

**Response of *Thuja occidentalis* and *Abies balsamea* Seedlings
to Stand Manipulations in Northern Minnesota Riparian Forests**

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

Brooke Karen Haworth

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

Dr. Andrew J. David, Dr. Charles R. Blinn

November, 2011

© Brooke Karen Haworth 2011

Acknowledgements

First and foremost, this research could not have been accomplished without the generous financial support I received from many sources: the USFS Northern Research Station in Grand Rapids, Minnesota; Katherine Hill Fellowships through the UMN Department of Forest Resources; UMN Graduate School Fellowships; Dr. Andrew David, UMN Department of Forest Resources; the Minnesota Logger Education Program; the Ruth Eden Trust; Drs. Leah and Ian Evison; and the Hendersonville, NC Chapter of P.E.O. Sisterhood.

I am indebted to many individuals for their professional assistance, guidance, and patience throughout this project, especially my advisors Drs. Andy David and Charlie Blinn and committee members Drs. Randy Kolka and Brian Palik. I received invaluable help in project design from Dr. Sandford Weisberg, statistical assistance from Dr. Chris Chizinski and the University of Minnesota Statistical Clinic, laboratory analysis from John Larson, and laboratory space from Dr. Paul Bolstad. I appreciated the kind help of the Department of Forest Resources administrative and office staff. I am grateful for copy editing provided by Beth Gaede.

Every field research effort can only be accomplished with the support of many people, and I was fortunate to have the assistance of a group of dedicated private individuals who gave generously of their personal time, energy, and camaraderie throughout the clear and inclement weather of this project – particularly Leah Evison, Jeff Couture, and Beth Gaede. I also thank Grand Rapids staff of the USFS Northern Research Station and the North Central Research and Outreach Center for their help in the field.

Finally, I am most grateful to the many friends and family members from whom I received the support and encouragement that sustained me throughout this process, reminding me to “not lose sight of the forest for the trees.” And for the inspiration that guided me, I thank my mother who kept the wonder alive, my father who set the bar high, and my sister who pointed the way.

Abstract

Northern white-cedar (*Thuja occidentalis* L.), a long-lived conifer closely associated with many riparian boreal forests of Minnesota, is an important species to riparian ecosystem health and to the forest products industry. Northern white-cedar is currently experiencing a decline in recruitment throughout much of its natural range, due primarily to herbivory by white-tailed deer (*Odocoileus virginianus*). Herbivory on northern white-cedar removes seedling and sapling size classes, and allows less browsed species (notably balsam fir (*Abies balsamea* (L.) Mill)) to further displace the northern white-cedar forest component. This study examined practices that could encourage advance regeneration of northern white-cedar in the riparian setting. The role of partial overstory removal and forest floor microsite was tested on the development of planted 3-0 seedlings of northern white-cedar and the potentially competitive species of balsam fir. Seedlings were planted in mound, pit, and slash microsites (important to seedling germination and establishment) in partially harvested and unharvested riparian areas, and assessed for survival and growth over a four-year period. The test was duplicated inside and outside of fenced plots to evaluate the impact of deer browse and to more fully understand the current dynamic between species.

Protected from herbivory, results indicated that partial harvest of the overstory contributed to significant seedling growth with both species demonstrating potential to recruit into taller height and larger basal diameter classes. Basal diameter growth rates were greater in northern white-cedar than balsam fir. Microsites of mound, pit, and slash did not contribute significantly to growth. Percent survival of northern white-cedar was

greater than balsam fir, which experienced lower survival in controls. Due to seasonal flooding, pits had a significant negative effect on survival of both species. When protected from herbivory, planted northern white-cedar seedlings were shown to be good candidates for outplanting in a variety of riparian settings, particularly partial harvest areas, and were competitive with balsam fir seedlings for up to four years in the field.

Percent browse frequency on unfenced seedlings was greater in harvest treatments and on mound microsites. Unfenced northern white-cedar seedlings were browsed at a significantly higher rate than balsam fir. Northern white-cedar showed significant mortality and no height increase in any treatments, with browse on seedlings overwhelming the benefits of overstory harvests. However, seedlings continued carbon allocation to basal diameter. In addition, northern white-cedar displayed survival resiliency, although reduced vitality, for the four years subjected to herbivory. Basal diameter increase and survival of browsed northern white-cedar seedlings are most likely due to their ability to replace browsed foliage in the current year. Unfenced balsam fir seedlings maintained growth responses to harvest treatments and did not experience significant mortality due to browse. Balsam fir seedlings exhibited the potential to recruit successfully into the overstory even under browse pressure, while northern white-cedar did not. Management activities that increase light availability while retaining some overstory structure, and selection of planting sites that limit or exclude browse, will result in the best chance for northern white-cedar seedlings to recruit into the sapling stage.

Table of Contents

Acknowledgements	i
Abstract	ii
Table of Contents	iv
List of Tables	viii
List of Figures	ix
Introduction	1
Bibliography to Introduction	4
Chapter 1: Northern White-cedar and Balsam Fir in the Riparian Forest: A Literature Review	6
Chapter 1 Synopsis	7
The riparian setting of northern white-cedar and balsam fir	8
Introduction to northern white-cedar	8
<i>Northern white-cedar forest types and associates</i>	10
<i>Northern white-cedar stand origins</i>	11
<i>Northern white-cedar soil and hydrologic environments</i>	11
<i>Northern white-cedar reproduction and growth</i>	12
<i>Northern white-cedar pathology and pests</i>	13
<i>Northern white-cedar wildlife and plant associates</i>	14
<i>Northern white-cedar forest products</i>	15
The northern white-cedar recruitment decline	15
<i>Early silviculture</i>	15
<i>Causes of northern white-cedar recruitment decline</i>	16
Northern white-cedar and white-tailed deer	17
<i>Ecological impacts of deer</i>	18
<i>Herbivory on northern white-cedar</i>	19
<i>Winter movement of deer</i>	20
<i>Winter diet of deer</i>	20
Northern white-cedar stand changes	22

Introduction to balsam fir	23
<i>Balsam fir forest types and associates</i>	24
<i>Balsam fir soil and hydrologic environments</i>	25
<i>Balsam fir reproduction and growth</i>	25
<i>Balsam fir pathology and pests</i>	26
<i>Balsam fir wildlife and plant associates</i>	28
<i>Balsam fir forest products</i>	29
Extent of the northern white-cedar and balsam fir forest resource in Minnesota	29
<i>Species comparison and life strategies</i>	31
Regeneration - the role of substrate and microtopography	32
<i>Mounds</i>	34
<i>Pits</i>	35
<i>Slash</i>	36
<i>Microsite regeneration studies</i>	36
<i>Beyond regeneration - the continuing role of microsites</i>	38
Chapter 1 Tables	39
Chapter 1 Figures	41
Chapter 1 Bibliography	43
Chapter 2: A Comparison of <i>Thuja occidentalis</i> and <i>Abies balsamea</i> Seedling Response to Partial Harvest and Microsite in Northern Minnesota Riparian Forests	52
Chapter 2 Synopsis	53
Introduction	55
<i>Recruitment decline</i>	55
<i>Role of microsites</i>	58
<i>Northern white-cedar microsite research</i>	59
Materials and Methods	60
<i>Site locations</i>	60
<i>Experimental design</i>	61
<i>Microsite description</i>	61
<i>Seedling measurements</i>	62
<i>Vegetation measurements</i>	64
<i>Soil measurements</i>	64
<i>Data Analysis</i>	65
Results	68
<i>Seedling survival</i>	68

<i>Seedling growth</i>	70
<i>Seedling growth correlated to environmental factors</i>	70
<i>Basal area</i>	70
<i>Additional northern white-cedar correlations</i>	70
<i>Additional balsam fir correlations</i>	71
Discussion	71
<i>Seedling survival</i>	71
<i>Seedling growth</i>	73
<i>Seedling growth correlated to environmental factors</i>	76
Recommendations	78
Chapter 2 Tables	81
Chapter 2 Figures	92
Chapter 2 Bibliography	109
Chapter 3: Deer Browse Effects on <i>Thuja occidentalis</i> and <i>Abies balsamea</i> Seedlings in Riparian Harvest Areas within Northern Minnesota	114
Chapter 3 Synopsis	115
Introduction	117
<i>Northern white-cedar introduction</i>	118
<i>Northern white-cedar and herbivory</i>	119
<i>Study description</i>	120
Materials and Methods	121
<i>Site locations and characteristics</i>	121
<i>Experimental design and trial installation</i>	122
<i>Data collection and analysis</i>	124
Results	128
<i>Percent browse frequency</i>	129
<i>Percent survival</i>	129
<i>Relative growth rate</i>	131
<i>Height and basal diameter</i>	132
<i>Northern white-cedar correlation analysis</i>	133
<i>Balsam fir correlation analysis</i>	134
Discussion	135
<i>Percent browse frequency</i>	135
<i>Percent survival</i>	139
<i>Species comparison: growth</i>	143

<i>Height and basal diameter</i>	146
<i>Correlation analysis</i>	147
<i>Northern white-cedar correlations</i>	147
<i>Balsam fir correlations</i>	149
Summary	150
Further Research	152
Chapter 3 Tables	154
Chapter 3 Figures	165
Chapter 3 Bibliography	176
Chapter 4: Recommendations for Management of Planted Northern White-cedar Seedlings in Riparian Forests within Northern Minnesota	181
Chapter 4 Synopsis	182
Background	183
Riparian harvest, microsite, and deer exclosure study	185
Study results and management applications	186
<i>Seedling Percent Survival</i>	186
<i>Seedling Growth</i>	187
<i>Competition</i>	189
<i>Effect of Herbivory</i>	190
<i>Site Effects</i>	193
Summary of northern white-cedar treatment means	194
Planting recommendations for northern white-cedar seedlings	196
Management recommendations for northern white-cedar seedlings	197
Chapter 4 Bibliography	198
Cumulative Bibliography	200

List of Tables

Chapter 1	39
Table 1.1. Northern white-cedar and balsam fir biological characteristics	40
 Chapter 2	 81
Table 2.1. Study site locations and information	82
Table 2.2. Experimental design components	83
Table 2.3. GLM of percent survival between species	84
Table 2.4. GLM of northern white-cedar height and basal diameter	85
Table 2.5. GLM of northern white-cedar RHG and RDG	86
Table 2.6. GLM of balsam fir height and basal diameter	87
Table 2.7. GLM of balsam fir RHG and RDG	88
Table 2.8. GLM of RHG and RDG between species	89
Table 2.9. Correlations between size and independent variables	90
Table 2.10. Correlations between RGR and independent variables	91
 Chapter 3	 154
Table 3.1. Study site locations and information	155
Table 3.2. GLM of browse frequency between species	156
Table 3.3. GLM of percent survival between species in fence treatments	157
Table 3.4. GLM of RHG between species in fence treatments	158
Table 3.5. GLM of RDG between species in fence treatments	159
Table 3.6. GLM of northern white-cedar height and basal diameter	160
Table 3.7. GLM of balsam fir height and basal diameter	161
Table 3.8. Correlations between percent browse frequency and independent variables	162
Table 3.9. Correlations between northern white-cedar size and independent variables	163
Table 3.10. Correlations between balsam fir size and independent variables	164

List of Figures

Chapter 1	41
Figure 1.1. Northern white-cedar and balsam fir resource in Minnesota	42
 Chapter 2	 92
Figure 2.1. Location of study sites in Minnesota	93
Figure 2.2. Conceptual model of experimental design	94
Figure 2.3. Idealized microsite plot layout	95
Figure 2.4. Percent survival of northern white-cedar and balsam fir	96
Figure 2.5. Percent survival over time of northern white-cedar and balsam fir	97
Figure 2.6. Northern white-cedar height and basal diameter	98
Figure 2.7. Balsam fir height and basal diameter	99
Figure 2.8. RHG and RDG of northern white-cedar and balsam fir	100
Figure 2.9. Correlations of northern white-cedar size and RGR to BA	101
Figure 2.10. Correlations of balsam fir size and RGR to BA	102
Figure 2.11. Correlations of northern white-cedar size and RGR to percent forest floor	103
Figure 2.12. Correlations of northern white-cedar size and RGR to percent herbaceous cover	104
Figure 2.13. Correlations of northern white-cedar size and RGR to percent woody cover	105
Figure 2.14. Correlations of balsam fir size and RGR to C:N ratio	106
Figure 2.15. Correlations of balsam fir size and RGR to forest floor depth	107
Figure 2.16. Correlations of balsam fir size and RGR to percent coarse fragments	108
 Chapter 3	 165
Figure 3.1. Location of study sites in Minnesota	166
Figure 3.2. Conceptual model of experimental design	167
Figure 3.3. Idealized microsite plot layout	168
Figure 3.4. Percent browse frequency on northern white-cedar and balsam fir	169
Figure 3.5. Percent survival of northern white-cedar and balsam fir by fence treatment	170
Figure 3.6. Percent survival over time by fence treatment of northern white-cedar and balsam fir	171
Figure 3.7. RHG of northern white-cedar and balsam fir in fence treatment	172
Figure 3.8. RDG of northern white-cedar and balsam fir in fence treatment	173
Figure 3.9. Northern white-cedar size in fence treatment	174
Figure 3.10. Balsam fir size in fence treatment	175

Chapter 4

Figure 4.1. Northern white-cedar timberland acres in Minnesota	184
Figure 4.2. Percent survival over time of northern white-cedar by fence treatment	187
Figure 4.3. Northern white-cedar size in fence treatment	188
Figure 4.4. Northern white-cedar relative growth rate in fence treatment	189
Figure 4.5. Percent browse frequency on northern white-cedar and balsam fir	190

Introduction

In the state of Minnesota an estimated 1.4 million hectares of forest land are potentially riparian, falling within sixty meters of a waterway (Palik et al. 2004). Today timber harvests are guided by voluntary site-level guidelines developed by the Minnesota Forest Resources Council (MFRC 2005). In 2003 a long-term study was initiated to evaluate the riparian portion of the timber harvest guidelines and their impacts on the riparian ecosystem (“RMZ Harvest” Internet-updated July 2008). Major project cooperators were the USDA Forest Service Northern Research Station in Grand Rapids and the University of Minnesota, supported by the Legislative-Citizen’s Commission on Minnesota Resources. The long-term study project was conducted at eight riparian sites across northern Minnesota and addressed the areas of terrestrial, fisheries and wildlife habitat. This master’s study falls under the terrestrial component of that larger project. It was conducted at three of the eight sites and was supported by funds from the Forest Service Northern Research Station.

A species closely associated with many riparian boreal forests is northern white-cedar (*Thuja occidentalis* L.). A long-lived conifer species, FIA inventory data indicates that its current cover within Minnesota is 4% of total forested acreage, most of it in riparian areas (MN DNR 2010). Beginning in the mid-20th century forest managers documented a recruitment decline throughout the managed range of the species. Attributed to a number of causes, the most important one has been identified as herbivory by increased populations of white-tailed deer (*Odocoileus virginianus*). Herbivory suppresses northern white-cedar at the seedling and sapling stages, removing advance

regeneration and allowing less heavily-browsed species (notably balsam fir (*Abies balsamea* (L.) Mill)) to replace the northern white-cedar component (Heitzman et al. 1999; Cornett et al. 2000; Rooney and Waller 2003; Hofmeyer et al. 2009; Larouche et al. 2010).

There is a need to examine management practices that will encourage the growth of northern white-cedar, but the loss of advance regeneration makes it difficult to study. Previous studies have examined the role of forest floor microsites and substrates in northern white-cedar regeneration (St. Hilaire and Leopold 1995; Cornett et al. 1997; Simard et al. 1998; Simard et al. 2003). However little is known about microsite contributions following seedling establishment, while additional studies have found that the conditions necessary for regeneration are not necessarily the same as those which favor sapling growth (Chimner and Hart 1996; Rooney et al. 2002; Dovčiak et al. 2003).

To learn more about the environmental conditions and management practices necessary to encourage advance regeneration of northern white-cedar, this master's project examined the continuing role of microsites and partial overstory removal on the development of seedlings. *T. occidentalis* and *A. balsamea* 3-0 seedlings were planted in mound, pit, and slash microsites in harvested and unharvested riparian areas, and assessed for survival and growth over a four-year period. The test was duplicated inside and outside of fenced plots to evaluate the impact of deer browse.

Chapter 1 is a literature review of the status of northern white-cedar in the riparian landscape. Three issues associated with the status of white-cedar populations are discussed including the role of microtopography, competition from balsam fir, and

browse by white-tailed deer. Species biology and interactions of northern white-cedar and balsam fir are discussed, along with current resource status in Minnesota.

Chapter 2 presents the riparian harvest study in which 3-0 seedling pairs of *T. occidentalis* and *A. balsamea* were planted within fenced plots, using the forest floor microsites of mound, pit and slash to compare seedling growth and survival response between control and partial harvest treatments. The microsite environment is examined further by the correlation of seedling height and basal diameter growth with vegetation cover and soil characteristics. These results are discussed with management implications for recruitment of northern white-cedar.

Chapter 3 addresses seedling growth and survival response of *T. occidentalis* and *A. balsamea* outside of fenced plots where they were vulnerable to deer browse. The extent of deer browse within the separate microsite and harvest treatments is discussed, along with an analysis of seedling response as affected by browse. Comparisons are made to unbrowsed seedling survival and growth inside fenced plots, with implications for the effect of browse on future stand development.

Chapter 4 presents planting and management recommendations for northern white-cedar seedlings based on a summary of the survival and growth results.

Bibliography to Introduction

Chimner, R. A., and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Canadian Journal of Forest Research* 26:389-93.

Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.

Cornett, M. W., P. B. Reich, and K. J. Puettmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* 4(3):353-64.

DeLong, H. B., V. J. Lieffers, and P. V. Blenis. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27:1452-57.

Heitzman, E., K. S. Pregitzer, R. O. Miller, M. Lanasa, and M. Zuidema. 1999. Establishment and development of northern white-cedar following strip clear cutting. *Forest Ecology and Management* 123:97-104.

Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.

Larouche, C., L. S. Kenefic, and J.-C. Ruel. 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.

Minnesota Department of Natural Resources. 2010. Minnesota's Forest Resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.

Minnesota Forest Resources Council. 2005. *Sustaining Minnesota Forest Resources: Voluntary Site-level Forest Management Guidelines for Landowners, Loggers and Resource Managers*. St. Paul, MN: Minnesota Forest Resources Council.

Palik, B., S. M. Tang, and Q. Chavez. 2004. *Estimating riparian area extent and land use in the Midwest*. Gen. Tech. Rep. NC-248. St. Paul, MN: USDA Forest Service, North Central Research Station.

RMZ Harvest [Internet]. [updated 2008 Jul 27]. St. Paul, MN: University of Minnesota, College of Food, Agriculture and Natural Resource Sciences; [cited 2009 Jul 14]. Available from: <http://rmzharvest.cfans.umn.edu/>.

Rooney, T. P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181(1):165-76.

St. Hilaire, L. R., and D. J. Leopold. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. 1995. *Canadian Journal of Forest Research* 25:261-69.

Chapter 1

Northern White-cedar and Balsam Fir in the Riparian Forest: a Literature Review

Chapter 1 Synopsis

Northern white-cedar (*Thuja occidentalis* L.), a coniferous species found in many riparian landscapes of northeastern North America, currently is experiencing recruitment failure across much of its range, primarily due to herbivory from white-tailed deer (*Odocoileus virginianus*). Balsam fir (*Abies balsamea* (L.) Mill.), a common cohort of northern white-cedar, frequently recruits more successfully into taller seedling classes in disturbance settings due to lack of browse pressure. Numerous studies have examined the detrimental effects of herbivory on northern white-cedar recruitment; others have focused on seedling regeneration and the roles of forest floor substrates and microsites. Further study is needed into the long-term roles of microsites, overstory harvest, and herbivory control in the development and eventual recruitment of northern white-cedar advance regeneration. This literature review was conducted to learn the extent of knowledge regarding the biology and stand dynamics of northern white-cedar and balsam fir, and their susceptibility to herbivory.

Key words: northern white-cedar, balsam fir, riparian, herbivory, microsite

The riparian setting of northern white-cedar

The riparian landscape of Minnesota, shaped by fluvial process and glacial deposition, supports diverse forest types. Riparian forests are contiguous wooded lands connected functionally to waterways and are delineated by geomorphology and hydrology (Ilhardt et al. 2000). These forests cycle energy and nutrients, sustain high floral and faunal diversity, mitigate flood events, and protect water quality through bank stabilization, sediment filtration, temperature moderation, and coarse and fine organic inputs (Crow et al. 2000; Palik et al. 2000).

Riparian forest composition is the result of diverse environmental interactions that affect the many stages of seedling establishment and eventual recruitment (Greene et al. 1999; Dovčiak et al. 2003). The main factors distinguishing the formation of riparian forests from upland forests are hydrologic processes and geomorphic constraints that play stronger roles in soil development and disturbance regimes within riparian landscapes. These in turn determine the composition of riparian plant communities in which species are adapted to gradients of water (Goebel et al. 2006).

Introduction to northern white-cedar

Northern white-cedar, *Thuja occidentalis* L., is a coniferous forest species of northeastern North America. Its range extends in the west from southeastern Manitoba across Canada east to the Atlantic Ocean, south into the northern Midwest states of Minnesota, Wisconsin, Michigan, eastward to the coast of Maine, and appearing locally

south to western North Carolina (approximately 97° W to 63°W longitude, 52°N to 43°N latitude).

Northern white-cedar is of medium height (15 meters or 50 feet on average), moderately to very shade tolerant, slow-growing in maturity, and long-lived with a life span of 400 years and more. It can withstand suppression for many years while retaining the ability to respond to release and is stable in pure stands in the absence of disturbance. It also occurs frequently as a component of mixed stands where it is over-topped by taller cohorts. Frequent associates include balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), black and white spruce (*Picea mariana* (Mill.) B. S. P. and *Picea glauca* (Moench) Voss), black ash (*Fraxinus nigra* Marsh), and red maple (*Acer rubrum* L.). The shorter-lived balsam fir is the only associate whose shade tolerance allows it to establish under northern white-cedar canopy (Johnston 1990).

Northern white-cedar has been called a bimodal species, as it appears in two different environments - low wetlands and dry uplands. The majority of northern white-cedar in Minnesota occurs in lowland areas (Cornett 2000; MN DNR 2010). Early studies found evidence of ecotype differences between lowland and upland cedar in Wisconsin (Habeck 1958; Musselman et al. 1975). If this is correct, there are ramifications for seed collection and dispersal to areas outside their provenance (Pregitzer 1990). More recent studies from Ontario have found no evidence of ecotypic differences; rather, differences are site or intra-stand specific (Matthes-Sears and Larson 1991; Matthes-Sears et al. 1991; Briand et al. 1992).

