Wagner, Robert G. 2005. **Effects of commercial thinning on physiological stress in balsam fir and red spruce.** In: Cooperative Forestry Research Unit: 2004-2005 annual report. Miscellaneous Report 438. Orono, ME: Maine Agricultural and Forest Experiment Station: 47-48.

Minocha, Rakesh; Thangavel, Palaniswamy; Dhankher, Om Parkash; Long, Stephanie. 2008. **Separation and quantification of monothiols and phytochelatins from a wide variety of cell cultures and tissues of trees and other plants using high performance liquid chromatography.** Journal of Chromatography A. 1207(1-2): 72-83.

Moores, Andrew R. 2003. **Understory growth dynamics and mensuration techniques in uneven-aged, mixed-species northern conifer stands.** Orono, ME: University of Maine. 105 p. M.S. thesis.

Moores, Andrew R.; Seymour, Robert S.; Kenefic, Laura S. 2004. **Understory height growth dynamics in uneven-aged, mixed-species northern conifer stands.** In: Ward, Jeffrey S.; Twery, Mark J., eds. Forestry across borders: proceedings of the New England Society of American Foresters 84th winter meeting; 2004 March 23-26; Quebec City, Canada. Gen. Tech. Rep. NE-314. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 12-14.

Moores, Andrew R.; Seymour, Robert S.; Kenefic, Laura S. 2007. **Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands.** Canadian Journal of Forest Research. 37(12): 2715-2723.

Momoshima, Noriyuki; Bondietti, Ernest A. 1990. **Cation binding in wood: applications to understanding historical changes in divalent cation availability in red spruce.** Canadian Journal of Forest Research. 20: 1840-1849.

Mount, Peter; Covell, Mildred R.; Young, Harold E. 1952. **Physical properties of forest soil as related to the site index of spruce – a progress report.** Technical Bulletin 16. Orono, ME: Maine Agricultural and Forest Experiment Station. 2 p.

Mount, Peter; Gove, William; Young, Harold E. 1952. **Site index for spruce-fir stands based on age at breast height and total height.** Technical Bulletin 13. Orono, ME: Maine Agricultural and Forest Experiment Station. 3 p.

Muszynski, Lech; Lagana, Rastislav; Shaler, Stephen M. 2003. **An optical method for characterization of basic hygromechanical properties of solid wood in tension.** In: Proceedings of the 8th international IUFRO wood drying conference; 2003 August 24-29; Brasov, Romania. Brasov, Romania: Transilvania University of Brasov: 77-82.

Muszynski, Lech; Lagana, Rastislav; Shaler, Stephen M. 2006. **Hygro-mechanical behavior of red spruce in tension parallel to the grain.** Wood and Fiber Science. 38(1): 155-165.

Olson, Matthew G. 2009. **Spatial and temporal patterns of tree regeneration in the Acadian Forest of central Maine.** Orono, ME: University of Maine. 120 p. Ph.D. dissertation.

Olson, Matthew G.; Wagner, Robert G. 2010. **Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes.** Canadian Journal of Forest Research. 40(10): 1993-2002.

Ostrofsky, William D. 1998. **Condition and development of root systems of fir and spruce following precommercial thinning.** Cooperative Forestry Research Unit: 1998 annual report. Miscellaneous Report 411. Orono, ME: Maine Agricultural and Forest Experiment Station: 9-11.

Patrick, David A. 2007. **The effects of forest practices on a Maine amphibian community.** Orono, ME: University of Maine. 119 p. Ph.D. dissertation.

Patrick, David A.; Calhoun, Aram J.K.; Hunter, Malcolm L., Jr. 2008. **The importance of understanding spatial population structure when evaluating the effects of silviculture on spotted salamanders (*Ambystoma maculatum*).** Biological Conservation. 141(3): 807-814.

Patrick, David A.; Harper, E.B.; Hunter, Malcolm L., Jr.; Calhoun, Aram J.K. 2008. **Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians.** Ecology. 89: 2563-2574.