Northern white-cedar forest types and associates

Upland stands occur on old field sites with calcareous mineral soils (Inceptisols and Entisols) over limestone, sandstone bluffs, and limestone cliffs (Johnston 1990). In northeastern Minnesota, upland cedar has been considered a climax species that occurs in the absence of disturbance (Grigal and Ohmann 1975). Upland stands appear in Minnesota's NPCC as *upland white-cedar forest* (FDn43c) with rotations of 220 years due to fire (MN DNR 2003). Ancient populations have also been found growing on the Niagara Escarpment in southeastern Ontario, Canada (Matthes-Sears et al. 1991; Briand et al. 1992).

Lowland northern white-cedar, the subject of this research project, occurs within Minnesota in the Laurentian Mixed Forest Province that encompasses the northeast third of the state. It comprises the majority of SAF forest cover type 37 (Northern white-cedar) and on lowland sites is most commonly associated with balsam fir, black and white spruce, tamarack, black ash, and red maple (Eyre 1980). Northern white-cedar associates with thirteen SAF forest cover types, seven of which occur in Minnesota. In Minnesota's Native Plant Community Classification (NPCC), it is described as *northern wet cedar forest* (WFn53), occurring along borders of wetland basins and slopes in areas of groundwater discharge, and as *northern cedar swamp* (FPn63), occurring adjacent to peatlands with mineral-rich, oxygenated subsurface water flow and high water tables. Historically both forest types have few major disturbances and long fire rotations of 800 and 600 years, respectively, with small-scale disturbances due to windthrow at 340 and

380 years respectively. It also appears as a subcanopy/canopy component in approximately 10 other NPCC forest types (MN DNR 2003).

Northern white-cedar stand origins

Today's upland northern white-cedar stands likely originated after clear-cut harvests beginning in the late 1800s and subsequent wildfires. Studies suggest that following these stand-level disturbances, northern white-cedar effectively re-established through natural seeding and advance regeneration, developing into second-growth even-aged stands that are today from 75 to 150 years old (Pregitzer 1990; Heitzman et al. 1997). Northern white-cedar also persists in mixed lowland forest gaps created by blowdown or cohort mortality, where regeneration from seed, advance reproduction, and vegetative reproduction allow it to maintain its position. Here the development of single or multiple cohort stands can depend upon disturbance severity and frequency (Pregitzer 1990; Heitzman et al. 1999). Heinselman describes white-cedar in northern Minnesota as "driven to the lakeshores by fire" (Heinselman 1973), where it survives in narrow borders around lake edges.

Northern white-cedar soil and hydrologic environments

This species typically grows in moist lowland areas with organic Histosol soils, acidic to neutral pH (5.5 to 7.2), and flowing mineral rich waters. Nelson (1951) places northern white-cedar in older bogs, where peat is fairly well decomposed; Stewart (1925) states that the best cedar swamps have a shallow peat depth and good drainage. The

species frequently occurs as a border of vegetation around wetlands, lakes and streams - areas common in northern Minnesota's glacial landscape.

Pregitzer (1990) described the hydrologic environment that is important to lowland northern white-cedar sites, one in which the lateral movement of water through the soil brings oxygen and nutrients to the root zone. As the hydraulic gradient lowers and water stagnates farther into the bog or water environment, soils and water become acidic, creating conditions that support different vegetation and confine northern white-cedar to the edges.

Northern white-cedar reproduction and growth

Northern white-cedar seeds require 50 percent of full sunlight to germinate and will establish only on specialized substrates with high moisture and warm temperatures (Johnston 1990). Following establishment, 45 percent sunlight results in the tallest growth, but full sun yields heaviest root and shoot growth (Logan 1969). Larouche et al. (2006) reported similar results with planted northern white-cedar seedlings in Maine showing that mean annual height increment was proportional to light intensity. Northern white-cedar therefore reproduces in gaps and on stand edges, and understory saplings may remain suppressed for many years until released. Given sufficient light, northern white-cedar seedlings grow quickly, although later stages of growth are much slower. A recent study of overstory trees in Maine found that basal growth of northern white-cedar was not correlated with increased light levels (Hofmeyer et al. 2009b).

Branch layering, an asexual vegetative reproduction strategy of northern white-cedar, is common in riparian areas. In this species, adventitious roots can originate from any part of branches or stems that are exposed to sufficient soil moisture. This occurs when low hanging branches or tree tip-ups come in contact with moist soils, where the presence of mosses often facilitates rooting. Windfall trees also create new shoots as horizontal branches are re-positioned to vertical, becoming new leaders. Layering can produce more than half of all new stems in swamp conditions and occurs more often in younger trees (Johnston 1990). Vegetative reproduction is more shade tolerant than reproduction from seedlings, perhaps because of access to an adequate root system. This may account for greater advance regeneration in the absence of disturbance (Curtis 1946).

Northern white-cedar pathology and pests

Common environmental causes of mature northern white-cedar mortality are windthrow, fire, ice damage, and flooding. Shallow roots create susceptibility to winds; thin and resinous bark leave trees vulnerable to fire; snow and ice break limbs and tree tops; road construction and beaver (*Castor canadensis*) activity impede drainage causing mortality from changing water levels (Johnston 1990). There are no major insects that afflict northern white-cedar at the stand level, but red carpenter (*Camponotus ferrugineus*) and black carpenter (*C. pennsylvanicus*) ants reduce timber value and weaken boles. Leafminers are common pests of foliage, but do not appreciably impair tree health. Fungal diseases of seedlings, roots, and butts are present but not highly

damaging. *Phomopsis juniperovora* and *Didymascella thujina* are foliage blights that attack seedlings and saplings. White stringy butt rot (*Poria subacida*), balsam butt rot (*Tyromyces balsameus*), and red-brown butt rot (*Phaeolus schweinitzii*) cause deformities and weaken trees (Johnston 1990).

Northern white-cedar wildlife and plant associates

Northern white-cedar stands and communities provide habitat for wildlife, including birds (warblers, white-throated sparrows, pileated woodpeckers) and small mammals (snowshoe hare (*Lepus americanus*), red squirrel (*Tamiascurus hudsonicus*), and porcupine (*Erethizon dorsatum*) (Johnston 1990)). White-tailed deer (*Odocoileus virginianus*) congregate in “cedar deeryards” during winter months, making use of lower snow depth, thermal cover, and palatable browse (Johnston 1990; Davis et al. 1998).

Northern white-cedar contributes to riparian forest functions by bank stabilization, nutrient and sediment filtration, aquatic environment shading, and coarse/fine carbon additions. Microsite relief variations associated with northern white-cedar swamps are created by the accumulation of coarse woody debris in varying decay stages, the movement of water and soil around surface roots, and tree tip-ups resulting in characteristic riparian pit-and-mound topography.

These micro-environments support plants with various water and nutrient requirements (Heitzman et al. 1999) such as ferns, lichens and mosses. Understory woody shrubs varies by site quality, with speckled alder (*Alnus rugosa*), red-osier dogwood (*Cornus stolonifera*), and fly honeysuckle (*Lonicera canadensis*) common on

better sites and labrador-tea (*Ledum groenlandicum*) and blueberries (*Vaccinium* spp.) on poorer sites (Johnston 1990). Herbaceous species include the threatened ram's head orchid (*Cypripedium arietinum*) and other orchids of the genera *Cypripedium* and *Platanthera*, bishop's cap (*Mitella nuda*), goldthread (*Coptis groenlandica*), creeping snowberry (*Gaultheria hispidula*), twinflower (*Linnaea borealis*), and jack-in-the-pulpit (*Arisaema triphyllum*) ("Hardwood and Conifer Swamps" Internet-updated May 2008).

Northern white-cedar forest products

Northern white-cedar has a light, strong and rot-resistant wood valued for lumber products. Historically the wood was used for cabin logs, railroad ties, shingles, barrels, telephone poles, and posts. Today cedar wood products most commonly consist of cabin logs, siding, and paneling. Specialty uses include cedar oil for perfumes and harvested boughs for holiday decoration (Johnston 1990; Heitzman et al. 1999).

The northern white-cedar recruitment decline

Early silviculture

Beginning in the 1940s wildlife biologists noted a reduction in northern white-cedar forage available for winter deer maintenance, attributed to the combined effects of logging and deer consumption (Aldous 1941; Aldous 1944). Early silviculture studies in Michigan examined differing management practices for these respective uses (Nelson 1951). Upland harvest treatments (partial cuts leaving a residual stand 1235 to 1850 stems ha⁻¹ (500 to 750 stems ac⁻¹)) were applied for commercial timber production. Heavier cuts were applied in young lowland stands where vegetative reproduction could

provide substantial production for deer browse. Seedling plantations were established in cutover areas, for deer browse and conversion from spruce-fir forest type. Silviculture guidelines implemented in the 1960s (many developed for the purpose of deeryard management) recommended narrow strip and small block clearcutting to allow seed input from adjacent uncut strips, accompanied by thin residual slash to encourage seedling establishment (Verme 1965; Johnston 1977; Miller 1990, Heitzman et al. 1999).

By the 1980s it became evident that harvest practices had not supported the successful recruitment of northern white-cedar. Advance regeneration had failed to recruit into tall height classes, with substantial seedling and sapling mortality. By 1990 state and federal agencies in the Lake States had enforced limited cutting of northern white-cedar in response to diminished establishment (Miller 1990). The absence of sapling and pole size classes from both pure and mixed stands seen today indicates that recruitment into existing stands may be insufficient to maintain viable populations (Heitzman et al. 1997 and 1999; Cornett et al. 2000a; Rooney et al. 2002; Forester et al. 2008; Hofmeyer et al. 2009a; Larouche et al. 2010).

Causes of northern white-cedar recruitment decline

Various factors have been implicated in the recruitment decline of northern white-cedar. Heinselman (1973) suggested that northern white-cedar in northeastern Minnesota had been driven to the edges of lakes by fire. Early road construction cut through many conifer swamps, impeding drainage and causing significant mortality (Stoekler 1967; Boelter and Close 1974; Forester 2008). Slow growth rates through the

range of sapling sizes contribute to a delay in recruitment to pole stage that is longer than other species in harvested mixedwood stands (Larouche et al. 2010). Research into regeneration mechanisms has found that harvest methods may remove or destroy necessary niches on the forest floor, such as hummocks (Chimner and Hart 1996) and nurse logs (Cornett et al. 2001). Simard et al. (1998), studying conifer establishment in Canada, found that northern white-cedar took fifty years to begin re-establishment following fire and was dependent upon the gradual decomposition of woody debris as necessary substrate.

Northern white-cedar and white-tailed deer

The foremost cause of current northern white-cedar recruitment failure is herbivory from white-tailed deer. The range and populations of white-tailed deer have risen significantly in the twentieth century due to increased forage, removal of natural predators, and modern hunting regulations (Van Deelen et al. 1996; Russell et al. 2001; Côte et al. 2004). A browsing ungulate of prairies and transition forests edges, their historic range in Minnesota was primarily southern and central. Available deer habitat area increased with logging and settlement in the early 1900s that converted mature conifer forests of the north to young hardwoods and agricultural lands. The resulting increase in deer numbers has had a detrimental impact on recruitment potential of northern white-cedar (Cole 1987; Alverson et al. 1988; Cornett et al. 2000a; Rooney and Waller 2003; Hofmeyer et al. 2009a).

Ecological impacts of deer

Waller and Alverson (1997) considered white-tailed deer a keystone herbivore, defined as one that affects distribution and abundance of other species as well as community structures at multiple trophic levels by modifying patterns of competition. Stromayer and Warren (1997) suggested that deer create alternate stable states in forest plant communities, i.e., vegetation layers that will not return to their previous structure if browse were eliminated. Rooney (2001) addressed the direct (species specific) and indirect (cascading) effects of deer browse which reduce vegetation complexity vertically and horizontally, thus affecting stratifications of plant and wildlife. Côté et al. (2004) discussed at length the history and extent of ecological impacts of abundant deer.

Studies specific to forest conifers echo these results. Zenner and Peck (2009) documented eastern white pine (*Pinus strobus* L.) loss in the understory and midstory of a north-central Minnesota conifer/hardwood forest that may change succession trajectory. Deer browse eliminated white pine seedlings, altered the woody shrub layer, affected shading of the regeneration layer, and modified resource competition. Balsam fir on Anticosti Island, Québec, has been heavily browsed by white-tailed deer since their introduction in the late 1890s. Studies show that browse over this period has resulted in canopy recruitment failure and a shift toward dominance of white spruce (*Picea glauca* Moench Voss) (Chouinard and Filion 2001; Tremblay et al. 2007). Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) have been implicated through a similar mechanism in suppression of western redcedar (*Thuja plicata*) in British Columbia, Canada, where

seedling mortality and growth suppression due to browse are to blame for the lack of recruitment into forest stands (Stroh et al. 2008).

Herbivory on northern white-cedar

The damaging effects of herbivory on northern white-cedar have been noted since the mid-1900s when Nelson (1951) and Aldous (1952) reported northern white-cedar deer yards depleted of foliage below the browse line and regeneration severely limited. Habeck (1960) described soil changes in northern white-cedar swamp yards where winter residence of deer broke and compacted peat substrates, resulting in a drop in water holding capacity and creation of a more mesic soil.

Current studies of ungulate and northern white-cedar interactions continue to document the effect upon recruitment. In a study in the Lake Superior highlands of Minnesota, Cornett et al. (2000a) found sufficient seed supply for northern white-cedar persistence but an absence of seedlings > 25 cm tall due to browse pressure; herbivory overwhelmed canopy influences and prevented recruitment. Rooney et al. (2002) examined regional establishment in the upper Midwest, demonstrating that attrition of northern white-cedar seedlings and lack of recruitment into small and large saplings was the result of deer browse. Light and basal area explained seedling numbers, but deer browse explained the loss of small and large saplings, replacing the normal process of self-thinning that occurs in tree populations as they progress through size classes. In the Chiquamegon-Nicolet National Forest of Wisconsin, Forester et al. (2008) similarly found the proportion of browse increased with sapling size, resulting in a higher

abundance of small seedlings (< 7.5 cm) with large saplings (> 100 cm) being almost absent.

Winter movement of deer

Seasonal migration of deer, prompted by the need for winter shelter, is toward areas of dense conifer stands that offer thermal protection. This is the time when northern white-cedar deer yards come under heavy browse pressure. During winter conditions, deer first choose protection from wind and deep snows and second choose to seek browse. This represents the biological trade-off between shelter and foraging: energy conservation under cover versus energy consumption to attain essential sustenance (Lefort et al. 2007). Studies show that deeper snow has a stronger effect upon winter mortality and migration patterns than lower temperatures.

Winter migration patterns differ between regions of winter severity, with obligate (every year) migration found in 89 percent of Minnesota does in northeastern Minnesota where winters are very severe, to conditional (occasional) in central Minnesota where winters are milder. Here depth of snow is more likely to promote migration than colder temperatures (Fieberg et al. 2008). Average migration distances from summer to winter habitat have been reported from 5.6 to 20 km (3.5 to 12.5 mi). However, once established for the winter, movements of deer in Minnesota average less than 4.8 km² (2 mi²) (Alverson et al. 1988).

Winter diet of deer

The winter diet of deer consists primarily of the terminal ends of deciduous

twigs, supplemented with arboreal lichens, litterfall, and conifer browse. A study in southeastern Quebec found that deer utilized treetop slash from commercial logging operations. The cuts attracted deer that were within two kilometers of the harvest. No feeding preference was found between fresh-cut and older-cut twigs, or between tree tops and saplings. A feeding preference was found for paper birch over trembling aspen (St-Louis et al. 2000). The diet of deer has a higher proportion of deciduous twigs in early winter, moving toward a more equal ratio of deciduous to coniferous fare in late winter, although when possible they will browse a mixture of both. From a dietary metabolism perspective, this demonstrates an energy maximizing strategy rather than a time minimizing one (Schmitz 1990).

In a browse test, northern white-cedar was preferred three to seven times over bigtooth aspen (*Populus grandidentata* Michx.), offering higher palatability, digestibility; and gross energy output (Ullrey et al. 1964). It was preferred ten times over balsam fir with higher digestibility, crude protein, fiber, and nutrition. Significant consumption of balsam fir resulted in loss of weight because of poor digestibility (Ullrey et al. 1968); it is considered starvation fare because of the low level of nutrients and high energy cost of digestion. Ditchkoff and Servelo (1998) tested digestible energy (DE) of winter diet. A measurement of energy efficiency of consumption, DE is measured in kilocalorie per gram (kcal/g) of dry matter. The DE of northern white-cedar was 2.46, eastern hemlock (*Tsuga canadensis*, another vital support conifer for deer which occurs primarily outside the range of Minnesota) 2.41, arboreal lichens (*Usnea* and *Evernia* spp.) 2.86, and

hardwood twigs 1.5-2.1. There was a negative relationship between kcal/g and twig diameter. Balsam fir was not tested because of poor digestibility and high concentrations of plant secondary compounds.

“Heavy browse” is a term frequently used when describing over-use of the northern white-cedar resources. Aldous (1952) defined this as complete removal of annual foliage growth, noting that annual browse by deer is frequently greater than annual growth. He found that removal of up to 20 percent of foliage in smaller trees would allow the sapling to continue to develop annual growth; in larger trees, removal of 50 percent of foliage below seven feet actually stimulated foliage production. The removal of all lower branch foliage did not retard tree growth because even without browse effect lower branches would have been lost to self-pruning.

Wildlife and timber management studies suggest that 8 deer/km² (21 deer mi²) are standard carrying capacity, but ecosystem studies find that a population level of 1-4 deer/km² (3 to 10 deer/mi²) is needed to avoid a detrimental impact to browse-sensitive species (Alverson et al. 1988). While not the normal feeding pattern, the daily consumption requirement for a healthy adult deer is 4.5 pounds of northern white-cedar foliage. This is the same amount of foliage provided by a three-inch diameter branch on a single mature northern white-cedar tree (Aldous 1941).

Northern white-cedar stand changes

The decrease of the northern white-cedar component in riparian stands has led to changes in stand composition. Northern white-cedar suppression in deeryards has been

reported to result in conversion to species that are not browsed as heavily. Associates such as balsam fir, red maple, alder, and aspens have replaced northern white-cedar where they previously shared space (Johnston 1972; Verme and Johnston 1986; Van Deelen et al. 1996; Davis et al. 1998). Balsam fir has emerged as the most frequent competitor for stand composition. In disturbance settings balsam fir frequently recruits more successfully into taller seedling classes (Johnston 1990; Miller et al. 1990; Chimner and Hart 1996; Schaffer 1996; Heitzman et al. 1997; Hofmeyer et al. 2009a; but see Cornett et al. 1997). In harvest settings, greater overstory removal often favors balsam fir reproduction over northern white-cedar, while red maple and alder are also common replacements (Nelson 1951; Johnston 1972; Chimner and Hart 1996).

Introduction to balsam fir

Balsam fir is a boreal conifer of wide range in Canada and the northern U.S. where it occurs in both pure and mixed stands. Its range extends from northwestern and central Alberta (60°N, 120°W) east across Canada, north to Greenland (83°N), across northern Quebec and Newfoundland to the Atlantic Ocean (53°W). The U.S. range extends through Minnesota (97°W), south to Iowa (40°N), across the Lake States to New England and the Atlantic Ocean (47°N, 67°W), and south locally in the Virginia and West Virginia mountains (36°N) (Frank 1990).

Balsam fir is classified as very shade tolerant and fast growing, reaches a medium height of 18 meters (60 ft), and potentially can live a maximum of 200 years. However, balsam fir stands usually break up before 90 years due to mortality from insect

infestations, trunk and root rots, and blowdown. Mean annual growth peaks about 60 years in even-age stands. Common forest associates are conifers (black and white spruce, eastern white pine (*Pinus strobus* L.), tamarack, northern white-cedar) and hardwoods (aspen, birch (*Betula alleghaniensis* Britton, *Betula papyrifera* Marsh.), red and sugar maple (*Acer saccharum* Marsh), black ash) (Frank 1990).

Balsam fir forest types and associates

Balsam fir occurs in Minnesota in the northeastern third of the state. This species is the primary component of SAF forest cover type 5 (Balsam fir) and appears in 22 eastern forest cover types (Frank 1990). Minnesota's NPCC lists balsam fir in approximately 25 forest types/subtypes (MN DNR 2003). For example, it is described as a canopy species in *northern mesic mixed forest* (FDn43), a fire-dependent forest type with rotations of 220 to 260 years. Balsam fir begins to replace pioneer deciduous species 35-55 years post-fire, moving into the mixed canopy 55-95 years post-fire and maintaining a presence until the next fire event. It is also listed as a frequent understory/canopy species in most subtypes of *northern* and *northern poor dry-mesic mixed woodland* (FDn32, FDn33) and as a canopy species in the early stages of *northern wet cedar forest* (WFn53) (MN DNR 2003).

Balsam fir has a stronger presence in today's forests due to historic logging of white pine that was replaced by forest types with a large balsam fir element, while subsequent fire suppression practices encouraged the accumulation of mature balsam stands (Blais 1983).

Balsam fir soil and hydrologic environments

Soil moisture is the most important site index indicator, with drainage and soil texture also important features. Balsam fir does not persist in flood-prone areas. It inhabits a wide range of organic and inorganic soils of glacial origin (Histosols, Inceptisols, Spodosols) with acidity between pH 5.0 and 7.0 (Frank 1990). It is not dominant and grows slowly in swamps, usually where the peat is less than 2.7 meters thick (Bakuzis and Hansen 1965). Balsam fir is a strong contender for space and over time can greatly increase annual volume ingrowth (Frank 1990). On wet-mesic sites, balsam fir will compete more successfully than associated hardwoods, but on mesic sites it is outgrown and often replaced by more tolerant hardwoods (Johnston 1986).

Balsam fir reproduction and growth

Balsam fir seeds require only ten percent of full sunlight to germinate, although seedlings grow best in 50 percent or higher. Germination occurs on a variety of substrates, with moisture availability the most important factor (Frank 1990). A nine-year light intensity study (Logan 1969) reported that for the first six years, balsam fir seedlings consistently showed slow height growth in all light treatments, with leader growth and branch elongation nearly the same. After that time, height growth increased more rapidly than branch elongation. In the same study, balsam fir expressed the greatest growth (determined by dry weight measure) in 45 percent light. Logan (1969) suggested that shade foliage had higher rates of photosynthesis per unit volume than sun foliage, which may help explain the high shade tolerance of this species. Balsam fir can withstand

suppression for many years in the understory, responding to release with a doubling of diameter growth rate within a few years (Johnston 1986). It has been found that a length of suppression between 30 and 100 years does not have an effect on cone production (Bakuzis and Hansen 1965).