Patrick, David A.; Hunter, Malcolm L., Jr.; Calhoun, Aram J.K. 2006. **Effects of experimental forestry treatments on a Maine amphibian community.** Forest Ecology and Management. 234(1-3): 323-332.

Philips, Leah M. 2002. **Crop tree growth and quality twenty-five years after precommercial thinning in a northern conifer stand.** Orono, ME: University of Maine. 87 p. M.S. thesis.

Ray, David G.; Keyser, Chad; Seymour, Robert S.; Brissette, John C. 2008. **Predicting the recruitment of established regeneration into the sapling size class following partial cutting in the Acadian Forest Region: using long-term observations to assess the performance of FVS-NE.** In: Havis, Robert N.; Crookston, Nicholas L., comps. Third Forest Vegetation Simulator conference; 2007 February 13-15; Fort Collins, CO. RMRS-P-54. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 186-200.

Ray, David G.; Saunders, Michael R.; Seymour, Robert S. 2009. **Recent changes to the northeastern variant of the Forest Vegetation Simulator (FVS-NE) and some basic strategies for improving model outputs.** Northern Journal of Applied Forestry. 26(1): 31-34.

Ray, David G.; Seymour, Robert S.; Keyser, Chad. 2006. **A test of FVS-NE for simulating the long-term growth dynamics of partially cut stands in the Acadian forest region.** In: Larocque, Guy R.; Fortin, Mathieu; Thiffault, Nelson, comps. Eastern Canada-USA forest science conference; 2006 October 19-21; Quebec: 118-123.

Rinaldi, Anthony M. 1970. **Deer and hare forage following strip clearcutting and slash disposal on the Penobscot Experimental Forest, Maine.** Orono, ME: University of Maine. 81 p. M.S. thesis.

Rushmore, Francis M. 1969. **Sapsucker damage varies with tree species and seasons.** Research Paper NE-136. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 19 p.

Rushmore, Francis M. 1973. **Techniques for calling sapsuckers and finding their nesting territories.** Research Paper NE-281. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 7 p.

Safford, Lawrence O. 1968. **Evaluation of growth characteristics of individual free-growing red spruce trees as a means of estimating forest productivity.** Orono, ME: University of Maine. 148 p. Ph.D. dissertation.

Safford, Lawrence O.; Frank, Robert M.; Little, Elbert L., Jr. 1969. **Trees and shrubs of the Penobscot Experimental Forest Penobscot County, Maine.** Research Paper NE-128. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 27 p.

Safford, Lawrence O.; Young, Harold E. 1968. **Nutrient content of the current foliage of red spruce growing on three soils in Maine.** Research in the Life Sciences, a quarterly report of the Maine Agriculture Experiment Station. Spring: 27-31.

Saunders, Michael R. 2006. **Dynamics of forest structure under different silvicultural regimes in the Acadian Forest.** Orono, ME: University of Maine. 249 p. Ph.D. dissertation.

Saunders, Mike R.; Wagner, Robert G. 2005. **Ten-year results of the Forest Ecosystem Research Program (FERP) - successes and challenges.** In: Peterson, C.E.; Maguire, D.A., eds. Balancing ecosystem values: innovative experiments for sustainable forestry; 2004 August 15-20; Portland, OR. Gen. Tech. Rep. PNW-635. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 147-153.

Saunders, Mike R.; Wagner, Robert G. 2008a. **Height-diameter models with random coefficients and site variables for tree species of central Maine.** Annals of Forest Science. 65: 203 (1-10).

Saunders, Mike R.; Wagner, Robert G. 2008b. **Long-term spatial and structural dynamics in Acadian mixedwood stands managed under various silvicultural systems.** Canadian Journal of Forest Research. 38: 498-517.

Schofield, Darci. 2003. **Vegetation dynamics and tree radial growth response in harvest gaps, natural gaps, and closed canopy conditions in Maine's Acadian Forest.** Orono, ME: University of Maine. 146 p. M.S. thesis.

Semlitsch, R.D.; Todd, Brian D.; Blomquist, Sean M.; Calhoun, Aram J.K.; Gibbons, J. Whitfield; Gibbs, James P.; Graeter, Gabrielle; Harper, Elizabeth B.; Hocking, Daniel; Hunter, Malcolm L., Jr.; Patrick, David A.; Rittenhouse, Tracy A.G.; Rothermel, Betsie B. 2009. **Effects of timber management on amphibian populations: understanding mechanisms from forest experiments.** Bioscience. 59: 853-862.

Sendak, Paul E. 2002. **Timber marking costs in spruce-fir: experience on the Penobscot Experimental Forest.** Northern Journal of Applied Forestry. 19(1): 22-24.

Sendak, Paul E.; Brissette, John C.; Frank, Robert M. 2003. **Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** Canadian Journal of Forest Research. 33: 2116-2128.

Sendak, Paul E.; Brissette, John C.; Frank, Robert M. 2004. **Managing stands of mixed northern conifers: 40-year results from the Penobscot Experimental Forest.** In: Ward, Jeffrey S.; Twery, Mark J., eds. Forestry across borders: proceedings of the New England Society of American Foresters 84th winter meeting; 2004 March 23-26; Quebec City, Canada. Gen. Tech. Rep. NE-314. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 19-21.

Sendak, Paul E.; Frank, Robert M.; Brissette, John C. 1996. **Financial analysis of northern conifer stands under various silvicultural treatments.** In: Sustaining forests, sustaining people: proceedings of the 1995 Society of American Foresters convention; 1996 October 28-November 1; Portland, ME. SAF-96-01. Bethesda, MD: Society of American Foresters: 368-369.

Sendak, Paul S.; Frank, Robert M.; Leak, William B. 2006. **Long-term data from silvicultural studies: interpreting and assessing old records for economic insights.** In: Irland, Lloyd C.; Camp, Ann E.; Brissette, John C.; Donohew, Zachary R., eds. Long-term silvicultural and ecological studies: results for science and management. Global Institute of Sustainable Forestry Research Paper 005. New Haven, CT: Yale University: 203-207.

Seymour, Robert S. 1995. **The northeastern region.** In: Barrett, John W., ed. Regional silviculture of the United States. 3rd ed. New York, NY: John Wiley & Sons: 31-79.

Seymour, Robert S. 2005. **Integrating disturbance parameters into conventional silvicultural systems: experience from the Acadian forest of northeastern North America.** In: Peterson, C.E.; Maguire, Douglas A., eds. Balancing ecosystem values: innovating experiments for sustainable forestry. Gen. Tech. Rep. PNW-GTR-635. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 41-48.

Seymour, Robert. 2008. **Natural disturbance-based multi-aged silviculture in the Acadian Forest of northeastern North America.** In: Society of American Foresters: 2007 national convention: sustaining America's forests; 2007 October 23-27; Portland, OR. [CD-ROM]. Bethesda, MD: Society of American Foresters.

Seymour, Robert S.; Guldin, James; Marshall, David; Palik, Brian. 2006. **Large-scale, long-term silvicultural experiments in the United States.** Allgemeine Forst und Jagd-Zeitung. 177(6/7): 104-112.

Seymour, Robert S.; Kenefic, Laura S. 1998. **Balance and sustainability in multi-aged stands: a northern conifer case study.** Journal of Forestry. 96(7): 12-16.

Seymour, Robert S.; Kenefic, Laura S. 2002. **Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands.** Canadian Journal of Forest Research. 32: 2032-2042.

Seymour, Robert S.; Zellers, Chris; Zeller, Kate. 2010. **Crop tree silviculture of white pine in mixed stands.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2009 annual report. Orono, ME: University of Maine: 23-27.

Smith, Kevin T.; Shortle, Walter C.; Jellison, Jody; Connolly, Jon; Schilling, Jonathon. 2007. **Concentrations of Ca and Mg in early stages of sapwood decay in red spruce, eastern hemlock, red maple, and paper birch.** Canadian Journal of Forest Research. 37: 957-965.

Sokol, Kerry A. 2001. **Implications of long-term diameter-limit harvesting: effects on radial growth of red spruce (*Picea rubens*) and genetic diversity of white pine (*Pinus strobus*).** Orono, ME: University of Maine. 118 p. M.S. thesis.