Balsam fir pathology and pests

Balsam fir is susceptible to a number of insects and diseases that shorten its potential lifespan. Spruce budworm (*Choristoneura fumiferana* Clemens) is the most serious insect pest, capable of causing large-scale disturbances and changes in forest composition. Damage ranges from low-level infestations that reduce vitality to periodic outbreaks causing defoliation and mortality on a regional basis. Impact is correlated with abundance of mature balsam, as stands under fifty years old are less affected (Johnston 1986). On lower slopes, balsam fir mortality due to spruce budworm infestation most often results in replacement by balsam fir, while hardwoods and non-host conifers tend to replace fir mortality on drier upper slopes (Bouchard et al. 2006). Spruce-fir stands in northeastern Minnesota, re-measured seventeen years following a spruce budworm outbreak, were found to have overstory composition changes from 79 percent fir and spruce basal area before to 31 percent afterward (Batzer and Popp 1985). However, 58 percent of understory stems 1.5 to 9.0 cm (0.6 to 3.5 in) DBH (diameter at breast height) were balsam fir, indicating that balsam fir would likely replace itself in the overstory. Batzer and Popp (1985) also found, contrary to Johnston (1986), that young and old balsam fir stands suffered the same mortality from spruce budworm. This discrepancy

could be due to their finding that mortality continued after the outbreak ended. Younger stands averaged more than twice as much balsam fir regeneration as older stands following the outbreak.

A scenario for gap recruitment was presented by Kneeshaw and Bergeron (1998) studying tree replacement in boreal forest gaps. They reported that balsam fir was the most plentiful gap-filler, with small gaps in early successional forests encouraging an increase in balsam fir dominance. Balsam fir reproduction was negatively correlated to gap size. Spruce budworm outbreaks in older fir forests created larger gaps that were colonized by a greater percentage of intolerant shrubs and hardwoods. They predicted an increase of balsam fir in early successional forests with smaller gaps, an increase of deciduous shrubs and hardwoods in older forests with larger gaps, and in the absence of fire, an increase in older forests of northern white-cedar.

Forest insects afflicting balsam fir to lesser degrees are hemlock looper, eastern blackheaded budworm, balsam fir bark beetle, balsam fir sawyer, and balsam fir seed chalcid. The most important diseases affecting balsam are trunk rots (primarily red heart rot (*Haematostereum sanguinolentum*)) and many root rots. Trunk rots cause boles to snap while root rots increase windthrow. Trees are prone to rots beginning about age 40; half of all firs are infected by age 70. Infection is less on wet-mesic sites, higher on drier and more productive sites (Johnston 1986; Frank 1990). Witches broom (*Melampsorella caryophyllacearum*) is a common cosmetic affliction. Fir is a shallow-rooted species, making it prone to windthrow, another frequent cause of mortality. Balsam fir-spruce

stands in New Brunswick, Canada, were found to decline by age 70 years, with blowdown the primary cause for 50 percent of tree deaths. Previous insect outbreaks contributed to the blowdown rate (Taylor and MacLean 2005).

Balsam fir wildlife and plant associates

Frequent understory shrub associates include beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), Labrador-tea (*Ledum groenlandicum*), and red raspberry (*Rubus idaeus* var. *strigosus*). Many of the same herbaceous species that are found on northern white-cedar forest floors also appear: twinflower (*Linnaea borealis*), bunchberry (*Cornus canadensis*), starflower (*Trientalis borealis*), creeping snowberry (*Gaultheria hispidula*), bluebead lily (*Clintonia borealis*), Canada mayflower (*Maianthemum canadense*), and various fern species. Forest floor associates can be an indicator of site quality. *Hylocomium* and *Hypnum* moss species indicate poor site quality and occur under pure balsam fir canopy (Frank 1990).

Balsam fir is an important species for wildlife habitat. It provides food and shelter for forest birds, in particular the ruffed grouse (*Bonasa umbellus* (Linnaeus)) and the spruce grouse (*Canachites canadensis* (Linnaeus)). Common songbirds are the warbler species, boreal chickadee (*Parus hudsonicus* Forster), and the yellow-bellied sapsucker (*Sphyrapicus varius* (Linnaeus)). Balsam fir provides important cover for small mammals such as snowshoe hare, marten, red squirrels, mice, and voles (Bakuzis and Hansen 1965). Moose (*Alces alces*) use fir for summer heat protection and winter cover, and feed extensively on foliage. White-tailed deer use lowland spruce-balsam fir stands for winter

cover, as stands more than 20 years old with basal area of at least 70 give moderate thermal protection (Johnston 1986). It is not a preferred browse species for deer but provides good fill, though it is lower in nutrient value than northern white-cedar. Balsam fir along waterways provides shading and cooler water temperatures for aquatic life and reduces beaver activity (Johnston 1986).

Balsam fir forest products

Balsam wood is lightweight and soft, and has low decay resistance. It is harvested primarily for pulpwood in making high quality paper, with smaller markets for lumber and oriented strand board (OSB). Specialty products are oleoresin from bark blisters used for mounting microscope slides, spirit varnishes, and boughs, which are harvested seasonally (Frank 1990).

Extent of the northern white-cedar and balsam fir forest resource in Minnesota

Northern white-cedar in Minnesota is harvested almost entirely for saw timber, with only minor markets for specialty products and fuel wood. The species is considered a potential resource for utilization and management if recruitment issues can be addressed. In 2007, across all ownership categories, the estimated average net annual growth was 193,678 cords; estimated annual mortality to growing stock was 119,933 cords; annual harvest was 8,800 cords, reflecting harvest policies that acknowledge lack of regeneration (MN DNR 2010). Currently Federal and state land managers in Minnesota practice no-cutting and leave-tree policies (MN DNR, Superior National

Forest, Chippewa National Forest pers. comm.). Because of this public harvest moratorium, mature northern white-cedar volume is currently increasing in Minnesota.

The balsam fir timber resource in Minnesota is reported by DNR's Forestry Division (2010) to depend upon the aspen and birch harvest, as 53% of balsam fir occurs in aspen and birch cover types. There are concerns about the amount of mortality from spruce budworm and basal rot, as well as for a high number of stands above 40 years old. In 2007 the estimated average net annual growth was 93,318 cords; estimated average annual mortality of growing stock was 116,892 cords; annual harvest was 165,600 cords (MN DNR 2010). Balsam fir volume is currently dropping in Minnesota.

The northern white-cedar cover type inhabits 231,887 hectares (573,000 acres) of timberland (4 percent of Minnesota timberland), while the balsam fir cover type occupies 155,805 hectares (385,000 acres for 2 percent of state timberland cover) (MN DNR 2010). However, more balsam fir is mixed in with other cover types than is northern white-cedar and may be under-reported by this amount.

USFS FIA data also show more volume acreage for the northern white-cedar forest type in Minnesota than for balsam fir forest type. 2005 net volume (in thousand cubic feet) of all live trees on Minnesota forest land was 1,028,694 for northern white-cedar and 677,900 for balsam fir. Net volume (in thousand cubic feet) of growing stock on timberland (defined as "forest land not restricted from harvesting and capable of growing trees at a rate of 20 cubic feet per acre per year") was 874,075 for northern white-cedar and 635,087 for balsam fir (Miles and Brand 2007).

In spite of these volume disparities, net volume of balsam fir growing stock in diameter classes 5.0 to 8.9 inches DBH exceeds that of northern white-cedar, showing a greater abundance of balsam fir in younger age categories (Figure 1) (Miles and Brand 2007). This also illustrates a difference in species' life history, where balsam fir reaches maximum productivity at a lesser DBH and a younger age than northern white-cedar.

The northern white-cedar cover type has 258,000 acres (45%) in old stands of greater than 100 years (rotation age 70 to 140 years), with less than 15,000 acres (2.6%) in stands younger than 30 years. The balsam fir cover type is also dominated by older stands, roughly 234,000 acres (61%) older than 40 years of age (average rotation length of 50 years); 130,000 acres (34%) is under 40 years (MN DNR 2010). While the northern white-cedar resource is reported to be growing more per annum and has a substantially lower harvest and mortality rate than balsam fir, it has little seedling regeneration and extremely low sapling numbers. Balsam fir, although exhibiting higher harvest and mortality levels and lower percent cover, shows greater growth potential in substantial regeneration and ingrowth.

Species comparison and life strategies

The comparison of northern white-cedar and balsam fir reveals different life strategies that allow for the co-existence of both species in pure and mixed stands (Table 1). Northern white-cedar requires specialized regeneration niches, uses layering as an alternate regeneration mechanism, grows slowly, matures after thirty years, and persists for up to 400 years, succumbing mainly to windthrow and fire (Johnston 1990). Balsam

fir regenerates across the forest floor, matures quickly in twenty years, and usually senesces before 100 years due to disease, insect infestation, or windthrow (Frank 1990). Advanced regeneration of both species responds to gap and stand level release, and as their populations fluctuate in shared spaces, survival of each is maintained.

However, the loss of northern white-cedar advance regeneration under current forest conditions could alter this balance. At present, northern white-cedar is long-lived with a low mortality rate, successful seedling regeneration but very little sapling survival, and an established mature population. Balsam fir is short-lived with a high mortality rate, substantial seedling regeneration, a sapling component, and mature stands with considerable fluctuation in structure. Without successful establishment, eventual senescence of northern white-cedar will leave forest stands with no younger generations. Balsam fir and hardwood species will recruit more effectively into forest gaps, further suppressing northern white-cedar recruitment.

Regeneration - the role of substrate and microtopography

To increase our understanding of conifer establishment, many studies have examined the role of forest floor substrate. Cornett et al. (1997; 1998; 2000b) used the concept of “safe-site” to describe seedbed and canopy type feedback loops that provide beneficial settings for seedling germination and establishment. Northern white-cedar germinants and seedlings were most successful where positive canopy feedbacks were present, as in decayed wood under a northern white-cedar canopy. They also did well in

substrates with higher soil moisture (except for pit areas), higher temperatures, thinner litter, and lower herbaceous cover, and under a conifer canopy.

Balsam fir germinants and seedlings did not depend as heavily on canopy feedback loops, were more widely dispersed throughout substrates, and most successful on level ground. Similar to northern white-cedar, germination was highest in substrates with thinner litter and warmer temperatures, and under a conifer canopy.

In a northern white-cedar restoration study, Cornett et al. (2001) found that artificial seedbeds under paper birch canopy had higher mortality than natural decayed logs or conifer canopy, most likely due to greater transpiration under higher light conditions; however, seedlings that survived had greater height growth. Overall, seedbed manipulation was not as advantageous to northern white-cedar colonization as natural conditions.

Many other studies have examined the role of microtopography (microsites) in conifer regeneration. Microsites are ground-level variations that affect vegetation on the scale of individual plants. Fine gradients of topography, temperature, nutrient, moisture, and light provide niche environments for specialized plant growth requirements (Cornett et al. 2001; Dovčiak et al. 2003; Simard et al. 2003).

Microsites are created by environmental incidents during the lifetime of the forest, such as mounds formed by tree fall and decay, pits formed by root displacement and slash piles formed by windfall (Cornett et al. 1997; Clinton and Baker 2000; Harrington and Bluhm 2001). Pit-mound or hummock-hollow topography is a common feature of

riparian forests, where hydrologic processes, wet soils, and shallow roots contribute to tree fall. Some microsites are created by harvest activities that leave slash residues and stump remnants (Freedman et al. 1996; Fraver et al. 2002). Microsites can also be destroyed or marginalized during harvest through mechanical means (Chimner and Hart 1996) or removal of coarse woody debris important for regeneration substrates (Freedman et al. 1996; Cornett et al. 1997; Simard et al. 1998).

Mounds

Mound microsites occur frequently in riparian landscapes in association with pit-mound topography. They are created by decomposition of stumps and boles and by soil slumps from the roots of tree fall. They provide nutrient resources, moisture retention, and protection from flooding. Various studies have examined specialized seedbed requirements for conifer regeneration, many of which require or are greatly encouraged by, decaying logs, mounds, and hummocks (Webb 1988; St. Hilaire and Leopold 1995; Chimner and Hart 1996; DeLong et al. 1997; Simard et al. 1998; Dovčiak et al. 2003; Simard et al. 2003). Northern white-cedar has a well-documented regeneration preference for decaying woody substrates (Nelson 1951; Holcombe 1976; Scott and Murphy 1987; Johnston 1990). Cornett et al. (2000b) examined the effects of seedbed and moisture availability on northern white-cedar germination and survival, concluding that both were highest under conditions of high moisture and non-litter, such as on decaying logs. In studies of upland northern white-cedar regeneration, Cornett et al. (1997; 2001) studied combined canopy and microsite influences which create feedback loops involving seed

rain, light input, litter type, and substrate. Under northern white-cedar canopy both germination and establishment were lower on mounds than on rotted wood, similar to level ground, and greater than in pits (except for one dry year when germination in pits was higher than on mounds).

Pits

Pit microsites are frequent components of riparian landscapes created by underlying substrate depressions and root removal during tree tip-up. They provide higher moisture and cooler soil temperatures (Cornett et al. 1997; Clinton and Baker 2000); however, pits also present establishment hazards, as they are vulnerable to flooding. Clinton and Baker (2000) compared characteristics of pits and mounds in the Coweeta Basin of North Carolina and found pits had higher soil moisture and seed deposition, lower soil temperature and photosynthetically active radiation (PAR), and similar concentrations of carbon and nitrogen.

Conifer seedling establishment does not occur often in pit microsites. Cornett et al. (1997) reported that pits had the lowest northern white-cedar germinant and seedling establishment of all forest floor microsites studied, except for one dry year. Webb (1988) found that balsam fir seedling colonization of windthrow pits in a Minnesota *Pinus-Abies* forest was low; Harrington and Bluhm (2001) found pits had lower seedling density and survival than intact forest floor in the Georgia Piedmont. In a Michigan fen, Chimner and Hart (1996) found that only 15% of deciduous shrub species, 11% of hardwood species, 6% of balsam fir and 3% of northern white-cedar occurred in pits.

Slash

Slash microsites consist of undecomposed woody debris on the forest floor such as branch litter, tree fall, and harvest residue. Forest Inventory Analysis (Chojnacky et al. 2004) categories of down woody materials include a living shrub/herb cover, defined as “understory shrubs and herbs of both live and dead plants that are still standing upright.” Slash offers shade, cooler soil temperatures, and some protection from browse predation (Verme and Johnston 1986; Peterson and Pickett 1995; Schaffer 1996). Seedling establishment of northern white-cedar is hindered by a heavy cover of slash, but a light cover is more favorable than none (Johnston 1990). In a Wisconsin study, Davis et al. (1998) reported that three years after harvest, a leave slash treatment had a higher density of regeneration of northern white-cedar and balsam fir than either a burn or full tree removal treatment. Curtis (1946) found native northern white-cedar seedlings in exposed areas on the lee of slash that mitigated desiccation and evaporation from drying winds and sun. Verme and Johnston (1986) established that northern white-cedar stems in harvested plots are tallest and most numerous when shaded by stumps or logs in the interior, and in the shadow of the uncut buffer zone on the south edge.

Microsite regeneration studies

Simard et al. (1998; 2003) studied conifer recruitment in northwestern Quebec, focusing on the seed to seedling recruitment stage. They determined that conifer initiation and establishment were most successful in well-lighted microsites with low litter and understory competition. Further, northern white-cedar seedlings were most often

restricted to decayed woody substrates, while balsam fir seedlings were more widely distributed.

A study in central New York of the relationship of hummock-hollow topography and bryophyte layers to conifer regeneration found that high hummocks covered with short mosses (*Hypnum* spp) provided safe sites for both northern white-cedar and balsam fir. Balsam fir had the highest density of seeds and seedlings, with both species exhibiting a gradient ranging from lowest germination in hollows and low hummocks to highest germination in high hummocks (St. Hilaire and Leopold 1995).

In a Michigan study of bryophyte flora of northern white-cedar seedbed logs, 73% of northern white-cedar germinants were associated with moss species on decaying logs and stumps, 19% emerged on raised humus over roots and rock, and 8% established on the forest floor (Holcombe 1976).

Hummock microtopography in a Michigan fen peatland provided unsaturated soil conditions that were necessary for successful regeneration of northern white-cedar. In contrast, areas with many pits and few hummocks contained prolific deciduous species and few northern white-cedar (Chimner and Hart 1996). A study in Quebec, Canada, found balsam fir seedlings up to six years old had a strong association with woody mounds covered by feather mosses that aided the infiltration of seedling roots into damp humus layers, while mosses that create thicker mats (*Hylocomium* spp.) inhibit establishment (Parent et al. 2003).

Beyond regeneration - the continuing role of microsites

Some studies suggest that conditions required for regeneration are not necessarily the same as those that favor the transitional stage of seedling to sapling growth. On South Manitou Island, Michigan, abundant northern white-cedar regeneration occurred on log substrates, but seedlings taller than 25 cm appeared only in or near canopy openings (Scott and Murphy 1987). Rooney et al. (2002) found in Michigan and Wisconsin that the percentage of northern white-cedar stems that originated on wood decreased as seedling stem size increased, while the percentage of larger stems originating on raised mounds and “other” substrates (non-tip-up mounds, pits, moss, and water) increased, suggesting that microsite substrates other than wood had higher survival value for seedlings past the germination stage.

The long-term role of microsites and light levels in northern white-cedar seedling development and eventual recruitment is not well studied. The absence of northern white-cedar advance regeneration in our forests deters the assessment of conditions that are important in the transition of seedlings to saplings. The following study was designed to examine the role of partial overstory removal and forest floor microsites in this next stage of seedling development.

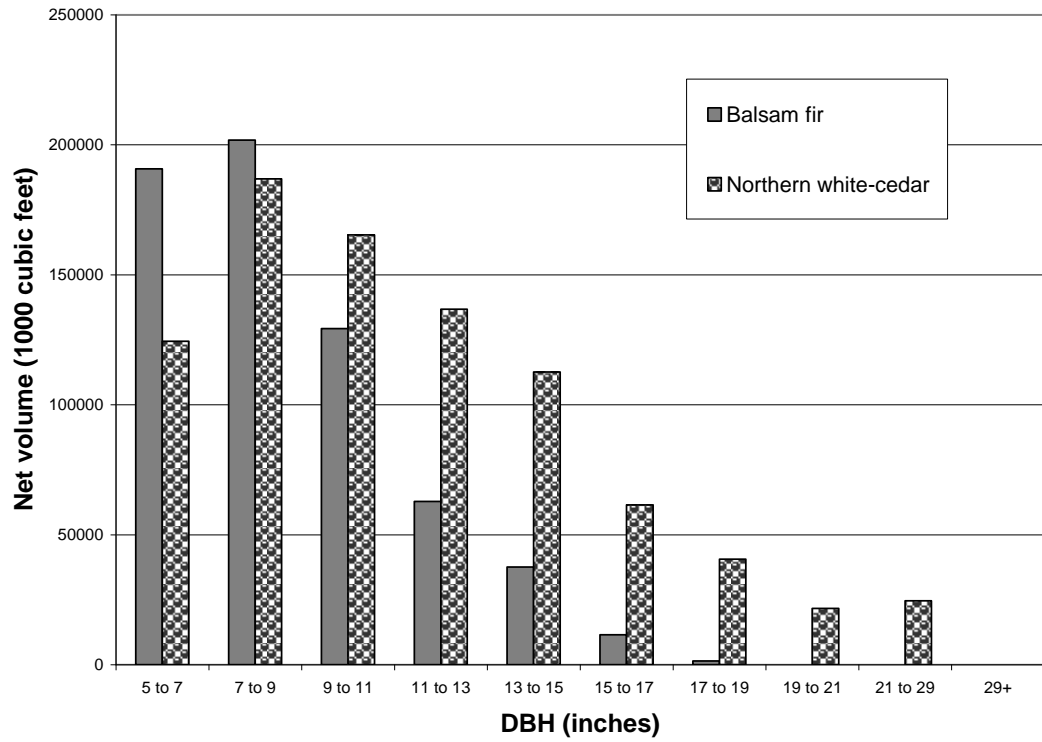
Chapter 1 Tables

Table 1.1. Comparison of lowland northern white-cedar and balsam fir biological characteristics (Frank 1990; Johnston 1990).

Characteristic	Northern white-cedar	Balsam fir
Flowering	monoecious	monoecious
Seed size	763,000/kg	131,000/kg
Seed range (windborn)	45–60m	25–60 m
Age at seeding	1 st at 30 yrs, best at 75 yrs	1 st at 20 yrs, best at > 20 yrs
Average maximum height	12–15 m	12–18 m
Average maximum DBH	30–60 cm	30–46 cm
Maximum age	> 400 yrs	200 (seldom)
Fire susceptibility	very sensitive	very sensitive
Site index at 50 yrs	5m (poor site) 12m (good site)	10m (poor site) 20m (good site)
Rotation years to merchantable volume	80–100 (poor site) 70–90 (good site)	65–70 (poor site) 45–59 (good site)
Light requirement	germination: 50% maximum seedling height: 45% maximum root + shoot mass: 100%	germination: 10% maximum seedling height: 45% maximum root + shoot mass: 45%
Pathology	curved butts, red heart fungus, leaf miners, flooding, windthrow, deer herbivory	spruce budworm, seed chalcid, witches broom, root and butt rots, windthrow
Rooting habit	seedling: initial taproot with lateral extensions; adult: shallow with spreading roots, often on soil surface	seedling: initial taproot strong, extending through duff to mineral soil, then spreading laterally; adult: shallow, in top of mineral soil under duff
Soil types	Histosols; pH of 5.5–7.2	Histosols, Inceptisols, Spodosols; pH of 5.0–7.0
Moisture requirements	Moist (51 cm– 40 cm annual)	Mesic (38 cm–140 cm annual)
SAF forest types	Type 37-Northern white-cedar; associate in 13 types	Type 5-Balsam fir; major component in types 33, 35; associate in 22 eastern types
MN NPCC	WFn53-Northern wet cedar forest FPn63-Northern cedar swamp Associate in approximately 10 types	FDn32-northern poor dry-mesic mixed woodland FDn33-northern dry-mesic mixed woodland FDn43-northern mesic mixed forest Associate in approximately 25 types

Chapter 1 Figures

Figure 1.1. Comparison of northern white-cedar and balsam fir resource: net volume of growing stock on Minnesota timberland by diameter class in thousand cubic feet (percent error = 1.31) (Data from Miles and Brand 2007)



Chapter 1 Bibliography

- Aldous, S. E. 1944. A deer browse survey method. *Journal of Mammalogy* 25(2):130-36.
- Aldous, S. E. 1952. Deer browse clipping study in the lake states region. *Journal of Wildlife Management* 16(4):401-09.
- Aldous, S. E. 1941. Deer management suggestions for northern white cedar types. *Journal of Wildlife Management* 5(1):90-94.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2(4):348-58.
- Bakuzis, E. V., and H. L. Hansen. 1965. *Balsam fir – a Monographic Review*. Minneapolis, MN: University of Minnesota Press.
- Batzer, H. O., and M. P. Popp. 1985. Forest succession following a spruce budworm outbreak in Minnesota. *Forestry Chronicle* 61(2):75-80.
- Blais, J. R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13:539-47.
- Boelter, D. H., and G. E. Close. 1974. Pipelines in forested wetlands. *Journal of Forestry* September:561-63.
- Bouchard, M., D. Kneeshaw, and Y. Bergeron. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology* 87(9):2319-29.
- Briand, C. H., U. Posluszny, and D. W. Larson. 1992. Comparative seed morphology of *Thuja occidentalis* (eastern white cedar) from upland and lowland sites. *Canadian Journal of Botany* 70(2):434-38.
- Chimner, R. A., and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Canadian Journal of Forest Research* 26:389-93.
- Chojnacky, D. C., R. A. Mickler, L. S. Heath, and C. W. Woodall. 2004. Estimates of down woody materials in eastern US forests. *Environmental Management* 33:Supplement 1: S44-55.
- Chouinard, A., and L. Filion. 2001. Detrimental effects of white-tailed deer browsing on balsam fir growth and recruitment in a second-growth stand on Anticosti Island, Québec. *Ecoscience* 8(2):199-210.

- Clinton, B. D., and C. R. Baker. 2000. Catastrophic windthrow in the southern Appalachians: Characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management* 126(1):51-60.
- Cole, G. F. 1987. Changes in interacting species with disturbance. *Environmental Management* 11(2):257-64.
- Cornett, M. W. "Ecological restoration of upland northern white cedar forests on the Lake Superior highlands." Ph.D. diss., University of Minnesota, 2000.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology* 9(4):386-96.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000a. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000b. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. *American Journal of Botany* 87(12):1807-14.
- Cornett, M. W., K. J. Puettmann, and P. B. Reich. 1998. Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. *Canadian Journal of Forest Research* 28:196-205.
- Cornett, M. W., P. B. Reich, and K. J. Puettmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* 4(3):353-64.
- Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics* 35:113-47.
- Crow, T. R., M. E. Baker, and B. V. Barnes. 2000. Diversity in riparian landscapes. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 43-65. Boca Raton, FL: Lewis Publishers.
- Curtis, J. D. 1946. Preliminary observations on northern white cedar in Maine. *Ecology* 27(1):23-36.

- Davis, A., K. Puettmann, and D. Perala. 1998. *Site preparation treatments and browse protection affect establishment and growth of northern white-cedar*. Research Paper NC-330. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- DeLong, H. B., V. J. Lieffers, and P. V. Blenis. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27:1452-57.
- Ditchkoff, S. S., and F. A. Servello. 1998. Litterfall: An overlooked food source for wintering white-tailed deer. *Journal of Wildlife Management* 62(1):250-55.
- Dovčiak, M., P. B. Reich, and L. E. Frelich. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. *Canadian Journal of Forest Research* 33:1892-1904.
- Eyre, F. H., ed. 1980. *Forest Cover Types of the United States and Canada*. Washington, D.C.: Society of American Foresters.
- Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. *Journal of Mammalogy* 89(6):1529-39.
- Forester, J. D., D. P. Anderson, and M. G. Turner. 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *American Midland Naturalist* 160:438-53.
- Frank, R. M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.
- Fraver, S., R. G. Wagner, and M. Day. 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.
- Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, G. Johnson, and S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental Reviews* 4: 238-265.
- Goebel, P. C., K. S. Pregitzer, and B. J. Palik. 2006. Landscape hierarchies influence riparian ground-flora communities in Wisconsin, USA. *Forest Ecology and Management* 230:43-54.

- Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Horin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29:824-39.
- Grigal, D. F., and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecological Monographs* 45:389-407.
- Habeck, J. R. 1960. Winter deer activity in the white cedar swamps of northern Wisconsin. *Ecology* 41(2):327-33.
- Hardwood and Conifer Swamps – White Cedar Swamp [Internet]. [updated 2008 May 29]. St. Paul, MN: University of Minnesota, College of Biological Sciences, Cedar Creek Ecosystem Science Reserve; [cited 2009 Apr 1]. Available from: <http://www.cedarcreek.umn.edu/conservation/habitats/swamp/>.
- Harrington, T. B., and A. A. Bluhm. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. *Forest Ecology and Management* 140:265-75.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-82.
- Heitzman, E., K. S. Pregitzer, and R. O. Miller. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Canadian Journal of Forest Research* 27:1953-61.
- Heitzman, E., K. S. Pregitzer, R. O. Miller, M. Lanasa, and M. Zuidema. 1999. Establishment and development of northern white-cedar following strip clear cutting. *Forest Ecology and Management* 123:97-104.
- Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009a. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.
- Hofmeyer, P. V., R. S. Seymour, and L. S. Kenefic. 2009b. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. *Northern Journal of Applied Forestry* 26(2):68-75.
- Holcombe, J. W. 1976. The bryophyte flora of *Thuja* seedbed logs in a northern white-cedar swamp. *The Michigan Botanist* 15:173-81.

- Ilhardt, B. L., E. S. Verry, and B. J. Palik. 2000. Defining riparian areas. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 23-41. Boca Raton, FL: Lewis Publishers.
- Johnston, W. F. 1972. *Balsam fir dominant species under rethinned northern white-cedar*. Research Note NC-133. St. Paul, MN: USDA Forest Service, North Central Forest Experiment station.
- Johnston, W. F. 1986. *Manager's handbook for balsam fir in the North Central States*. General Technical Report NC-111. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- Johnston, W. F. 1977. *Manager's handbook for northern white cedar in the North Central States*. General Technical Report NC-35. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- Johnston, W. F. 1990. *Thuja occidentalis* L. Northern white-cedar. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.
- Kneeshaw, D. D., and Y. Bergeron. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*: 79(3):783-94.
- Larouche, C., L. S. Kenefic, and J.-C. Ruel. 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, C., J.-C. Ruel, J.-M. Lussier, and L. Kenefic. 2006. Regeneration of *Thuja occidentalis* L. in mixedwood stands on mesic sites after partial cuts in Quebec. In: Larocque, G.R., M. Fortin, and N. Thiffault, editors: Conference handbook, 2nd ed. Forest Science across the Borders - Conference of the Eastern CANUSA; Oct. 19-21, 2006; Quebec City, Quebec, Canada. 90-94.
- Lefort, S., J.P. Tremblay, F. Fournier, F. Potvin, and J. Huot. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range. *Ecoscience* 14(1):109-16.
- Logan, K. T. 1969. *Growth of tree seedlings as affected by light intensity: IV. Black spruce, white spruce, balsam fir and eastern white cedar*. Publication No.1256. Canadian Forestry Service Department of Fisheries and Forestry.

- Matthes-Sears, U., and D. W. Larson. 1991. Growth and physiology of *Thuja occidentalis* L. from cliffs and swamps: Is variation habitat or site specific? *Botanical Gazette* 152(4):500-508.
- Matthes-Sears, U., S. C. Stewart, and D. W. Larson. 1991. Sources of allozymic variation in *Thuja occidentalis* in southern Ontario, Canada. *Silvae Genetica* 40(3-4):100-105.
- Miles, P. D., and G. J. Brand. 2007. *Minnesota's forest resources in 2005*. Resource Bulletin NRS-6. Newton Square, PA: USDA Forest Service, Northern Research Station. 33 p.
- Miller, R. O. 1990. Ecology and management of northern white-cedar. In *Proceedings of Regenerating conifer cover in deer yards workshop*, 1-13. North Bay, Ontario.
- Miller, R. O., M. Lanasa, D. Elsing, and M. Zuida. 1990. Northern white-cedar: stand assessment and management options. In *Proceedings of Northern white-cedar in Michigan Workshop*, 1-6. Sault Ste. Marie, MI.
- Minnesota Department of Natural Resources. 2003. Field guide to the native plant communities of Minnesota: The Laurentian Mixed Forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR St. Paul, MN.
- Minnesota Department of Natural Resources. 2010. Minnesota's forest resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.
- Musselman, R. C., D. T. Lester, and M. S. Adams. 1975. Localized ecotypes of *Thuja occidentalis* L. in Wisconsin. *Ecology* 56:647-55.
- Nelson, T. C. 1951. A Reproduction study of Northern White Cedar. Game Division, Michigan Department of Conservation.
- Palik, B., J. Zasada, and C. W. Hedman. 2000. Ecological principles for riparian silviculture. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 233-54. Boca Raton, FL: Lewis Publishers.
- Parent, S., M.-J. Simard, H. Morin, and C. Messier. 2003. Establishment and dynamics of balsam fir seedling bank in old forests in northeastern Quebec. *Canadian Journal of Forest Research* 33:597-603.
- Peterson, C. J., and S. T. A. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76(3):763-74.

- Pregitzer, K. S. 1990. The ecology of northern white-cedar. In *Proceedings of Northern white cedar in Michigan*, ed. D. O. Lantagne, 8-14. Research Report 512. East Lansing, MI: Michigan Agricultural Experiment Station.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* 74(3):201-08.
- Rooney, T.P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181(1):165-76.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. *American Midland Naturalist* 146(1): 1-26.
- Schaffer, W. W. 1996. *Silvicultural guidelines for the eastern white cedar*. Technical Report TR-006, Ontario: Ontario Ministry of Natural Resources, Southern Region Science & Technology Transfer Unit.
- Schmitz, O. J. 1990. Management implications of foraging theory: Evaluating deer supplemental feeding. *Journal of Wildlife Management* 54(4):522-32.
- Scott, M. L., and P.G. Murphy. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *American Midland Naturalist* 117(1):10-16.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: The importance of substrate. *Journal of Vegetation Science* 9(4):575-82.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. *Canadian Journal of Forest Research* 33:672-81.
- Smith, J. R., R. A. Sweitzer, and W. F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. *Journal of Wildlife Management* 71(8):2719-26.
- Stewart, G. 1925. Forest types of the northern swamps. *Journal of Forestry* 23:160-72.

- St. Hilaire, L. R., and D. J. Leopold. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. 1995. *Canadian Journal of Forest Research* 25:261-69.
- St-Louis, A., J.-P. Ouellet, M. Crête, J. Maltais, and J. Huot. 2000. Effects of partial cutting in winter on white-tailed deer. *Canadian Journal of Forest Research* 30:655-61.
- Stoeckeler, J. H. 1967. *Wetland road crossings: Drainage problems and timber damage*. Research Note NC-27. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station. 4p.
- Stroh, N., C. Baltzinger, and J-L. Martin. 2008. Deer prevent western redcedar (*Thuja plicata*) regeneration in old-growth forests of Haida Gwaii: Is there a potential for recovery? *Forest Ecology and Management* 255:3973-79.
- Stromayer, K. A., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25(2):227-34.
- Taylor, S. L., and D. A. MacLean. 2005. Rate and cause of decline of mature and overmature balsam fir and spruce stands in New Brunswick, Canada. *Canadian Journal of Forest Research* 35: 2479-90.
- Tremblay, J.-P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2007. Long-term decline in white-tailed deer browse supply: Can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology* 83:1087-96.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, B. E. Brent, and K. E. Kemp. 1968. Digestibility of cedar and balsam fir browse for the white-tailed deer. *Journal of Wildlife Management* 32:162-71.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, P. K. Ku, and L. D. Fay. 1964. Digestibility of cedar and aspen browse for the white-tailed deer. *Journal of Wildlife Management* 28(4):791-97.
- Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A Comparison of presettlement and present-day forests in two northern Michigan deer yards. *American Midland Naturalist* 135(2):181-94.
- Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan: Their ecology and management. *Journal of Forestry* 63(7):523-29.

Verme, L. J., and W. F. Johnston. 1986. Regeneration of northern white cedar deeryards in upper Michigan. *The Journal of Wildlife Management* 50(2):307-13.

Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: A keystone herbivore. *Wildlife Society Bulletin* 25(2):217-26.

Webb, S. L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. *Canadian Journal of Forest Research* 18:1186-95.

Zenner, E. K., and J. E. Peck. 2009. Maintaining a pine legacy in Itasca State Park. *Natural Areas Journal* 29(2):157-66.

Chapter 2

A Comparison of *Thuja occidentalis* and *Abies balsamea* Seedling Response to Partial Harvest and Microsite in Northern Minnesota Riparian Forests

Chapter 2 Synopsis

Northern white-cedar (*Thuja occidentalis* L.), a long-lived riparian conifer of boreal forests, currently suffers recruitment decline throughout much of its range, reducing the northern white-cedar forest presence. Herbivory by increased populations of white-tailed deer (*Odocoileus virginianus*) suppresses northern white-cedar at the seedling and advance regeneration stages, while forest disturbance generates changes in stand composition that favor less heavily browsed species, notably balsam fir (*Abies balsamea* (L.) Mill.). Many studies identify beneficial regeneration microsites for northern white-cedar, but little is known about microsite contributions following establishment. This study in northern Minnesota compared responses of planted seedlings of northern white-cedar and balsam fir inside fenced exclosures and examined the continuing role of microsites (mound, pit, slash), partial overstory removal, and unharvested controls in seedling survival and growth. After four years in the field, general linear model (GLM) analysis of survival between species was significantly higher for northern white-cedar than balsam fir overall, although both species suffered significant mortality in pits. Overstory had no effect on northern white-cedar survival, but balsam fir survival was significantly lower in controls. GLM analysis of growth showed that harvests yielded significant increases in height, basal diameter, and relative growth rate over controls for both species, but no microsites had any significant effect on growth for either species. Relative basal diameter growth (RDG) was greater for northern white-cedar than for balsam fir, although relative height growth (RHG) was not. Correlation analysis of environmental variables revealed a significant negative correlation between basal area and all growth parameters for both species. Northern white-cedar height and

basal diameter showed correlations to percent forest floor cover (negative), percent herbaceous cover (positive), and percent woody cover (positive). Balsam fir height, basal diameter, RHG, and RDG showed positive correlations to C:N ratio and forest floor depth.

Key words: northern white-cedar, balsam fir, microsite, recruitment decline, partial overstory harvest, relative growth rate

Introduction

Northern white-cedar (*Thuja occidentalis* L.) is a long-lived conifer of boreal forests. This bimodal species inhabits moist lowland areas with organic soils, neutral pH, and flowing, mineral-rich waters and also occurs in uplands on calcareous sites. Most current stands of northern white-cedar in the northeastern and north central United States originated from clearcut harvests and subsequent wildfires that began in the mid-1800s. Studies have found that following these stand-level disturbances, northern white-cedar successfully re-established through natural seeding and advance regeneration, and developed into second-growth, even-aged stands that today are 75 to 150 years old (Pregitzer 1990; Heitzman et al. 1997).

Silviculture guidelines for northern white-cedar regeneration implemented in the mid-20th century, many intended for deer yard management, recommended narrow strip and small block clearcutting with a thin residual slash covering. This allowed sufficient seed rain from adjacent uncut strips and a protective cover for seedling establishment (Verme 1965; Johnston 1977; Miller 1990, Heitzman et al. 1999). Nelson (1951) advocated a selective cut, leaving 500 to 750 stems ac⁻¹ (1235 to 1850 stems ha⁻¹) to increase seedling reproduction while suppressing shrub and hardwood competition.

Recruitment decline

By the 1980s it became evident that these harvest practices had not sustained the successful regeneration of northern white-cedar. Forest managers reported the lack of advance regeneration and recruitment (Heitzman et al. 1999; Rooney et al. 2002; Hofmeyer et al. 2009a; Larouche et al. 2010). This trend was also present in Minnesota forests, where the natural range of northern white-cedar encompassed the northeastern

third of the state. Estimates indicate northern white-cedar composed 8% of the pre-settlement landscape in northeastern Minnesota, while currently it makes up 4% of the state's forests (Cornett et al. 2000a; MN DNR 2010).

By 1990 state and federal agencies in the Lake States had enforced limited cutting of northern white-cedar in response to diminished establishment (Miller 1990). Today the absence of northern white-cedar sapling and pole size classes from both pure and mixed stands indicates that recruitment into existing stands may be insufficient to maintain viable populations (Heitzman et al. 1997; Cornett et al. 2000a; Rooney et al. 2002; Forester et al. 2008; Larouche et al. 2010).

Various factors have been implicated in the loss of northern white-cedar advance regeneration. Heinselman (1973) suggested that northern white-cedar in northeastern Minnesota had been driven to the edges of lakes by fire. Early road construction cut through many conifer swamps, impeding drainage and causing significant mortality (Stoeckler 1967; Boelter and Close 1974; Forester et al. 2008). Slow growth rates from small to medium to large sapling sizes contribute to a delay of recruitment to pole stage that is longer than other associated species (Larouche et al. 2010).

Research into regeneration mechanisms suggests that harvest methods may remove or destroy necessary regeneration niches on the forest floor such as hummocks (Chimner and Hart 1996) and nurse logs (Cornett et al. 2001). Simard et al. (1998), studying conifer establishment in Canada, found that northern white-cedar took 50 years to begin re-establishment following fire and was dependent upon the gradual decomposition of woody debris for necessary substrate. However, observations of northern white-cedar stands indicate that seedling regeneration and establishment are

present in sufficient quantity and therefore are not the underlying causes of recruitment decline (Heitzman et al. 1997; Cornett et al. 2000a; Forester et al. 2008).

The foremost cause of current northern white-cedar recruitment failure is herbivory from white-tailed deer (*Odocoileus virginianus*) (Scott and Murphy 1987; Pregitzer 1990; Heitzman et al. 1997; Davis et al. 1998; Heitzman et al. 1999; Forester et al. 2008). Northern white-cedar foliage is the preferred winter browse for deer, which exert heavy feeding pressure on all stages of tree growth (Johnston 1972; Davis et al. 1998). Deer populations have risen significantly in the 20th century due to increased forage made available by the conversion of forests to agricultural lands and the removal of natural predators (Cornett et al. 2000a; Rooney and Waller 2003). The ranges of northern white-cedar and white-tailed deer in Minnesota, once primarily separate, now overlap (Cornett et al. 2000a).

The decrease of a northern white-cedar component in riparian forests has led to changes in stand composition. Associates such as balsam fir (*Abies balsamea* (L.) Mill.), red maple (*Acer rubrum* L.), alder (*Alnus* spp.), and aspen (*Populus tremuloides* Michx., *Populus grandidentata* Michx.) have replaced northern white-cedar where they previously shared space (Johnston 1972; Verme and Johnston 1986; Davis et al. 1998).

Balsam fir has emerged as the most frequent competitor for overstory dominance. In harvest settings, overstory removal often favors balsam fir reproduction over northern white-cedar, while red maple and alder are also common replacements (Nelson 1951; Johnston 1972; Chimner and Hart 1996). In natural disturbances balsam fir frequently recruits more successfully into taller seedling classes (Johnston 1990; Miller et al. 1990; Schaffer 1996; Heitzman et al. 1997). Kneeshaw and Bergeron (1998) predicted that

balsam fir will increase in early successional forests with smaller gaps, while woody shrubs and trees will increase in larger gaps of older successional forests, and northern white-cedar will increase in older forests with nurse logs and the absence of fire.

Characteristics that help balsam fir compete successfully against northern white-cedar include a larger seed, ability to regenerate on diverse substrates, a stronger initial taproot, and higher shade tolerance of seedlings (Cornett et al. 1997; Simard et al. 1998). In addition, it is not a preferred species for deer herbivory. Balsam fir is able to recruit more quickly into gaps created by its own and northern white-cedar senescence, further suppressing northern white-cedar establishment.

Role of microsites

Microsites are created during the lifetime of the forest by environmental incidents. For example, mounds are formed by tree fall and decay, pits by root displacement, and slash piles by windfall and harvest residue (Freedman et al. 1996; Cornett et al. 1997; Clinton and Baker 2000; Harrington and Bluhm 2001; Fraver et al. 2002). Microsites can be destroyed during harvest activities (Chimner and Hart 1996) or marginalized by removal of coarse woody debris (Freedman et al. 1996; Cornett et al. 1997; Simard et al. 1998). Mounds provide organic soils, nutrients, moisture, and protection from flooding (Webb 1988; St. Hilaire and Leopold 1995; Chimner and Hart 1996; DeLong et al. 1997; Simard et al. 1998; Dovčiak et al. 2003; Simard et al. 2003). In comparison to mounds, pits present higher moisture and seed deposition, lower soil temperatures, lower germination rates, similar carbon and nitrogen concentrations, and a higher danger of flooding (Webb 1988; Cornett et al. 1997; Clinton and Baker 2000; Harrington and Bluhm 2001). Slash microsites contribute shade, cooler root temperatures, and protection

from browse predation (Verme and Johnston 1986; Peterson and Pickett 1995; Schaffer 1996; Larouche et al. 2010).

Northern white-cedar microsite research

Much of northern white-cedar research to date has focused on microsite conditions that are required for seed germination and seedling establishment. Effects of various canopy and seedbed conditions have been studied by Cornett et al. (2000b; 2001) and Simard et al. (2003). Other studies have examined the role of forest floor microsites and substrates in conifer regeneration (St. Hilaire and Leopold 1995; Chimner and Hart 1996; DeLong et al. 1997; Cornett et al. 1998; Simard et al. 1998; Dovčiak et al. 2003; Forester et al. 2008).

During the early stages of tree growth (seed germination, initial seedling establishment, and early seedling growth), the biological conditions required for success of individuals at particular stages are often not the same as the conditions required at previous stages (St. Hilaire and Leopold 1995; Simard et al. 1998; Scott and Murphy 1987; Rooney et al. 2002; Simard et al. 2003). There has been little examination of the continuing role of forest floor microsites in the growth of northern white-cedar seedlings past the first year of seedling establishment.

This project examined the effect of partial overstory removal and the role of mound, pit, and slash microsites on the survival and growth of northern white-cedar and balsam fir seedlings after establishment in harvested riparian management zones (RMZs) of northern Minnesota. The goal was to gain insight into the management practices and environmental conditions that might encourage growth of northern white-cedar over balsam fir within managed riparian forests. The questions addressed were: (1) do partial

overstory removal and microsite type influence the survival of planted northern white-cedar and balsam fir seedlings? and (2) do partial overstory removal and microsite type influence northern white-cedar and balsam fir seedling growth response as demonstrated by height and basal diameter growth? Answers to these questions will help guide practices that encourage the establishment and recruitment of northern white-cedar in managed riparian areas.

Materials and Methods

Site locations

This study was conducted as part of a broader study, originating in 2003, that investigated the ecological effects of riparian harvests on forest productivity, wildlife habitat, and aquatic ecosystems in the Laurentian Mixed Forest Province of northeastern Minnesota (“RMZ Harvest” Internet-updated July 2008). This landscape province is characterized by mixed hardwood and conifer forests, peatlands, and lakes. The current project was conducted on three of the eight sites from the larger study including Shotley Brook (48°N, 94.5°W), Nemadji State Forest (46.4°N, 92.3°W), and East Branch Beaver River (47.3°N, 91.3°W) (Figure 2.1).

Sites were harvested in the winter of 2003-04 on frozen ground with conventional harvesting equipment (i.e., a tracked feller-buncher with grapple skidder). The current study was installed in May 2004; growth data were collected in the autumns of 2005, 2006, and 2007; survival and browse data were collected each spring and autumn; environmental data were collected in the summer of 2006. Pre-harvest basal area, post-harvest residual basal area (RBA), and forest composition were obtained from Kastendick 2005 (Table 2.1).