Sokol, Kerry A.; Greenwood, Michael S.; Livingston, William L. 2004. **Impacts of long-term diameter-limit harvesting on residual stands of red spruce in Maine.** Northern Journal of Applied Forestry. 21(2): 69-73.

Solomon, Dale S.; Frank, Robert M. 1983. **Growth response of managed uneven-aged northern conifer stands.** Research Paper NE-517. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 17 p.

Solomon, Dale S.; Gove, Jeffrey H. 1999. **Effects of uneven-age management intensity on structural diversity in two major forest types in New England.** Forest Ecology and Management. 114(2-3): 265-274.

Solomon, Dale S.; Hosmer, Richard A. 1986. **Fiber: a growth model for forest types in the Northeast.** In: Wiant, H.V.; Yandle, D.O.; Kidd, W.E., eds. Forestry microcomputer software symposium; 1986 June 30-July 2; Morgantown, WV. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 131-145.

Solomon, Dale S.; Hosmer, Richard A.; Hayslett, Homer T., Jr. 1986. **A two-stage matrix model for predicting growth of forest stands in the Northeast.** Canadian Journal of Forest Research. 16: 521-528.

Solomon, Dale S.; Hosmer, Richard A.; Hayslett, Homer T., Jr. 1987. **Fiber handbook: a growth model for spruce-fir and northern hardwood forest types.** NE-RP-602. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 19 p.

Solomon, Dale S.; Seegrist, Donald W. 1983. **Growth and yield analysis of thinned uneven-aged spruce and fir stands in Maine.** In: Proceedings: planning, performance, and evaluation of growth and yield studies; 1979 September; Oxford, England. IUFRO Subject Group S4.01, Occasional Paper 20. University of Oxford Press: Commonwealth Forestry Institute: 149-156.

Spencer, Katherine J. 2010. **Addressing the age-related growth decline in red spruce productivity: integrating physiological and genomic approaches.** Orono, ME: University of Maine. 71 p. M.S. thesis.

Strojny, Carol A. 2004. **Effects of harvest gaps and natural canopy gaps on amphibians within a northeastern forest.** Orono, ME: University of Maine. 87 p. M.S. thesis.

Strojny, Carol A.; Hunter, Malcolm L., Jr. 2010a. **Comparing relative abundance of amphibians in forest canopy gaps of natural origin vs. timber harvest origin.** Animal Biodiversity and Conservation. 33: 1-13.

Strojny, Carol A.; Hunter, Malcolm L., Jr. 2010b. **Log diameter influences detection of eastern red-backed salamanders (*Plethodon cinereus*) in harvest gaps, but not in closed-canopy forest conditions.** Herpetological Conservation and Biology. 5: 80-85.

Su, Jeffrey C. 1999. **Insect diversity in forests and its relationship to plant diversity, structural diversity, and forest management.** Orono, ME: University of Maine. 79 p. Ph.D. dissertation.

Su, Jeffrey C.; Woods, Stephen A. 2001. **Importance of sampling along a vertical gradient to compare the insect fauna in managed forests.** Environmental Entomology. 30(2): 400-408.

Swift, Edwin; Penner, Margaret; Gagnon, Rolland; Knox, Jason. 2007. **A stand density management diagram for spruce-balsam fir mixtures in New Brunswick.** Forestry Chronicle. 83(2): 187-197.

Thomas, Shelly L. 2007. **Effects of forest management on click beetle (Coleoptera: Elateridae) assemblages in the Acadian Forest of Maine.** Orono, ME: University of Maine. 174 p. Ph.D. dissertation.

Tian, Suzhong. 2002. **Effect of precommercial thinning on root development and root and butt decay incidence of red spruce and balsam fir.** Orono, ME: University of Maine. 265 p. Ph.D. dissertation.

Tian, Suzhong; Ostrofsky, William D. 1999. **Condition and development of root systems of balsam fir and red spruce in pre-commercially thinned and unthinned stands.** Cooperative Forestry Research Unit: 1999 annual report. Miscellaneous Report 417. Orono, ME: Maine Agricultural and Forest Experiment Station: 21-22.