Experimental design

Each site contained an upstream uncut control and a downstream harvested area within the riparian management zone. The RMZs were along one side of a waterway with control and harvest dimensions 46 m deep x 183 m wide, separated by an uncut buffer 46 m deep x 61 m wide. Upland clearcuts (137 m deep x 183 m wide) were made above each test area (Figure 2.2). The target RBA for the harvest treatments was $11.6 \text{ m}^2\text{hc}^{-1}$, but actual RBA differed to some extent by site. Shotley Brook was $20.1 \text{ m}^2\text{hc}^{-1}$ RBA, East Branch Beaver River was $15.5 \text{ m}^2\text{hc}^{-1}$ RBA, and Nemadji State Forest was $11.2 \text{ m}^2\text{hc}^{-1}$ RBA (Kastendick 2005) (Table 2.1). Actual RBA was used in data analysis. In Minnesota $11.6 \text{ m}^2\text{hc}^{-1}$ is the recommended harvest level for uneven-age management of trout streams. Harvests were conducted according to riparian guidelines (MFRC 2005).

Three replicates each of mound, pit, and slash microsites were established on existing landforms in the control and harvest areas. There were nine microsite plots per overstory treatment, 18 plots per site, and a total of 54 plots at all three locations. Four seedlings each of 3-0 northern white-cedar and balsam fir were planted and tagged per microsite plot.

Microsite description

At each site, each of three microsite treatments was replicated three times within the control and harvest areas. The microsites of mound, pit, and slash were selected for this project because of earlier studies that illustrated their roles in northern white-cedar and balsam fir regeneration (Shaffer 1996; Cornett et al. 1997; Simard et al. 1998; Chimner and Hart 1996; Cornett et al. 2000b, 2001; Rooney et al. 2002; Dovčiak et al.

2003). Microsite selection was made from features that occurred from natural and harvest events throughout the control and harvest RMZs.

Most mound microsites selected were the residue of old tree stumps, evidenced by the presence of large aging stump structures and the surrounding mound of organic soil. All fit into decay class 4 (wood is mostly rotten) as described by Fraver et al. (2002). A few mounds were organic soil hummocks of unknown origin.

Pit microsites were distinct depressions of various origins in the forest floor. These were formed by weathered tree root tip-ups, abandoned stream or oxbow channels, or dips in underlying substrate.

Slash microsites were naturally occurring piles of coarse and fine woody debris of different dimensions. They ranged from solid boles of windthrown trees to tree top logging residue. Seedlings were planted as close as possible along the north side of slash features to maximize contributions of shading and soil temperature moderation.

To eliminate potential deer browse, prior to planting each microsite plot was enclosed by polypropylene fencing 2.8 m tall x 3 m x 3 m upheld by steel fence poles. The effects of deer browse were determined by duplicating plantings outside of each fenced plot in an adjoining or nearby microsite of the same type, for an additional 432 seedling individuals. Chapter 3 documents the impacts of browsing on seedling growth.

Seedling measurements

Seedlings were planted in May 2004 and followed for four growing seasons. Four northern white-cedar and four balsam fir seedlings were planted inside each fenced plot approximately 0.5 m apart, alternating individuals by species (Figure 2.3), for a total of 216 northern white-cedar and 215 balsam fir individuals (one balsam fir was

unintentionally not planted). The seedlings were field grown for three years (3-0) by the Minnesota DNR nurseries from native seed collected within the north central zone. Seedling measurements taken were height in centimeters (ground level to tip of the longest leader), basal diameter in millimeters (an average of two measurements at ground level), and survival (individuals that died before the end of data collection in 2007 were eliminated from the growth analysis). Baseline seedling measurements of height and basal diameter were taken within one month of planting and a metal identification tag was attached with a copper wire around the base of each stem. A standard metal tape measure was used to measure heights to the half centimeter. Basal diameter was measured with a Spi dial caliper in 0.1 mm increments. Growth data were collected annually each autumn beginning after the second growing season; survival data were collected each spring and autumn. All analysis was performed on final measurements from the fourth growing season.

Analysis of initial seedling heights inside fence exclosures revealed a significant difference at the overstory treatment level at the time of planting. Seedlings of both species were significantly taller in the harvest areas at planting (northern white-cedar height in controls = 21.1 cm \pm 1.10, in harvests = 24.2 cm \pm 1.75, $p = 0.04$; balsam fir height in controls = 10.6 cm \pm 0.71, in harvests 12.95 cm \pm 0.60, $p = 0.02$). Unintended planting bias may have occurred, although separate crews planted each site. To avoid this in the future, seedlings could be selected within a pre-determined range of height and basal diameter, and assigned to plots through a random selection process prior to field planting.

Vegetation measurements

Associated forest floor and vegetation cover was assessed once during the study (the third summer in the field). Data were collected for the parameters of percent forest floor cover (exposed area with no vegetation cover, litter may or may not be present), percent moss cover, percent herbaceous cover (grass plus forbs), percent woody cover (shrub cover with stems < 2.5 cm diameter at breast height (DBH) and foliage height < 1.3 m), and overstory basal area (BA) (Table 2.2). Stems < 2.5 cm diameter with foliage > 1.3 m height were neglected. Percent covers were compiled per plot from visual estimates of four one-meter quadrats that were then averaged for each cover category. Overstory basal area was measured per plot by prism (factor 10) and included woody stems > 2.5 cm diameter at breast height (DBH).

Soil measurements

The forest floor at all locations was a variable mix of deciduous leaves and conifer needles. Forest floor depth (in centimeters) was measured twice per plot at random points and averaged. Soil samples were collected to investigate the planting environment of seedling roots. Samples were collected by site within a 24-hour window and more than 48 hours after the last rain. One sample was collected inside of each fenced plot. After removing the surface litter, a 10 x 10 mm steel cylinder was inserted into the ground, and an O horizon soil sample was extracted. The soil cores were double-bagged in plastic and stored in bulk coolers at 23° C (45° F) until processing.

Soil parameters analyzed in the laboratory were percent coarse fragments, gross bulk density, percent carbon, percent nitrogen, and C:N ratio (Table 2.2). Soil samples were air-dried and sieved by hand through a 2-mm stainless steel sieve to remove coarse

fragments, creating mineral soil samples of < 2-mm size fraction. Sub-samples were oven-dried to obtain residual water content of air-dried soil sample to express gross bulk density on an oven-dry basis. Coarse fragments and mineral soil samples were weighed and entered into a spreadsheet to calculate the percent coarse fragment content and soil gross bulk density using the following formulas:

(1) *Percent coarse fragments*

$$= \frac{\text{weight of } > 2\text{mm size fraction, } g}{\text{weight of } > 2\text{mm} + < 2\text{mm size fractions, } g} \times 100$$

$$(2) \text{ Gross bulk density} = \frac{\text{whole soil core dry weight (oven dry basis), } g}{\text{soil core volume, } \text{cm}^3 = 709}$$

Analysis was conducted following Forest Inventory Analysis laboratory protocol (Amacher et al. 2003).

Soil samples for elemental analysis were placed in glass vials that were rolled to homogenize the contents. Analysis for percent carbon and nitrogen was done on a Leco TruSpec CHN determinator with a range for carbon of 0.005% to 50% precision of 0.5% RSD and for nitrogen from 0.008% to 100% with a precision of 0.5% RSD. The detection method for carbon was an optimized, low-noise, non-dispersive infrared absorption cell, and for nitrogen an optimized, low-drift, thermal conductivity cell. Results were entered into a spreadsheet to calculate carbon to nitrogen ratio (C:N ratio).

Data analysis

Statistical analysis was performed with SAS/STAT® software Version 9.1.3 for Windows. General Linear Model (GLM) analysis (Type III Sum of Squares) was used for

seedling survival and growth response due to 100 percent mortality in some pit microsites and variable species mortality, which caused unbalanced data. Site was used as a blocking factor, allowing any true differences between site conditions to be lumped with the error term, producing a more stringent F-test. Significance was based on $p \leq 0.05$. Tukey's Studentized Range HSD test ($\alpha = 0.05$) was used to identify which means were significantly different from each other when a significant difference was discovered by the model.

The experimental design was a 2x3x2 factorial. Independent variables were species (northern white-cedar and balsam fir), overstory treatment (control and harvest), microsite treatment (mound, pit, slash). Interactions between variables (referred to as "interaction" or denoted with "x") were added to the model. Dependent variables were percent survival, height, basal diameter, relative height growth (RHG), and relative basal diameter growth (RDG). Variables were constructed as follows:

(a) Percent survival was calculated by species per plot as:

$$\text{Percent survival} = \left(\frac{\# \text{ of survived seedlings}}{4} \right) \times 100$$

with 4 being the number of planted seedlings per species per plot (with 3 used for the plot with an unplanted seedling). Plot data were used for correlation analysis and aggregated for GLM analysis and figure construction.

(b) Relative growth rate (RGR) is the increase in log seedling growth over a period of time and was calculated by species per seedling as:

$$\text{RGR} = \frac{\log N \text{ final value} - \log N \text{ initial value}}{4}$$

with final value being the last measured value, initial value being the measured value at planting, and 4 being the length

of study time in growing seasons. Seedling data were then averaged per plot for correlation analysis; plot averages were aggregated for GLM analysis and figure construction.

Different growth habits of northern white-cedar and balsam fir make comparisons based on height and basal diameter difficult. Northern white-cedar has a relative distribution of leaf area in the upper crown with small branch diameters; balsam fir has a relative distribution of leaf area lower in the crown with larger branches (Weiskittel et al. 2009; Weiskittel et al. 2010). RGR, based on growth rate ratios, was deemed the most accurate means of assessment between species with differing growth traits. RGR analysis is conventionally measured in dry weight (Harper 1977), but for this study was measured in height and basal diameter to allow non-destructive sampling.

Simple linear regression was used to compare response variables (height, basal diameter, and RGR) to independent variables (vegetation and soil measurements) to identify correlations that might help explain the responses identified by GLM analysis. The coefficient was calculated by Pearson product moment correlation; the significance probability was calculated for $\alpha = 0.05$.

Variable transformations were performed for each level of analysis to meet assumptions of normality and variance. GLM analysis was performed at the interaction mean level, $n = 3$. Correlation was performed at the plot mean level, $n = 46$ plots for northern white-cedar, $n = 44$ plots for balsam fir. The original number of plots established was 54, but some suffered complete mortality and so were not included in the growth analysis.

Results

Seedling survival

After four seasons in the field, percent survival was significantly higher for northern white-cedar than for balsam fir (82.0% and 67.0% respectively, $p = 0.004$) (Table 2.3, Figure 2.4a). With species pooled, percent survival in pit microsites (47.9%) was significantly lower than in mounds (91.4%) or slash (85.4%) ($p < .0001$). With species pooled, percent survival in controls (67.4%) was significantly lower than in harvest treatments (82.4%) ($p = 0.01$). Species x overstory interaction was almost significant ($p = 0.06$), with balsam fir survival in controls (54.3%) much lower than harvests (79.6%) or northern white-cedar controls (80.6%) and harvests (85.2%) (Figure 2.4b).

No significant differences were found by GLM for species x microsite x overstory interactions ($p = 0.92$); however, Tukey's HSD did find significance between the highest and lowest values (Figure 2.4c). Northern white-cedar survival in control x mound interactions (100%), harvest x mound (100%), and harvest x slash (100%) were much higher than balsam fir survival in control x pit interactions (30.6%). Northern white-cedar cumulative survival dropped substantially in pits during the first year in the field, while balsam fir cumulative survival dropped initially in pits and consistently in the controls each of the first four years in the field (Figure 2.5).

Seedling growth

Overstory treatment had a significant effect on northern white-cedar seedling height, where harvest treatments resulted in taller seedlings (63.2 cm) than controls (40.9 cm) ($p = 0.0003$) (Table 2.4, Figure 2.6a). Harvest treatments also resulted in greater

basal diameters (8.2 mm) than controls (5.3 cm) ($p = 0.0004$). Neither microsite treatment nor overstory x microsite interaction had a significant effect on northern white-cedar height or basal diameter (Figure 2.6b and c). Overstory treatment also had a significant effect on relative growth rate, where harvest treatment resulted in greater RHG (0.23) than control (0.17) ($p < 0.0001$), as well as greater RDG (harvest 0.25, control 0.18; $p = 0.01$) (Table 2.5). Neither microsite treatments nor overstory x microsite interactions had any significant effect on northern white-cedar RGR response.

Overstory treatment had a similar significant effect on balsam fir seedling height and basal diameter. Harvest treatments resulted in taller seedlings (35.9 cm) than controls (18.8 cm) ($p = 0.001$), as well as larger basal diameters (harvest 6.9 mm, control 4.3 mm; $p = 0.0001$) (Table 2.6, Figure 2.7a). Neither microsite treatment nor overstory x microsite interaction had a significant effect on either balsam fir size measurements (Figure 2.7b and c). Overstory treatment also had a significant effect on relative growth rate for balsam fir. Harvest treatment resulted in greater RHG (0.23) than control (0.13) ($p = 0.0026$) and greater RDG (harvest 0.19, control 0.09; $p = 0.001$) (Table 2.7). Neither microsite treatments nor overstory x microsite interactions had any significant effect on balsam fir RGR response.

GLM comparison of RHG between species showed no significant differences between species overall ($p = 0.75$) or for species x overstory, species x microsite, or species x overstory x microsite (Table 2.8, Figure 2.8a). Overall RDG of northern white-cedar (0.21) was significantly higher than that of balsam fir (0.14) ($p < 0.0001$) (Figure 2.8b).

Seedling growth correlated to environmental factors

Basal area

Both northern white-cedar (NWC) and balsam fir (BF) showed a significant negative correlation in height to BA (NWC: $p < 0.0001$, $r = -0.64$; BF: $p = 0.0001$; $r = -0.58$) and a corresponding negative correlation in basal diameter to BA (NWC: $p < 0.0001$, $r = -0.60$; BF: $p = 0.0001$, $r = -0.55$) (Table 2.9, Figures 2.9a and 2.10a). RGR correlation analysis for both species also showed significant negative correlations to BA for RHG (NWC: $p = 0.002$, $r = -0.45$; BF: $p = 0.02$, $r = -0.35$) and RDG (NWC: $p = 0.0003$, $r = -0.51$; BF: $p = 0.01$, $r = -0.40$) (Table 2.10, Figures 2.9b and 2.10b).

Additional northern white-cedar correlations

In northern white-cedar seedlings, negative correlations were found between all growth parameters and percent forest floor cover: height ($p = 0.0001$, $r = -0.54$), basal diameter ($p = 0.001$, $r = -0.46$) (Table 2.9), RHG ($p = 0.002$, $r = -0.46$), and RDG ($p = 0.01$, $r = -0.36$) (Table 2.10, Figures 2.11a and b). Northern white-cedar height to percent herbaceous cover was positively correlated ($p = 0.003$, $r = 0.42$); so too were basal diameter ($p = 0.01$, $r = 0.37$) (Figure 2.12a) and RHG ($p = 0.01$, $r = 0.40$), but not RDG ($p = 0.24$, $r = 0.18$) (Figure 2.12b). Similarly, height to percent woody shrub cover had a weak positive correlation ($p = 0.03$, $r = 0.31$); so too did basal diameter ($p = 0.01$, $r = 0.40$) (Figure 2.13a) and RDG ($p = 0.01$, $r = 0.36$), but not RHG ($p = 0.58$, $r = 0.09$) (Figure 2.13b).

Weak positive correlations were found for northern white-cedar basal diameter to percent soil carbon ($p = 0.05$, $r = 0.29$), percent nitrogen (almost at $p = 0.09$, $r = 0.26$), and percent coarse fragments ($p = 0.03$, $r = 0.33$) (Table 2.9, figures not shown); RDG

also had close to significant correlations for percent carbon ($p = 0.07$, $r = 0.28$) and percent nitrogen ($p = 0.06$, $r = 0.28$) (Table 2.10, figures not shown).

Additional balsam fir correlations

In balsam fir seedlings, positive correlations were found between all growth parameters and soil C:N ratio: height ($p = 0.01$, $r = 0.41$), basal diameter ($p = 0.05$, $r = 0.30$) (Table 2.9, Figure 2.14a), RHG ($p < 0.0001$, $r = 0.59$), and RDG ($p = 0.02$, $r = 0.34$) (Table 2.10, Figure 2.14b). Balsam fir seedling height ($p = 0.01$, $r = 0.39$) and basal diameter ($p = 0.04$, $r = 0.31$) showed a positive correlation to forest floor depth (Figure 2.15a), as well as RHG ($p = 0.001$, $r = 0.48$), but not RDG ($p = 0.09$, $r = 0.26$) (Figure 2.15b). Negative correlations were found for height and RHG to percent moss cover ($p = 0.02$, $r = -0.36$ and $p = 0.002$, $r = -0.47$, respectively) (figure not shown). Weak positive correlations were found for height, RHG, and (nearly) RDG to percent woody cover ($p = 0.01$, $r = 0.38$; $p = 0.03$, $r = 0.33$; and $p = 0.06$, $r = 0.29$, respectively) (figures not shown). Weak positive correlations were found for height, RHG, and RDG to percent coarse fragments ($p = 0.02$, $r = 0.34$; $p = 0.01$, $r = 0.41$; and $p = 0.04$, $r = 0.31$, respectively) (Figures 2.16a and b).

Discussion

Seedling survival

Northern white-cedar seedlings percent survival was similar in control and harvest, where overall survival rates were not significantly different between overstory treatments. Transplant seedlings were able to remain alive in the lower light environment of full overstory controls. This result differs from earlier studies, which report lack of germination and establishment, and higher mortality for small seedlings (< 30 cm tall and

≤ one year old) under natural canopy (Simard et al. 1998, Cornett et al. 2001), and implies that older seedlings are not subject to similar constraints.

Among microsite treatments, survival of northern white-cedar in pits was significantly lower than in mounds and slash. During the first two seasons in the field, those pits subject to seasonal flooding suffered almost complete mortality. Cornett (1996) also found almost complete mortality of northern white-cedar germinants in pits that experienced seasonal inundation. Mounds and slash provided conditions that were beneficial for planted seedling survival, with percent survival statistically similar.

Balsam fir percent survival was significantly lower overall than that of northern white-cedar. Transplant mortality may have been a factor for balsam fir, which had 26 seedlings die in the first summer after planting, compared to one mortality for northern white-cedar. Balsam fir percent survival was also significantly lower in unharvested control areas, with results showing the negative effect of lower light available under full overstory. This result disagrees with Logan (1969), who stated that balsam fir's low light tolerance at a young age is based "more on its ability to survive than on its ability to grow in low light."

Pit microsites again showed the effect of seasonal flooding on balsam fir with the significantly lowest percent survival, while mounds and slash were statistically similar.

These results address the first question examined by this study: do partial overstory harvest and microsites influence seedling survival? After four years in the field, northern white-cedar has significantly higher survival overall than balsam fir. Northern white-cedar percent survival was not affected by overstory treatment, while

balsam fir survival was lower in controls. At this age, planted northern white-cedar appears to be more shade-tolerant than balsam fir.

Both species suffered lower survival in pit environments, which was attributed to seasonal flooding of riparian areas. Clearly three-year old planted seedlings are still at flood risk from periodic inundation. Survival was lowest for both species at Site 1, Shotley Brook, where northern white-cedar survival overall was 59.7% and balsam fir survival was 45.8%. At Site 1 the groundwater was close to the surface, and all pit plots were subject to annual floodplain submersion.

Among our treatments, our results show that the best places to plant seedlings to maximize survival for both species were mound and slash microsites within partially harvested RMZs. However, northern white-cedar seedlings consistently out-performed balsam fir seedlings for percent survival (northern white-cedar 80.6%, balsam fir 54.3%), indicating that northern white-cedar could be favored over balsam fir by planting in unharvested areas.

Seedling growth

Partial overstory removal was a significant positive treatment for both northern white-cedar and balsam fir seedling growth. RMZ harvests proved significantly advantageous over unharvested controls for height and basal diameter responses of both species. This is consistent with silvicultural practice, which holds that overstory removal generates a release response in advance regeneration (Simard et al. 1998; Nyland 2002). Cornett et al. (2000a) reported similar results from an extended height growth simulation of northern white-cedar seedlings planted in the Lake Superior Highlands. Nearly half of seedlings under a more open *Betula papyrifera* canopy reached 2.1 m in 60 years,

compared to only 6% of seedlings under a denser *Thuja occidentalis* canopy. Larouche et al. (2006) reported similar results with planted northern white-cedar seedlings in Maine showing that mean annual height increment was proportional to light intensity.

However, there may be a limit to the amount of overstory removal that is advantageous. Manager's recommendations for northern white-cedar (Johnston 1977) state that reproduction grows best in half to full sunlight. Logan (1969) found that both northern white-cedar and balsam fir seedlings of ages two to nine years grew best in 45% over 100% available light. A recent study of overstory trees in Maine found that basal area growth of northern white-cedar was not correlated with site class or increased light levels, while balsam fir basal area growth and light exposure were correlated (Hofmeyer et al. 2009b).

No significant microsite influence or overstory x microsite interaction was detected for seedling growth response of either species. Over a four -year period, microsites (mound, pit, and slash) did not significantly influence either northern white-cedar or balsam fir seedling growth. This differs from microsite contributions to conifer seed germination and seedling establishment, where mound and slash microsites are important refuges, and pit microsites provide necessary (but often an excess) of moisture (Cornett et al. 2001; Dovčiak et al. 2003; Simard et al. 2003).

These results address the second question examined by this study: do partial overstory removal and microsites influence seedling growth? Our results indicate that at this seedling age, partial overstory removal positively affects seedling development of both northern white-cedar and balsam fir, but neither microsite nor overstory x microsite interaction plays a statistically significant role in growth response.

Partial overstory removal emerged again as the most influential treatment for both northern white-cedar and balsam fir seedling rate of growth. RHG and RDG responses were significantly higher in RMZ harvests than in unharvested controls. Also, no microsite or overstory x microsite interactions produced significant RGRs. This implies that by this age, seedlings do not depend upon microsite niche characteristics for successful growth rates, but instead respond most strongly to higher light environments afforded by partial overstory removal. This differs in part from results reported by Reich et al. (1998) for a greenhouse germination and growth study of boreal tree species. In that study, northern white-cedar germinants showed greater RGR of basal diameter at lower light levels (5% of full sunlight) than at higher levels (25%). This disparity might be attributed to different allocation patterns of seedlings in different growth stages (seedlings less than six months old in the 1998 study versus those seven years old in the current study), but such a determination is outside the scope of this study.

RGR analysis determined that at this age northern white-cedar responded with faster basal diameter growth, and to a lesser extent height growth, than balsam fir. Northern white-cedar true height was significantly higher than that of balsam fir in mound and slash microsites of both control and harvest overstory treatments. While this could be explained by differing growth habits between the species, gaining height and acquiring the higher stratum position can afford substantial advantage in the competition for light.