Tian, Suzhong; Ostrofsky, William D. 2000. **Condition and development of root systems of balsam fir and red spruce in precommercially thinned and unthinned stands.** Cooperative Forestry Research Unit: 2000 annual report. Miscellaneous Report 424. Orono, ME: Maine Agricultural and Forest Experiment Station: 28-29.

Tian, Suzhong; Ostrofsky, William D. 2001. **Condition and development of root systems of balsam fir and red spruce in precommercially thinned and unthinned stands.** Cooperative Forestry Research Unit: 2001 annual report. Miscellaneous Report 428. Orono, ME: Maine Agricultural and Forest Experiment Station: 36.

Tian, Suzhong; Ostrofsky, William D. 2007. **Butt and root decay in precommercially thinned spruce-fir stands.** Northern Journal of Applied Forestry. 24(2): 129-133.

Tsomides, Leonidas; Gibbs, K. Elizabeth; Jennings, Daniel T. 1982. **Species of Odonata feeding on Lepidoptera in spruce-fir forests of Maine.** Research in the Life Sciences, a report of the University of Maine at Orono, Life Sciences and Agricultural Experiment Station. 30(1): 1-12.

Wagner, Robert G.; Keefe, Robert F. 2005. **Growing space allocation to residual stands following commercial thinning treatments.** In: Cooperative Forestry Research Unit: 2004-2005 annual report. Miscellaneous Report 438. Orono, ME: Maine Agricultural and Forest Experiment Station: 42-46.

Wagner, Robert G.; Seymour, Robert S. 2005. **Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2004-2005 annual report. Miscellaneous Report 438. Orono, ME: Maine Agricultural and Forest Experiment Station: 34-41.

Wagner, Robert G.; Seymour, Robert S.; McConville, Daniel J. 2001. **Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2001 annual report. Miscellaneous Report 428. Orono, ME: Maine Agricultural and Forest Experiment Station: 23-35.

Wagner, Robert G.; Seymour, Robert S.; McConville, Daniel J.; Opland, Dawn M. 2002. **Commercial Thinning Research Network.** In: Cooperative Forestry Research Unit: 2002 annual report. Miscellaneous Report 431. Orono, ME: Maine Agricultural and Forest Experiment Station: 23-28.

Ward, Margaret H. 2005. **Age-related trends in red spruce needle anatomy and their relationship to declining productivity.** Orono, ME: University of Maine. 97 p. M.S. thesis.

Wave, Herbert E.; Wentworth, David F.; Chapman, Gordon L. 1952. **A pruning time study for spruce and white pine in unevenaged, natural stands.** Technical Bulletin 15. Orono, ME: Maine Agricultural and Forest Experiment Station. 2 p.

Weaver, Jamie K. 2007. **Substrate availability and regeneration microsites of tolerant conifers in mixed-species stands in Maine.** Orono, ME: University of Maine. 80 p. M.S. thesis.

Weaver, Jamie; Kenefic, Laura S.; Brissette, John C.; Seymour, Robert S. 2006. **Coarse woody material as a regeneration substrate: impacts of management.** In: Proceedings, Society of American Foresters 2006 national convention; 2006 October 25-29; Pittsburgh, PA. [CD-ROM]. Bethesda, MD: Society of American Foresters.

Weaver, Jamie K.; Kenefic, Laura S.; Seymour, Robert S.; Brissette, John C. 2009. **Decaying wood and tree regeneration in the Acadian Forest of Maine, USA.** Forest Ecology and Management. 257(7): 1623-1628.

Weiskittel, Aaron R.; Kenefic, Laura S.; Seymour, Robert S.; Phillips, Leah M. 2009. **Long-term effects of precommercial thinning on stem dimensions, form and branch characteristics of red spruce and balsam fir crop trees in Maine, USA.** Silva Fennica. 43(3): 397-409.