However, these dynamics are expected to change over time as seedling growth habits change. Logan (1969) reported from long-term field experiments that northern white-cedar seedlings up to six years were faster growing in height than balsam fir.

Balsam fir height growth was poor up to six years, during which time branch elongation was substantial. Between 6 and 9 years, height growth rate increased over branch elongation, with this trend predicted to continue. No such increase in growth rate was noted for northern white-cedar.

Seedling growth correlated to environmental factors

A consistent negative correlation was found between growth responses and RGR of northern white-cedar and balsam fir to BA (Tables 2.9 and 2.10). This mirrors the results of the GLM analysis, where it was found that both species responded to partial overstory removal by allocating resources to height and basal diameter growth. In the remaining correlation analysis, there were virtually no situations where correlations were shared between species. The lack of shared correlations between species' growth and environmental variables may be an indication of the different resources accessed by each species, and of the different ways in which those resources are used. This type of comparison could help explain how northern white-cedar and balsam fir can co-exist or alternatively how one species might gain an advantage over the other in certain resource environments.

Northern white-cedar height, basal diameter, RHG, and RDG had negative correlations to percent forest floor and positive correlations to percent herbaceous (height, basal diameter, RHG) and percent woody cover (height, basal diameter, RDG). Percent forest floor was greater where overstory was greater (i.e., in controls) (personal observation), and conversely herbaceous and woody cover was greater where overstory was lower (i.e., in harvest areas). It is therefore likely that the growth response of seedlings is a response to light availability. The consistency of northern white-cedar

correlation to these variables indicates that (a) seedling growth responds to light conditions in a manner similar to herbaceous and woody plants, and (b) light availability affects northern white-cedar seedling growth more than the competition for soil resources presented by neighborhood herbaceous and woody growth. The absence of significant correlation between northern white-cedar seedling height or RHG and nutrient soil factors (C:N ratio, percent carbon, percent nitrogen) seems to support the latter argument, at least in the case of height growth. Light availability appears to be the most important factor, of those variables measured, in northern white-cedar seedling growth at this stage of development.

Northern white-cedar basal diameter and RDG were found to have positive correlations (significant or almost significant) to percent soil carbon and percent soil nitrogen. This may indicate that these soil resources are accessed for basal diameter growth in all treatments and may partially account for the faster growth rate of northern white-cedar basal diameter over that of balsam fir. Further study regarding soil resource contributions and resource allocation in northern white-cedar seedling growth is indicated.

A positive correlation was found between all balsam fir growth variables (height, basal diameter, RHG, and RDG) and C:N ratio. In this study C:N values ranged between 12 and 33, with most values below 20 and a mean value of 17.5. In a study in Quebec, Canada, Roy et al. (2000) reported positive correlations between height increase of balsam fir advance regeneration and soils with C:N ratios between 25 and 35. These positive correlations may imply a preference of balsam fir for higher C:N ratios.

Balsam fir height, basal diameter, and RHG correlated positively to forest floor depth. Simard et al. (1998) also found that the occurrence of balsam fir seedlings was positively associated with leaf and needle litter, while northern white-cedar seedlings were not. Though forest floor in this study was not analyzed for identifiable components, deeper litter was associated with greater deciduous leaf-fall (personal observation), which has higher nitrogen content than conifer litter (Fisher and Binkley 2001). This also may indicate the presence of an active decomposition zone in the O horizon, with a greater incidence of soil microbes generating a pool of plant-available nitrogen. The correlations found between balsam fir growth variables to C:N ratio and forest floor depth may suggest that balsam fir is better able than other species to take advantage of a wider range of C:N ratios and available nitrogen supplies to partially compensate for the limiting factor of overstory density. Height, basal diameter, and RHG were positively correlated to percent coarse fragments, which may indicate better growth in soils with aeration and drainage, as indicated in the literature (Frank 1990).

Recommendations

In the riparian landscape, local site conditions of topography, hydrology, and soils influence local forest development. The use of site replicates in the overall study design (Shotley Brook, Nemadji State Forest, and East Branch Beaver River) was a way of addressing this variability by combining growth means that developed under different local conditions into an ideal average; these could then be used to make general management recommendations. However, an examination of treatments affecting northern white-cedar and balsam fir seedlings could not ignore these local site differences. For example, frequent flooding at Site 1, Shotley Brook led to significantly

higher mortality for both species than at Site 3, East Branch Beaver River. Mean growth for northern white-cedar varied substantially between Site 1-Harvest located in the floodplain (49.6 cm height, 6.3 mm basal diameter) and Site 3-Harvest located on a terrace above a steep river bank (75.1 cm height, 10.1 mm basal diameter). The same difference in mean growth for balsam fir height existed between Site 1 harvest x mound (18.6 cm) and Site 3 harvest x mound (46.4 cm). These numbers illustrate that landscape site differences should be considered when applying results reported by this study. Although northern white-cedar performance in this study indicates that it would be a good candidate for planting in a variety of riparian landscape locations, further monitoring is needed to determine the influence of local site conditions in successive life stages.

It should be remembered that this study was conducted inside fences to exclude the effects of herbivory by white-tailed deer. What we observed was the potential for northern white-cedar to grow into stands of variable harvest in the absence of browse. Given current deer populations, fencing of planted seedlings is suggested. Other methods of protection from herbivory should be investigated, including individual barriers such as tree tubes and bud-capping, the use of repellents, and planting inside slash cover.

General recommendations for planting northern white-cedar in riparian management areas include the following: (1) avoid pit areas due to high mortality during seasonal flooding; (2) for faster growth, plant in areas of partial harvest (plantings in harvests to approximately $11.6 \text{ m}^2 \text{hc}^{-1}$ RBA result in better growth than in un-harvested areas); (3) for slower growth rates but good survival, plant in no-harvest or low-harvest

areas; (4) remove balsam fir advance regeneration that may also be encouraged by partial harvest.

In this study, planted seedlings of northern white-cedar and balsam fir responded in height and basal diameter growth in a similar manner to the same treatments. However, RGR and percent survival analysis indicate that planted balsam fir seedlings do not have a competitive advantage over planted northern white-cedar seedlings up to four years in the field. Results suggest that, in the absence of deer browse, planted northern white-cedar would have at least four years in which to establish before having to compete with balsam fir.

Chapter 2 Tables

Table 2.1. Study site locations and local site information. Data is from Kastendick 2005 and author field data (*).

Site name	Latitude Longitude	County	Waterbody width (m)	Soil Type*	Relief (m)*		Primary pre- harvest timber species present	Mean (±SE) pre- harvest RMZ basal area (m ² hc ⁻¹)	Mean (±SE) post- harvest RMZ basal area (m ² hc ⁻¹)
					Control	Harvest			
Shotley Brook	N 48.05958 W 94.55176	Beltrami	4.6	Deep sandy loam	0-2	0-2	Northern hardwoods, aspen, lowland hardwoods	33.6 (4.9)	20.1 (3.7)
Nemadji State Forest	N 46.42021 W 92.31652	Carlton	1	Sandy loam, sandy clay loam	0-20	0-4	Northern hardwoods and aspen	20.8 (5.4)	11.2 (4.3)
East Branch Beaver River	N 47.33702 W 91.36048	Lake	5.5	Shallow sandy loam, shallow clay loam	0-10	0-25	Birch, aspen, lowland hardwoods, balsam fir	22.7 (3.1)	15.5 (2.8)

Table 2.2. Experimental design components.

Sites with latitude, longitude	Shotley Brook 48.0°N, 94.5°W Nemadji State Forest 46.4°N, 92.3°W East Branch Beaver River 47.3°N, 91.3°W
Overstory treatments	Control uncut Harvest to 11.6 m ² hc ⁻¹ RBA
Microsite treatments	mound pit slash
Seedling species	northern white-cedar balsam fir
Growth variables	survival height (in cm) basal diameter (in mm)
Vegetation variables	percent forest floor cover percent moss cover percent herbaceous cover percent woody cover basal area
Soil variables	forest floor depth percent carbon percent nitrogen C:N ratio gross bulk density percent coarse fragments

Table 2.3. General linear model output between species (Spp: northern white-cedar and balsam fir) for percent survival after four years in the field, in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; transformation: Θ = square; NR = not reported because Site was used as the blocking factor.

<u>Survival Θ ($r^2 = 0.77$)</u>				
<u>Source</u>	<u>DF</u>	<u>SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	8.20×10^7	NR	NR
Species	1	5.21×10^7	10.61	0.0036
Microsite	2	1.55×10^8	15.81	<.0001
Overstory	1	4.11×10^7	8.36	0.0085
Spp x Ms	2	1.52×10^6	0.16	0.8572
Spp x OS	1	1.89×10^7	3.85	0.0625
Ms x Os	2	9.18×10^6	0.93	0.4078
Spp x Ms x Os	2	8.13×10^5	0.08	0.9208
Model	13	3.61×10^8	5.65	0.0002
Error	22	1.08×10^8		
Corrected Total	35	4.68×10^8		

Table 2.4. General linear model output for northern white-cedar seedling height and basal diameter in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; transformations: Φ = log, \square = inverse; NR = not reported because Site was used as the blocking factor.

<u>Source</u>	<u>DF</u>	<u>Height Φ ($r^2 = 0.86$)</u>			<u>Basal diameter \square ($r^2 = 0.87$)</u>		
		<u>SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.0210	NR	NR	0.0052	NR	NR
Overstory	1	0.1292	35.16	0.0003	0.0138	33.26	0.0004
Microsite	2	0.0207	2.82	0.1181	0.0023	2.71	0.1260
Os x Ms	2	0.0046	0.63	0.5594	0.0006	0.68	0.5325
Model	7	0.1765	6.86	0.0072	0.0221	7.59	0.0052
Error	8	0.0294			0.0033		
Corrected Total	15	0.2059			0.0254		

Table 2.5. General linear model output for northern white-cedar seedling relative height growth and relative diameter growth in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; Transformations: Ω = cube, UT = untransformed; NR = not reported because Site was used as the blocking factor.

<u>Source</u>	<u>Relative height growth Ω ($r^2 = 0.93$)</u>				<u>Relative diameter growth UT ($r^2 = 0.66$)</u>		
	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.00002	NR	NR	0.0015	NR	NR
Overstory	1	0.0002	64.55	<.0001	0.0190	14.24	0.0054
Microsite	2	0.00002	3.49	0.0813	0.0002	0.09	0.9144
Os x Ms	2	0.00002	3.73	0.0717	0.0008	0.30	0.7492
Model	7	0.0004	14.40	0.0006	0.0209	2.23	0.1416
Error	8	0.00002			0.0107		
Corrected Total	15	0.0004			0.0317		

Table 2.6. General linear model output for balsam fir seedling height and basal diameter in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; transformations: Φ = log, UT = untransformed; NR = not reported because Site was used as the blocking factor.

Source	DF	Height Φ ($r^2 = 0.86$)			Basal diameter UT ($r^2 = 0.80$)		
		SS	F-stat	P-value	SS	F-stat	P-value
Site	2	0.0741	NR	NR	1.5812	NR	NR
Overstory	1	0.2902	37.21	0.0003	26.8063	28.55	0.0007
Microsite	2	0.0001	0.01	0.9940	0.6822	0.36	0.7063
Os x Ms	2	0.0125	0.80	0.4828	3.4193	1.82	0.2230
Model	7	0.3731	6.84	0.0073	30.3433	4.62	0.0237
Error	8	0.0624			7.5126		
Corrected Total	15	0.4355			37.8558		

Table 2.7. General linear model output for balsam fir seedling relative height growth and relative diameter growth in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; transformations: $\sqrt{\cdot}$ = arcsine square root; NR = not reported because Site was used as the blocking factor.

<u>Source</u>	<u>DF</u>	<u>Relative height growth $\sqrt{\cdot}$ ($r^2 = 0.88$)</u>			<u>Basal diameter $\sqrt{\cdot}$ ($r^2 = 0.83$)</u>		
		<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.1150	NR	NR	0.0042	NR	NR
Overstory	1	0.0615	18.45	0.0026	0.0346	31.66	0.0005
Microsite	2	0.0020	0.30	0.7463	0.0012	0.56	0.5930
Os x Ms	2	0.0080	1.21	0.3479	0.0032	1.49	0.2827
Model	7	0.1941	8.32	0.0039	0.0432	5.65	0.0132
Error	8	0.0267			0.0087		
Corrected Total	15	0.2208			0.0519		

Table 2.8. General linear model output between species (Spp: northern white-cedar and balsam fir) for (a) relative height growth and (b) relative diameter growth in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; transformations: UT = untransformed; NR = not reported because Site was used as the blocking factor.

	<u>Relative height growth^{UT} ($r^2 = 0.63$)</u>				<u>Relative diameter growth^{UT} ($r^2 = 0.82$)</u>			
<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.0272	NR	NR	2	0.0026	NR	NR
Species	1	0.0003	0.10	0.7551	1	0.0385	30.78	<.0001
Overstory	1	0.0501	16.32	0.0008	1	0.0526	42.04	<.0001
Microsite	2	0.0007	0.11	0.8980	2	0.0002	0.08	0.9279
Os x Ms	2	0.0016	0.26	0.7715	2	0.0036	1.46	0.2595
Spp x Os	1	0.0022	0.71	0.4090	1	0.0011	0.92	0.3510
Spp x Ms	2	0.0088	1.43	0.2654	2	0.0027	1.08	0.3592
Spp x Os x Ms	2	0.0062	1.01	0.3826	2	0.0004	0.17	0.8490
Model	13	0.0959	2.40	0.0431	13	0.1051	6.47	0.0002
Error	18	0.0553			18	0.0225		
Corrected Total	31	0.1512			31	0.1276		

Table 2.9. Correlations ($\alpha = 0.05$) between dependent (height and basal diameter) and independent (vegetation and soil) variables for northern white-cedar and balsam fir seedlings after four years in the field; (-) indicates a negative correlation. See *Vegetation and Soil analysis* sections for explanation of variables. Transformations: Θ = square root, \bullet = inverse square root, Φ = log, UT = untransformed, \ominus = square, \ominus = inverse square.

Vegetation variable	Northern white-cedar (n = 46)				Balsam fir (n = 44)			
	Height Θ		Basal diameter \bullet		Height Φ		Basal diameter \bullet	
	P value	r	P value	r	P value	r	P value	r
% Forest floor cover Θ	0.0001	- 0.54	0.001	- 0.46	0.42	- 0.13	0.17	- 0.21
% Moss cover Θ	0.67	- 0.07	0.89	0.02	0.02	- 0.36	0.20	- 0.21
% Herbaceous cover ^{UT}	0.003	0.42	0.01	0.37	0.78	0.04	0.41	0.13
% Woody cover Θ	0.03	0.31	0.01	0.40	0.01	0.38	0.16	0.21
Basal area Φ	< .0001	- 0.64	< .0001	- 0.60	0.0001	- 0.58	0.0001	- 0.55
Soil variable								
	P value	r	P value	r	P value	r	P value	r
% Carbon Φ	0.30	0.16	0.05	0.29	0.75	0.05	0.95	0.01
% Nitrogen Θ	0.39	0.13	0.09	0.26	0.28	- 0.17	0.66	- 0.07
C:N ratio \ominus	0.55	0.09	0.31	0.16	0.01	0.41	0.05	0.30
Gross bulk density Θ	0.66	- 0.07	0.24	- 0.18	0.42	0.13	0.62	0.08
% Coarse fragments Θ	0.12	0.23	0.03	0.33	0.02	0.34	0.15	0.22
Forest floor depth ^{UT}	0.83	0.03	0.91	- 0.02	0.01	0.39	0.04	0.31

Table 2.10. Correlations ($\alpha = 0.05$) between dependent (relative height growth (RHG) and relative basal diameter growth (RDG)) and independent (vegetation and soil) variables for northern white-cedar and balsam fir seedlings after four years in the field; (-) indicates a negative correlation. See *Vegetation and Soil analysis sections* for explanation of variables. Transformations: Φ = log, \bullet = inverse square root, \uparrow = arcsine square root, Θ = square root, UT = untransformed, \ominus = square, \boxminus = inverse square.

Vegetation variable	Northern white-cedar (n = 45)				Balsam fir (n = 44)			
	RHG Φ		RDG \bullet		RHG \uparrow		RDG \uparrow	
	P value	r	P value	r	P value	r	P value	r
% Forest floor cover \ominus	0.002	- 0.46	0.01	0.36	0.18	0.20	0.80	- 0.04
% Moss cover \ominus	0.56	- 0.09	0.30	0.16	0.002	- 0.47	0.15	- 0.23
% Herbaceous cover ^{UT}	0.01	0.40	0.24	- 0.18	0.15	- 0.22	0.62	- 0.08
% Woody cover \ominus	0.58	0.09	0.01	- 0.36	0.03	0.33	0.06	0.29
Basal area Φ	0.002	- 0.45	0.0003	0.51	0.02	- 0.35	0.01	- 0.40
Soil variable								
	P value	r	P value	r	P value	r	P value	r
% Carbon Φ	0.67	0.07	0.07	0.28	0.37	- 0.14	0.97	- 0.01
% Nitrogen \ominus	0.63	0.06	0.06	0.28	0.07	- 0.28	0.48	- 0.11
C:N ratio \boxminus	0.88	0.02	0.95	0.01	<.0001	0.59	0.02	0.34
Gross bulk density \ominus	0.44	0.12	0.40	- 0.13	0.73	0.05	0.59	0.08
% Coarse fragments \ominus	0.74	0.05	0.20	0.19	0.01	0.41	0.04	0.31
Forest floor depth ^{UT}	0.16	0.22	0.59	0.08	0.001	0.48	0.09	0.26

Chapter 2 Figures

Figure 2.1. Location of study sites in Minnesota. Site 1 = Shotley Brook, Beltrami County; Site 2 = Nemadji State Forest, Carlton County; Site 3 = East Branch Beaver River, Lake County. (MNMapper Jul 2009).

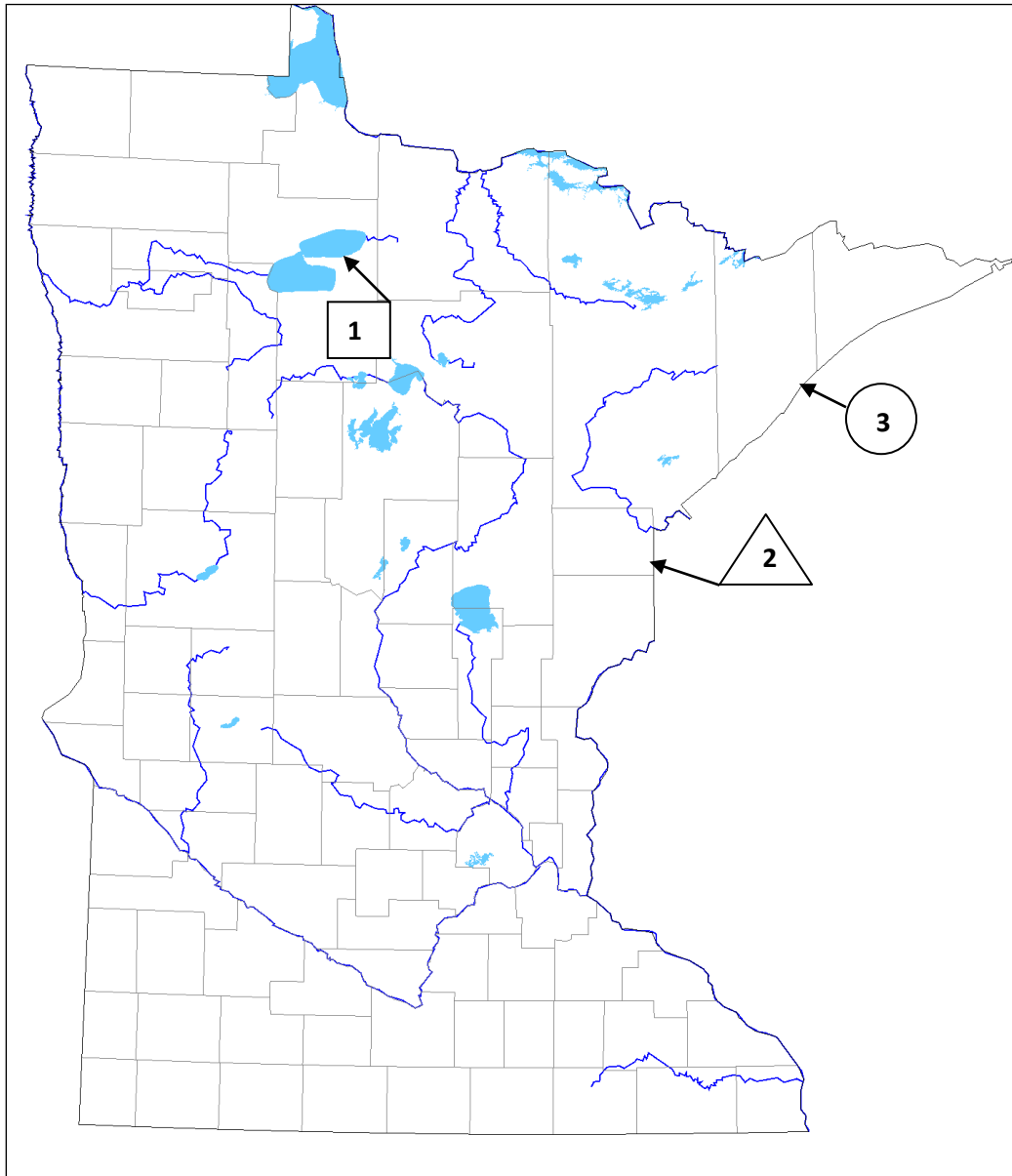


Figure 2.2. Conceptual model of experimental design at each of three study sites. M = mound microsite, P = pit microsite, S = slash microsite. Control and partial harvest areas measure 46 m deep by 183 m wide; buffer areas measure 46 m deep by 61 m wide. Illustration is not to scale.

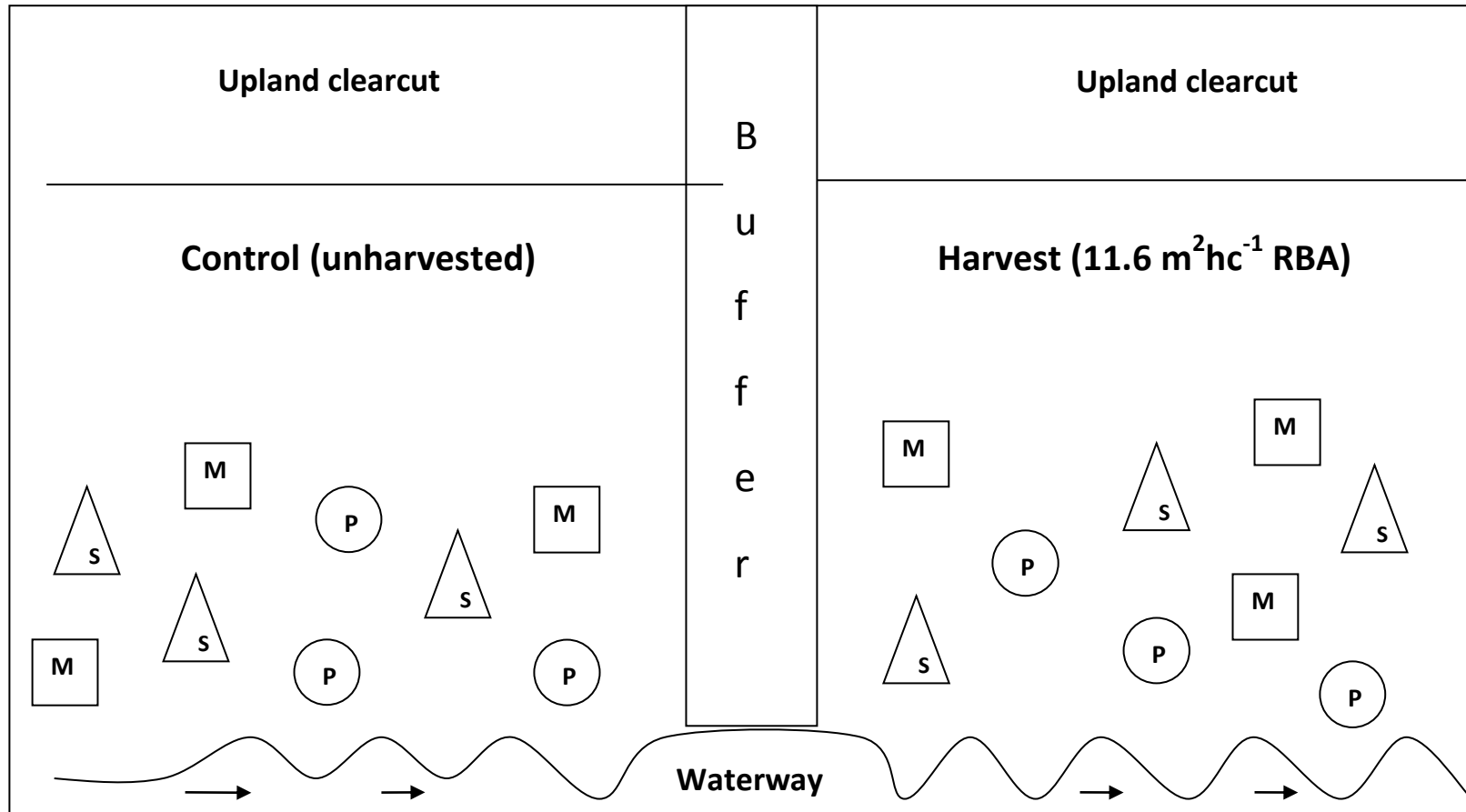


Figure 2.3. Idealized microsite plot with planted seedlings. Squares (Nwc) represent northern white-cedar seedlings, circles (Bf) represent balsam fir seedlings.

Fenced area ~ 3m x 3m

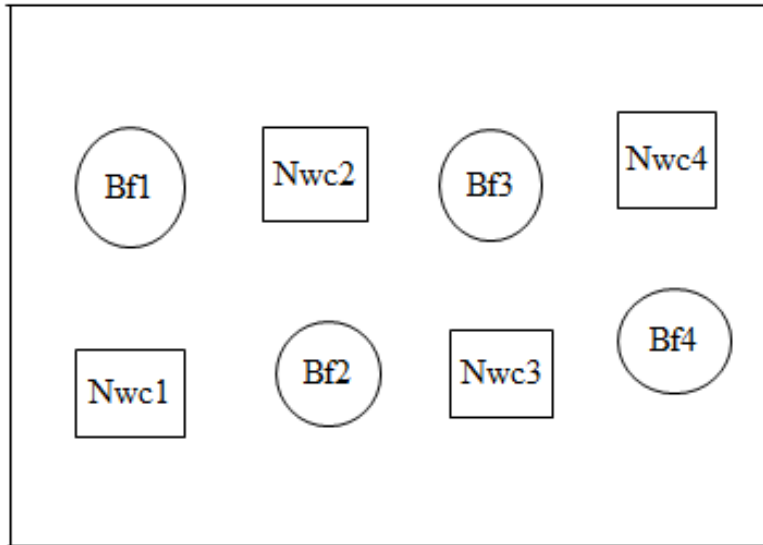
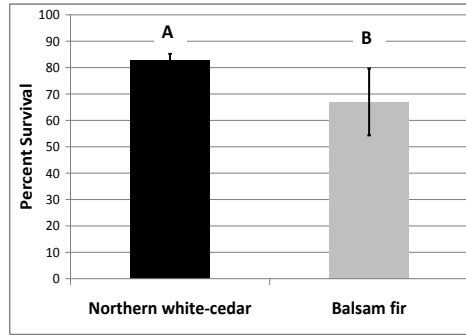
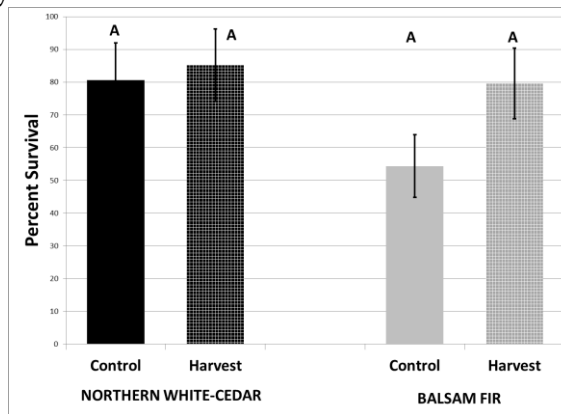


Figure 2.4. Percent survival after four years in the field of northern white-cedar and balsam fir seedlings for (a) species, (b) species x overstory, and (c) species x overstory x microsite interactions. Tukey's HSD test for means was performed between columns; means with the same letter (A,B; a,b) are not significantly different at $\alpha = 0.05$. Column bars show standard errors for $n = 3$.

(a) Species



(b) Species x overstory



(c) Species x overstory x microsite

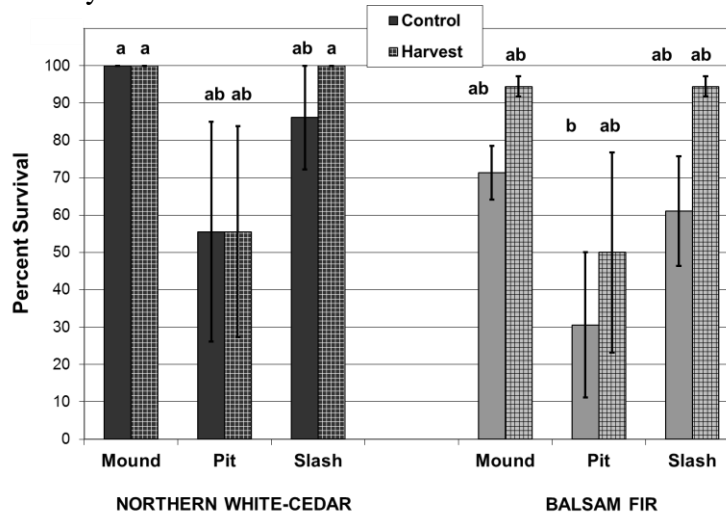
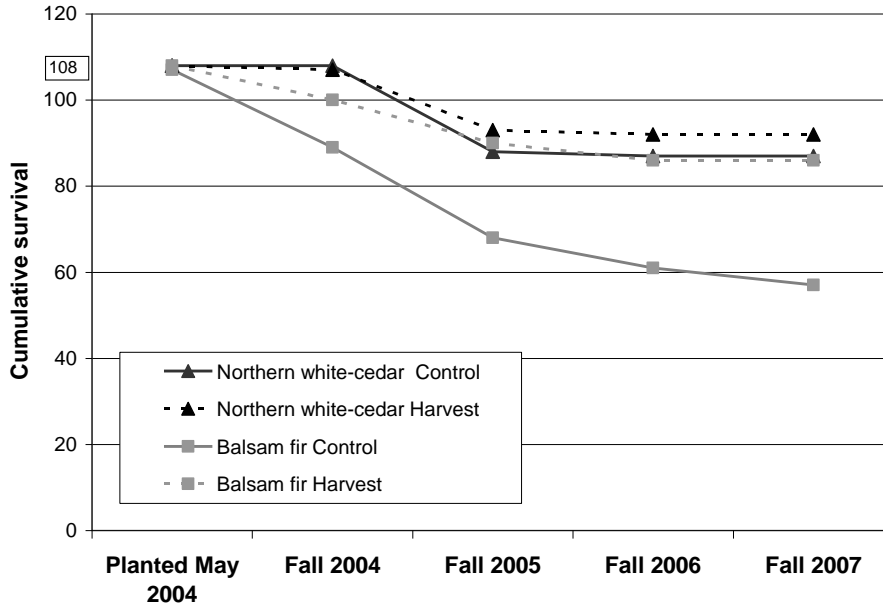


Figure 2.5. Northern white-cedar (NWC) and balsam fir (BF) cumulative annual seedling survival by (a) overstory treatment, beginning n = 108 and (b) microsite treatment, beginning n = 72. The sharp decline in survival for Fall 2005 is due to spring flooding of pits.

(a)



(b)

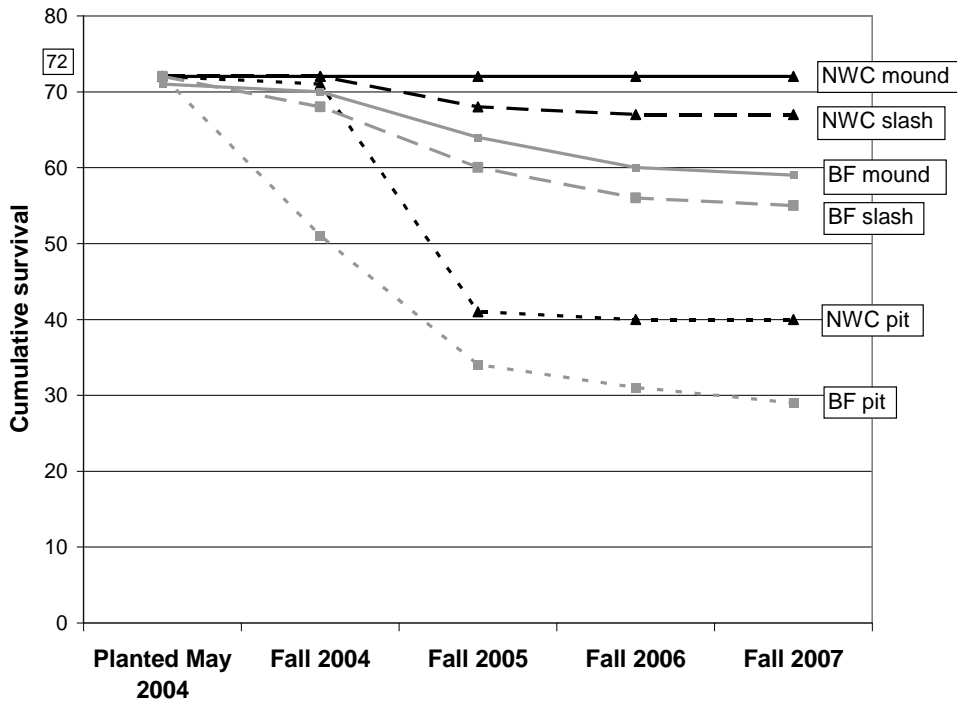
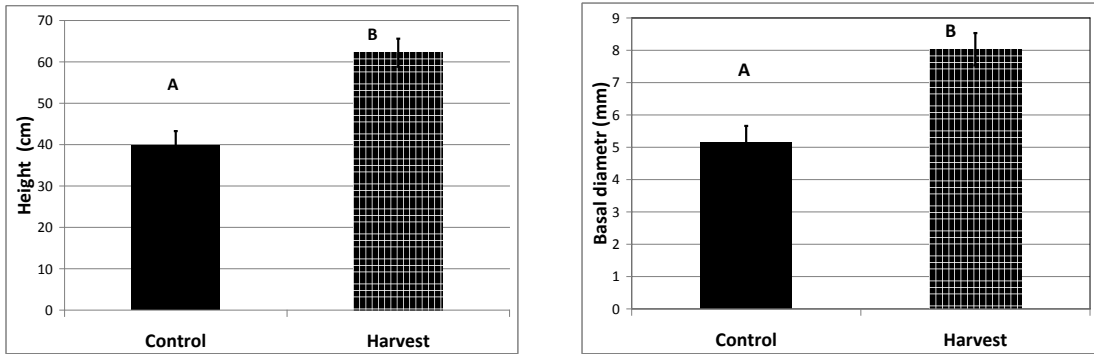
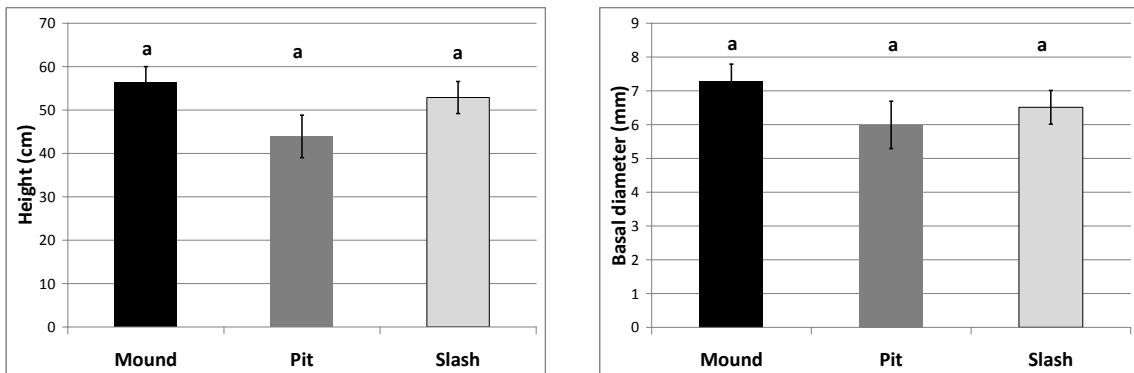


Figure 2.6. Northern white-cedar height and basal diameter after four years in the field for (a) overstory treatment, (b) microsite treatment, and (c) overstory x microsite treatment. Tukey's HSD test for means was performed between columns; means with the same letter (A,B; a,b,c) are not significantly different at $\alpha = 0.05$. Column bars show standard errors for $n = 3$.

(a) Overstory treatment



(b) Microsite treatment



(c) Overstory x microsite treatment

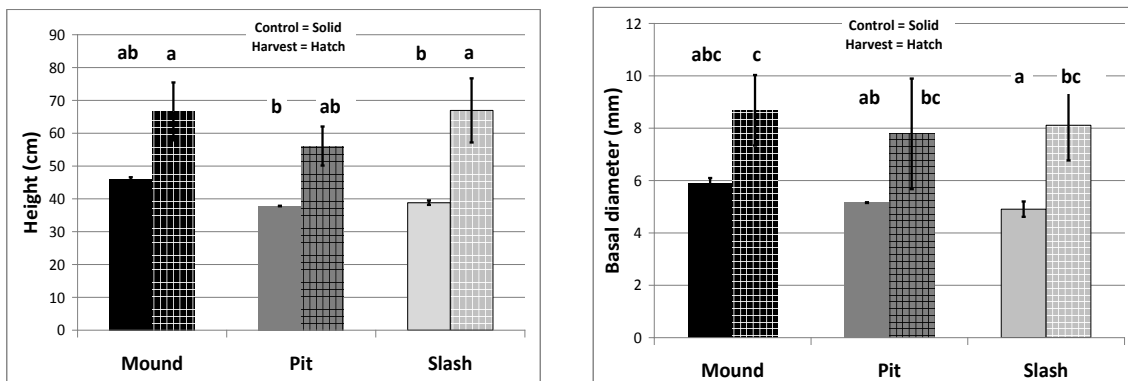
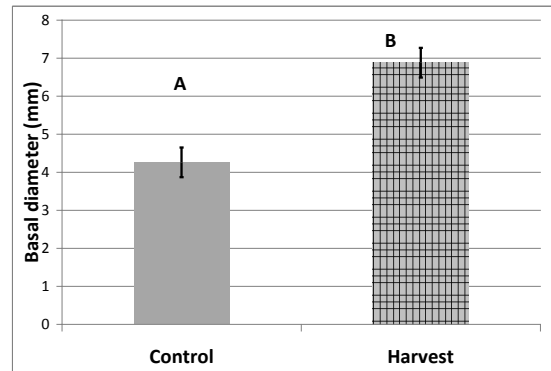
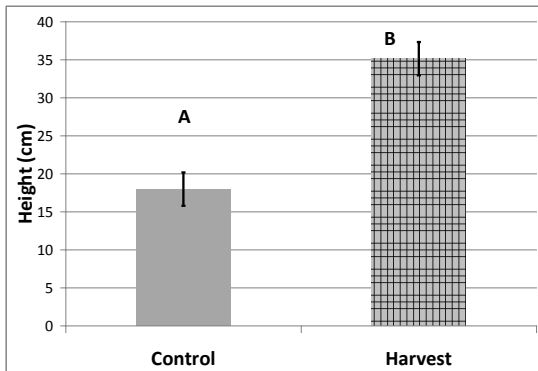
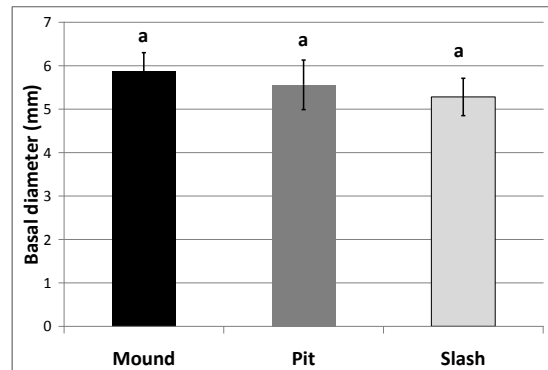
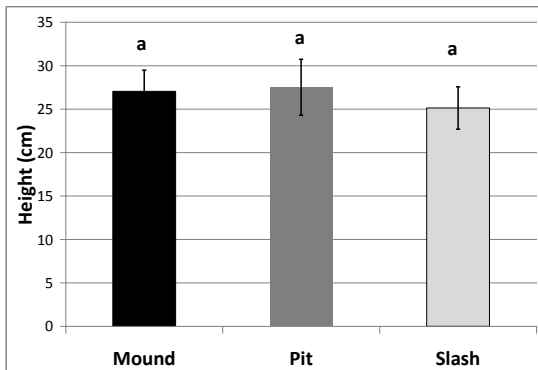


Figure 2.7. Balsam fir height and basal diameter after four years in the field for (a) overstory treatment, (b) microsite treatment, and (c) overstory x microsite treatment. Tukey's HSD test for means was performed between columns; means with the same letter (A,B; a,b,c) are not significantly different at $\alpha = 0.05$. Column bars show standard errors for $n = 3$.

(a) Overstory treatment



(b) Microsite treatment



(c) Overstory treatment x microsite

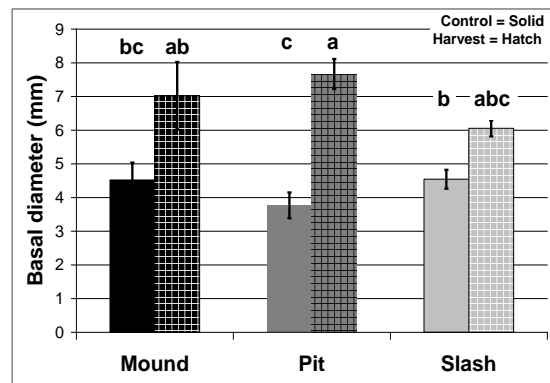
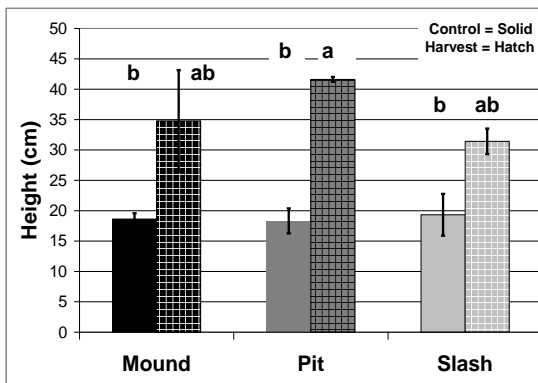


Figure 2.8. Control vs. Harvest comparison after four years in the field of northern white-cedar and balsam fir seedling growth in overstory x microsite interactions for (a) relative height growth and (b) relative diameter growth. Tukey's HSD test for means was performed between columns; means with the same letter (A,B; a,b) are not significantly different ($n = 2$ or 3 , $\alpha = 0.05$).

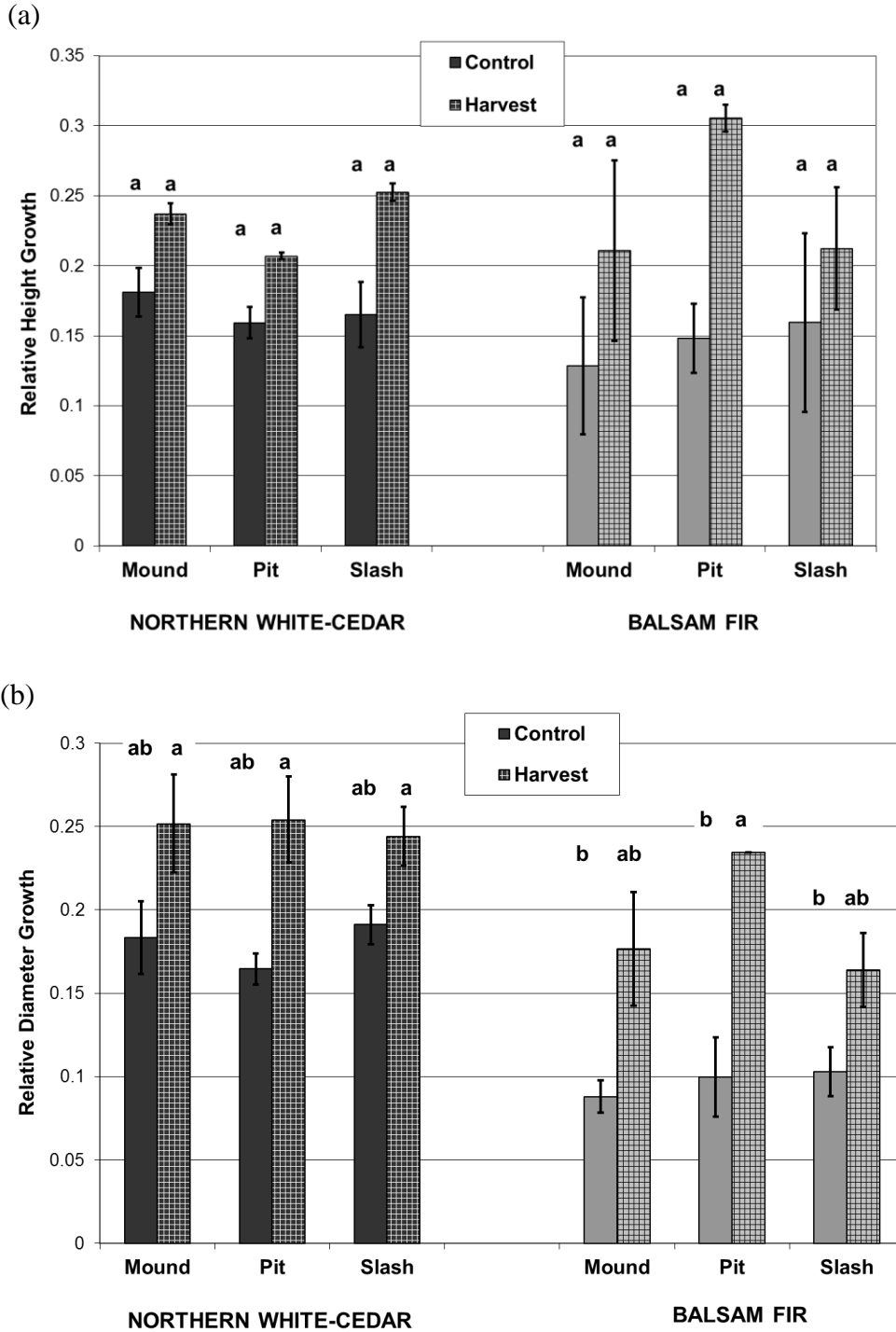


Figure 2.9. Significant correlations ($\alpha = 0.05$, $n = 46$; correlation coefficient is displayed in the upper right corner) of northern white-cedar seedling (a) height and basal diameter and (b) relative height growth and relative diameter growth to basal area. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were negative (data not shown). The inverse square root transformation of basal diameter in (a) and RDG in (b) changes slope direction for the transformed values.