Weiskittel, Aaron. R.; Kershaw, John A., Jr.; Hofmeyer, Philip V.; Seymour, Robert S. 2009. **Species differences in total and vertical distribution of branch- and tree-level leaf area for the five primary conifer species in Maine, USA.** Forest Ecology and Management. 258(7): 1695-1703.

Weiskittel, Aaron R.; Seymour, Robert S.; Hofmeyer, Philip V.; Kershaw, John A., Jr. 2010. **Modelling primary branch frequency and size for five conifer species in Maine, USA.** Forest Ecology and Management. 259(10): 1912-1921.

Weiskittel, Aaron R.; Wagner, Robert G.; Seymour, Robert S. 2010. **Refinement of the Forest Vegetation Simulator, northeastern variant growth and yield model.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2009 annual report. Orono, ME: University of Maine: 44-48.

Welbourn, W. Calvin; Jennings, Daniel T. 1991. **Two new species of erythraeidae (Acari: prostigmata) associated with the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), in Maine.** The Canadian Entomologist. 123: 567-580.

Wilson, Geoffrey F. 1997. **Modeling early regeneration processes in mixed species forests of Maine: germinant emergence and early survival.** Orono, ME: University of Maine. 93 p. M.S. thesis.

Wilson, Geoffrey F.; Maguire, Douglas A. 1996. **Simulation of early regeneration processes in mixed-species forests of Maine, USA: germination, survival, and height growth.** In: Skorsgaard, J.P.; Johannsen, V.K., eds. Modeling regression success and early growth of forest stands. Horsholm, Denmark: Danish Forest and Landscape Research Institute: 530-539.

Young, Harold E. 1954. **Forest soils-site index studies in Maine.** Soil Science Society of America Journal. 18: 85-87.

Young, Harold E. 1955. **Local pulpwood volume tables.** Technical Bulletin 37. Orono, ME: Maine Agricultural and Forest Experiment Station. 5 p.

Zellers, Christopher E. 2010. **The growth, yield, and financial performance of isolated eastern white pine (*Pinus strobus* L.) reserve trees.** Orono, ME: University of Maine. 73 p. M.S. thesis.

Zellers, Christopher E.; Seymour, Robert S.; Weiskittel, Aaron; Benjamin, Jeffrey. 2009. **The growth, yield and financial performance of isolated archetypal eastern white pine trees.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2008 annual report. Orono, ME: University of Maine: 29-31.

Zellers, Kate E. 2010. **Patterns of regeneration of eastern white pine (*Pinus strobus* L.) as influenced by large isolated reserve trees and precommercial thinning.** Orono, ME: University of Maine. 86 p. M.S. thesis.

Zellers, Kate E.; Seymour, Robert S.; Livingston, William H.; Wagner, Robert G. 2009. **Patterns of regeneration of eastern white pine as influenced by large, isolated crop trees and precommercial thinning.** In: Meyer, Spencer R., ed. Cooperative Forestry Research Unit: 2008 annual report. Orono, ME: University of Maine: 27-28.

ACKNOWLEDGMENTS

Invaluable assistance was provided by University of Maine student employee John Misener and staff of the University of Maine Fogler Library and National Forest Service Library. U.S. Forest Service retirees Robert M. Frank, Jr., Lawrence Safford, and Timothy Stone helped us determine if some publications originated from the PEF. Mac Hunter of the University of Maine provided useful lists of theses and publications that originated from the Maine Land-Use Effects on Amphibian Populations (LEAP) study. A draft of this bibliography was reviewed by Robert Frank and Robert Seymour (University of Maine).

ABOUT THE AUTHORS

Stephanie L. Adams was a graduate research assistant at the University of Maine, School of Forest Resources, Orono, Maine.

John C. Brissette is a project leader and research forester with the U.S. Forest Service, Northern Research Station, Durham, New Hampshire. Mailing address: U.S. Forest Service, Northern Research Station, 271 Mast Road, Durham, NH 03824; contact at 603-868-7632, or jbrissette@fs.fed.us.

Michael E. Day is an associate research professor at the University of Maine, School of Forest Resources, Orono, Maine.

Alison C. Dibble is a botanist and volunteer with the U.S. Forest Service, Northern Research Station, Bradley, Maine.

Robert M. Frank, Jr., is retired from the U.S. Forest Service, Northeastern Forest Experiment Station, Bradley, Maine. He was a research forester at the Penobscot Experimental Forest.

Michael S. Greenwood is retired from the University of Maine, School of Forest Resources, Orono, Maine. He was the Ruth Hutchins Professor of Tree Physiology and Forestry.

Jody Jellison is a professor at Virginia Tech, Department of Plant Pathology, Physiology, and Weed Science, and associate director of the Agricultural Experiment Station, Blacksburg, Virginia.

Laura S. Kenefic is a research forester with the U.S. Forest Service, Northern Research Station, Bradley, Maine and is the Station's lead scientist at the Penobscot Experimental Forest. Mailing address: School of Forest Resources, 5755 Nutting Hall, University of Maine, Orono, ME 04469; contact at 207-581-2794, or lkenefic@fs.fed.us.

Alan J. Kimball is an associate professor at the University of Maine, School of Forest Resources, and forest manager, University Forests Office, Orono, Maine.

Spencer R. Meyer is an associate scientist at the University of Maine, Center for Research on Sustainable Forests, Orono, Maine.

Andrew S. Nelson is an assistant professor at the University of Arkansas at Monticello, Monticello, Arkansas.

Matthew B. Russell is a postdoctoral research associate at the University of Minnesota, Department of Forest Resources, St. Paul, Minnesota.

Mike R. Saunders is an associate professor at Purdue University, Department of Forestry and Natural Resources, West Lafayette, Indiana.

Jonathan S. Schilling is an associate professor at the University of Minnesota, Department of Bioproducts and Biosystems Engineering, St. Paul, Minnesota.

Robert S. Seymour is the Curtis Hutchins Professor of Silviculture at the University of Maine, School of Forest Resources, Orono, Maine.

Walter C. Shortle is a senior research plant pathologist with the U.S. Forest Service, Northern Research Station, Durham, New Hampshire.

Kevin T. Smith is a plant physiologist with the U.S. Forest Service, Northern Research Station, Durham, New Hampshire.

Katherine Spencer is a project supervisor with the Alberta Environmental and Sustainable Resource Development.

Robert G. Wagner is the Henry W. Saunders Distinguished Professor in Forestry at the University of Maine, School of Forest Resources, and director of the Cooperative Forestry Research Unit, Orono, Maine.

Kenefic, Laura S.; Brissette, John C., compilers. 2014. **Penobscot Experimental Forest: 60 years of research and demonstration in Maine, 1950-2010.** Gen. Tech. Rep. NRS-P-123. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 185 p.

The Penobscot Experimental Forest (PEF) in Maine has been the site of U.S. Department of Agriculture, Forest Service, Northern Research Station (previously Northeastern Forest Experiment Station) research on northern conifer silviculture and ecology since 1950. Purchased by forest industry and leased to the Forest Service for long-term experimentation, the PEF was donated to the University of Maine Foundation in 1994. Since that time, the University and the Forest Service have worked in collaboration to advance the PEF as a site for research, demonstration, and education. This publication reports the history of the PEF during its first 60 years (1950 to 2010) and presents highlights of research accomplishments in silviculture, ecology, ecophysiology, nutrient cycling, botany, and other areas. Issues of data management and forest management planning are addressed. Also included is a bibliography of publications originating from research on the PEF, as well as recollections of a research forester stationed there for 30 years.

More than half a century of work on the PEF has served as an important source of information for practitioners and policy makers in the Acadian Forest region of the northeastern United States and adjacent Canada, and informed the practice of silviculture nationally and internationally. Long-term consistency in treatment application and measurement; stand-level replication; and accessible, digital data, metadata, and records archives have facilitated hundreds of studies and made the PEF an invaluable and highly influential research site.

KEY WORDS: silviculture, Acadian Forest, northern conifers, red spruce, balsam fir, eastern hemlock

Northern Research Station

www.nrs.fs.fed.us