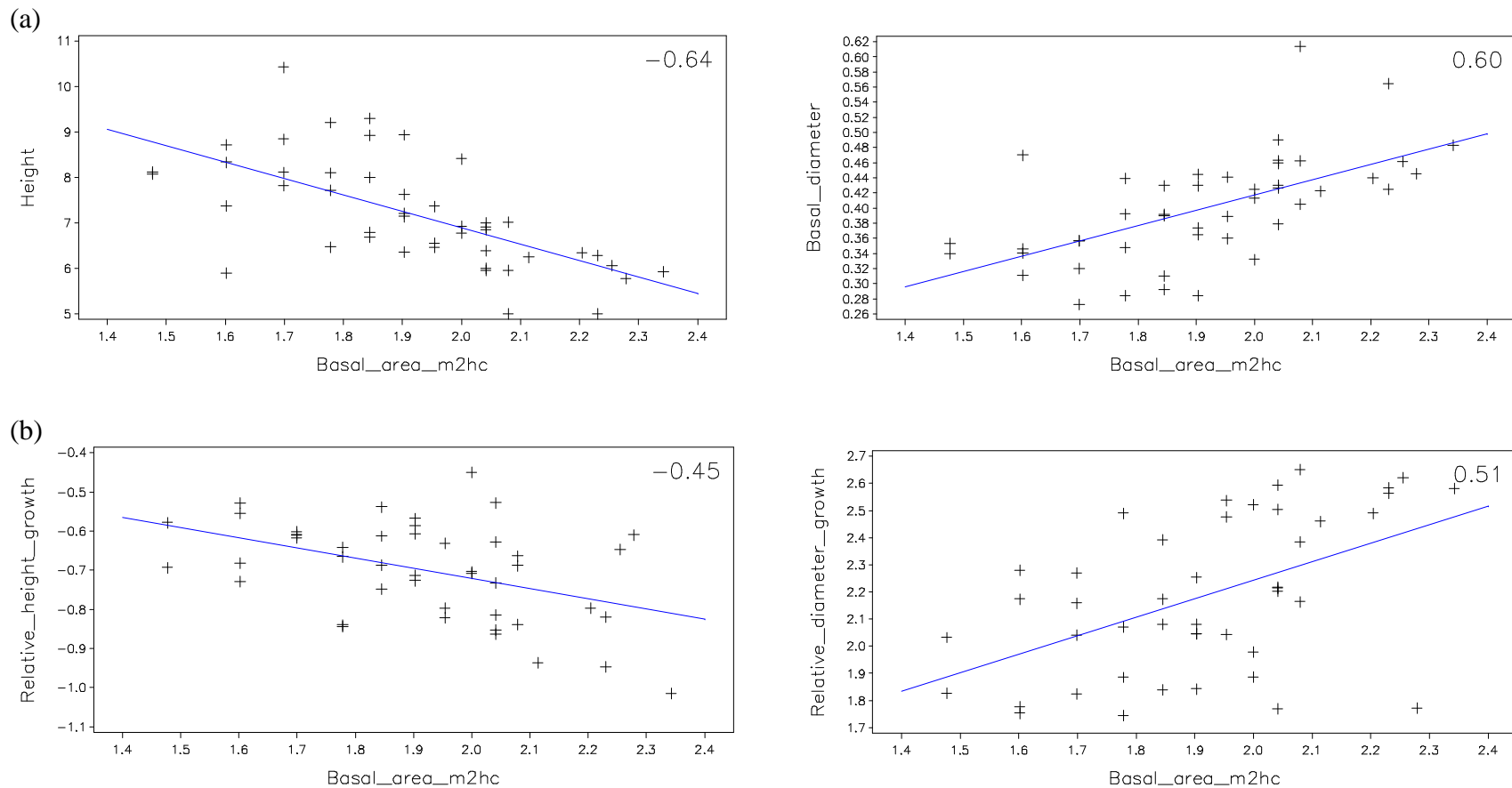


Figure 2.10. Significant correlations ($\alpha = 0.05$, $n = 44$; correlation coefficient is displayed in the upper right corner) of balsam fir seedling (a) height and basal diameter and (b) relative height growth and relative diameter growth to basal area. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were negative (data not shown). The inverse square root transformation of basal diameter in (a) changes slope direction for the transformed values.

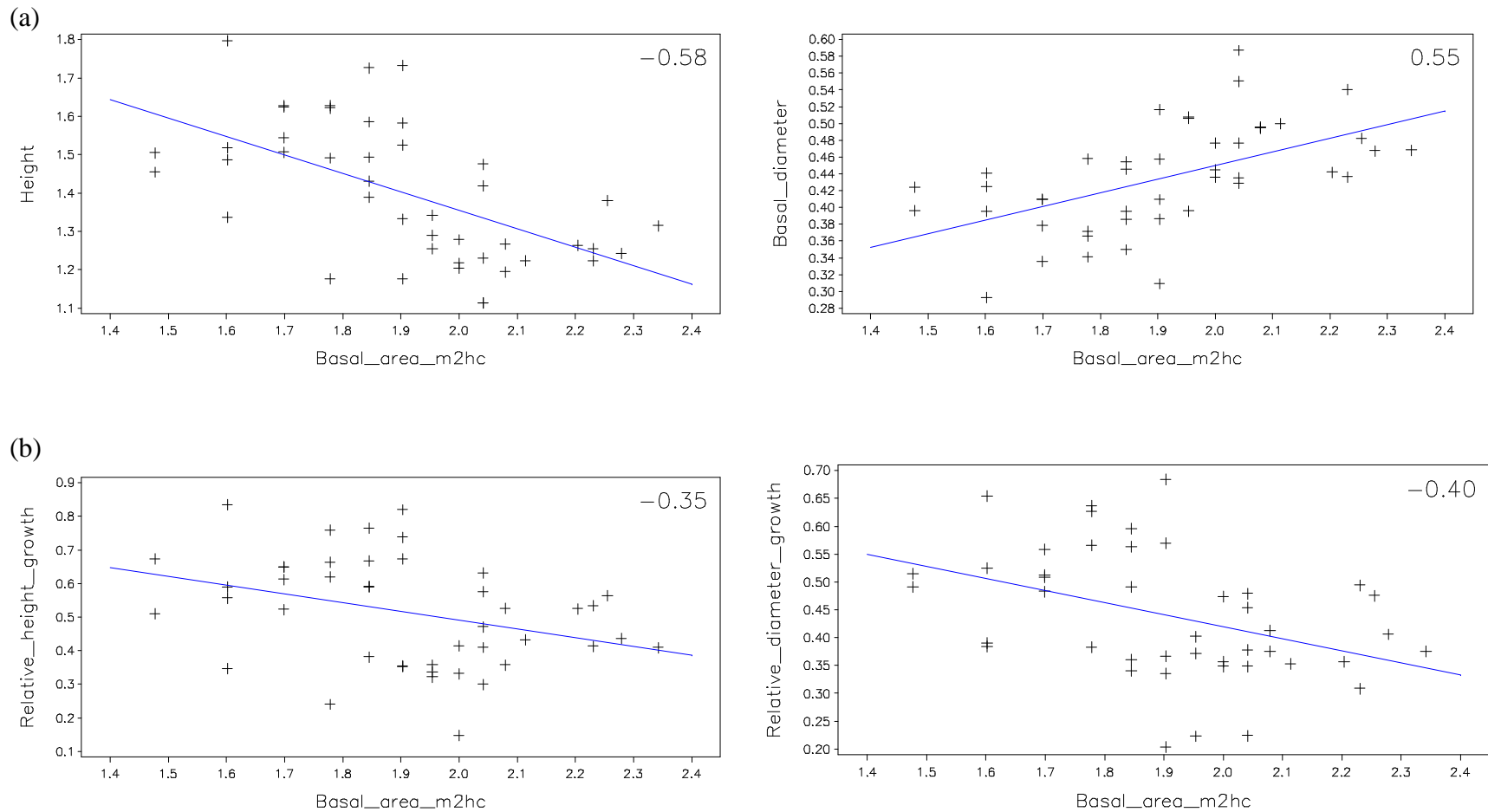


Figure 2.11. Significant correlations ($\alpha = 0.05$, $n = 46$; correlation coefficient is displayed in the upper right corner) of northern white-cedar seedling (a) height and basal diameter and (b) relative height growth and relative diameter growth to percent forest floor. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were negative (data not shown). The inverse square root transformation of basal diameter in (a) and RDG in (b) changes slope direction for the transformed values.

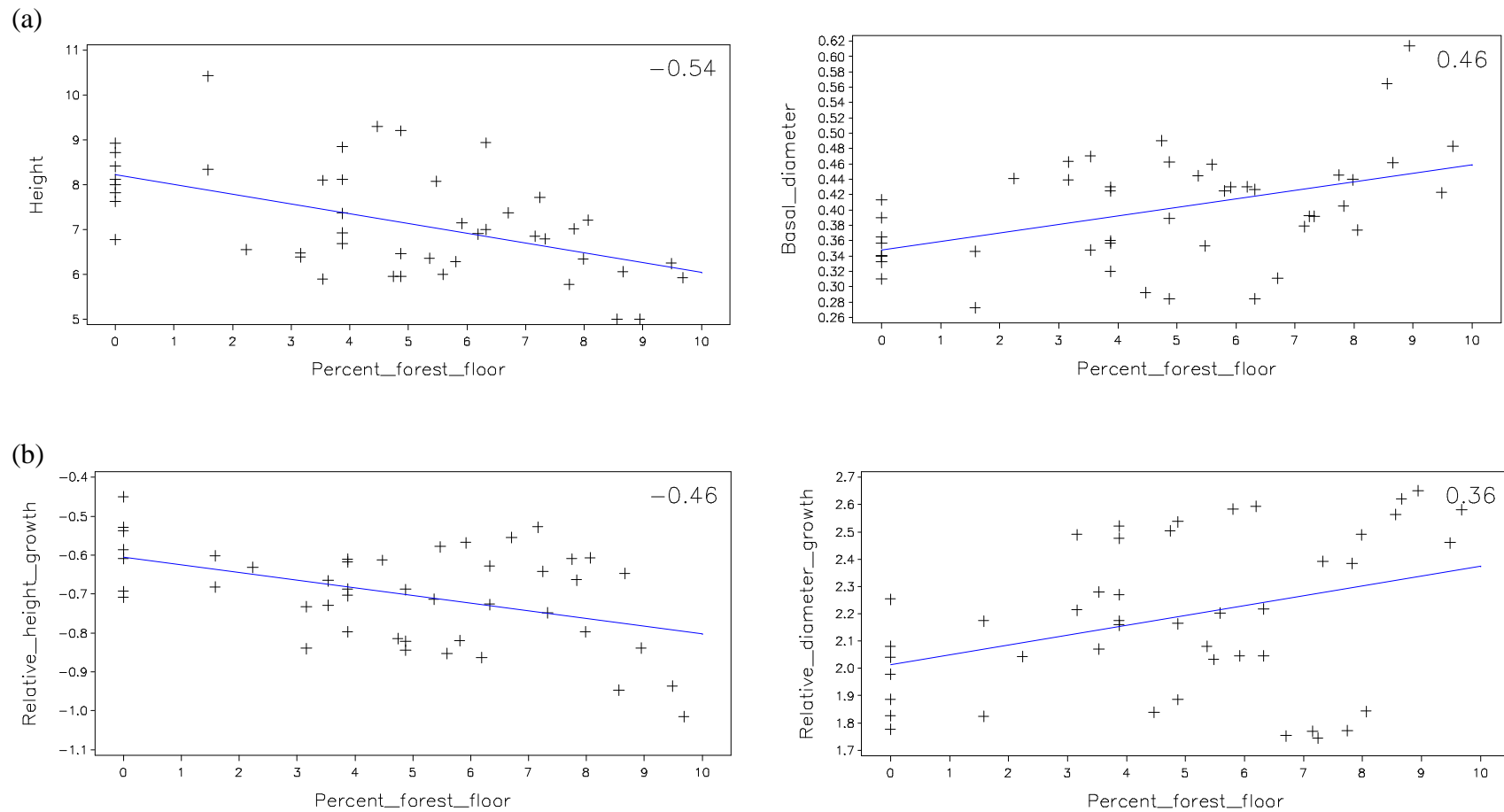


Figure 2.12. Significant correlations ($\alpha = 0.05$, $n = 44$; correlation coefficient is displayed in the upper right corner) of northern white-cedar seedling (a) height and basal diameter and (b) relative height growth to percent herbaceous cover. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were positive (data not shown). The inverse square root transformation of basal diameter in (a) changes slope direction for the transformed values.

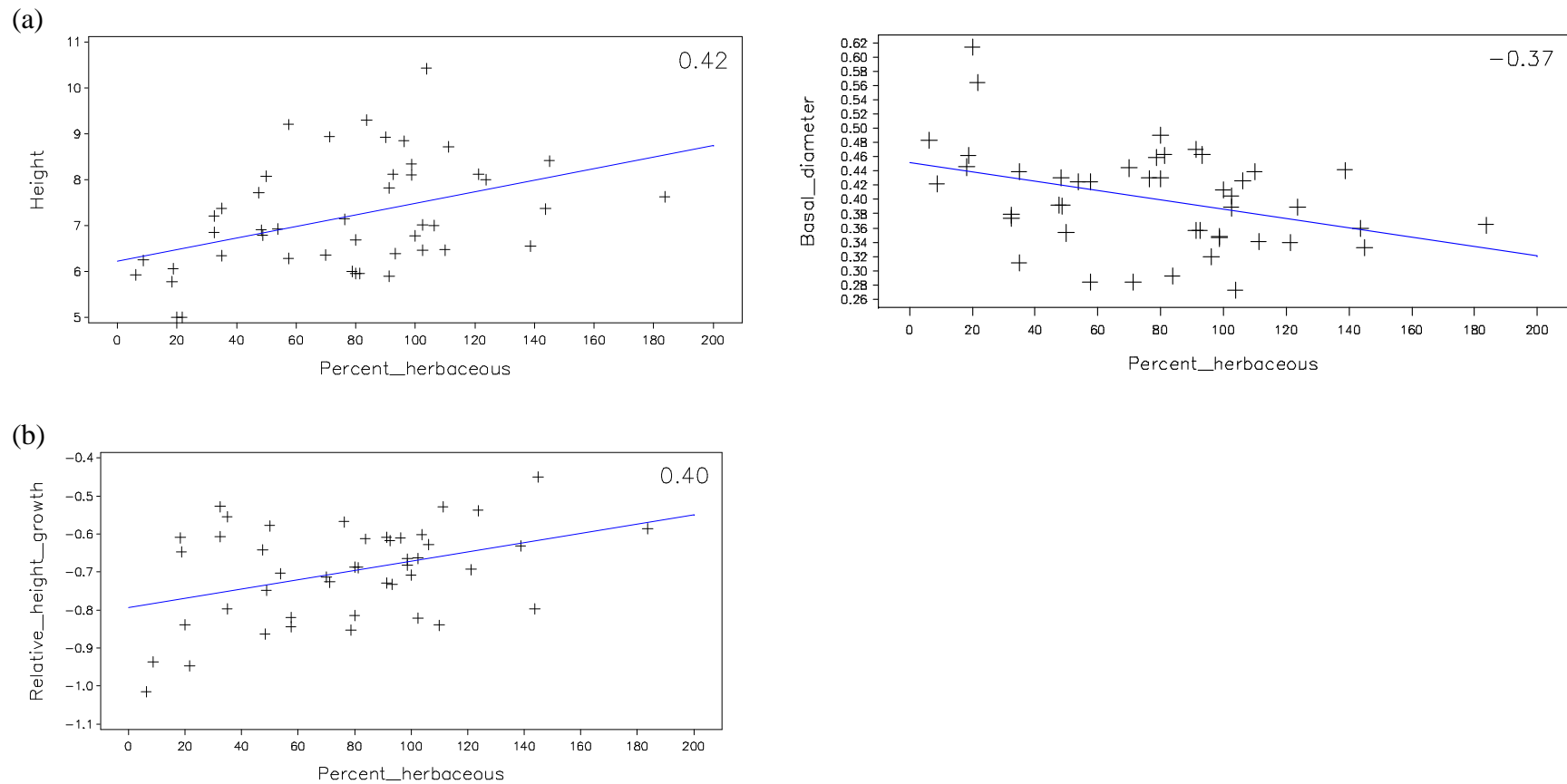


Figure 2.13. Significant correlations ($\alpha = 0.05$, $n = 4$; correlation coefficient is displayed in the upper right corner) of northern white-cedar seedling (a) height and basal diameter and (b) relative diameter growth to percent woody cover. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were positive (data not shown). The inverse square root transformation of basal diameter in (a) and RDG in (b) changes slope direction for the transformed values.

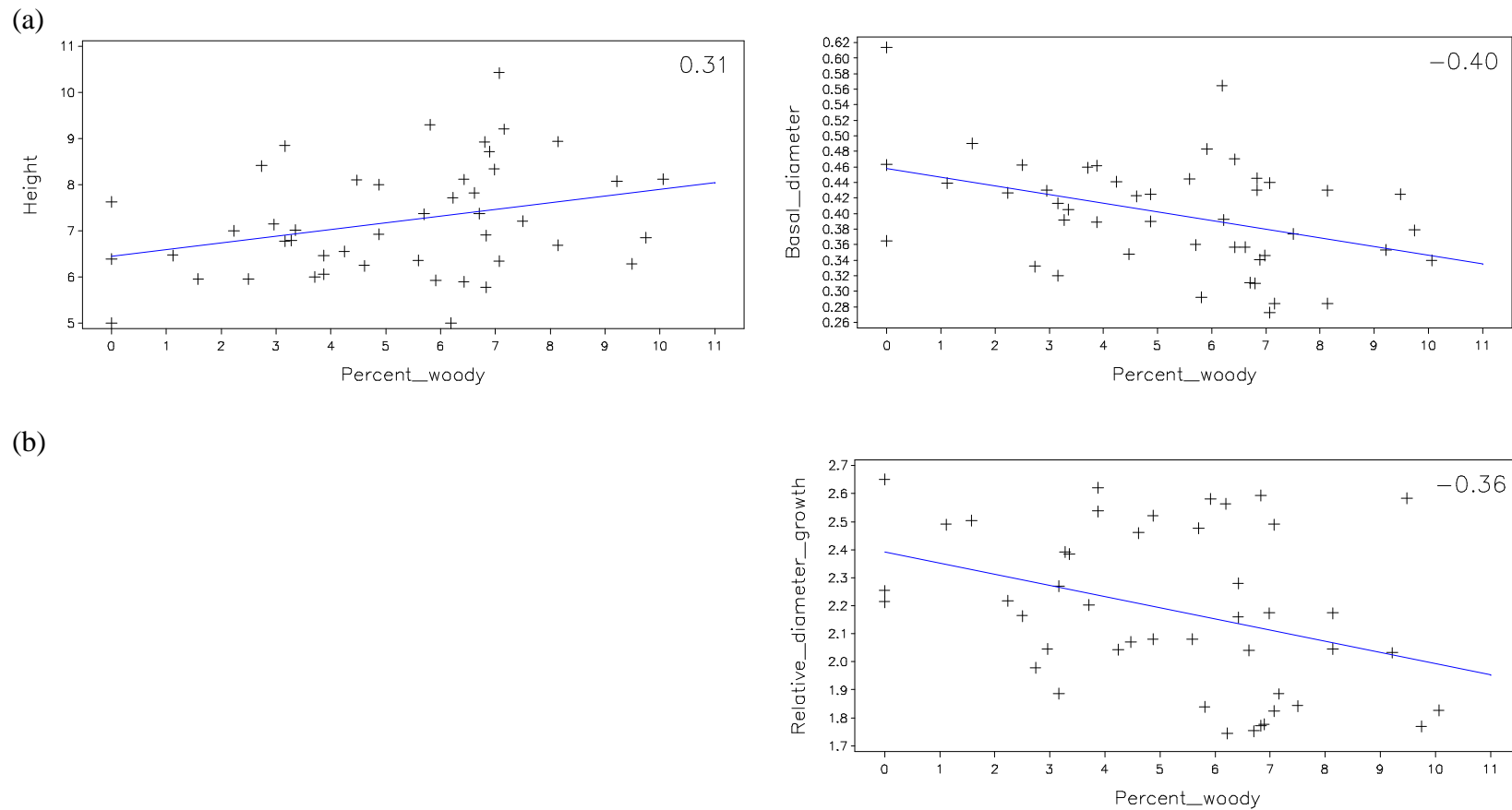


Figure 2.14. Significant correlations ($\alpha = 0.05$, $n = 44$; correlation coefficient is displayed in the upper right corner) of balsam fir seedling (a) height and basal diameter and (b) relative height growth and relative diameter growth to C:N ratio. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were positive (data not shown). The inverse square transformation for C:N ratio changes slope direction for the transformed values. The additional inverse square root transformation of basal diameter in (a) returns the slope to positive.

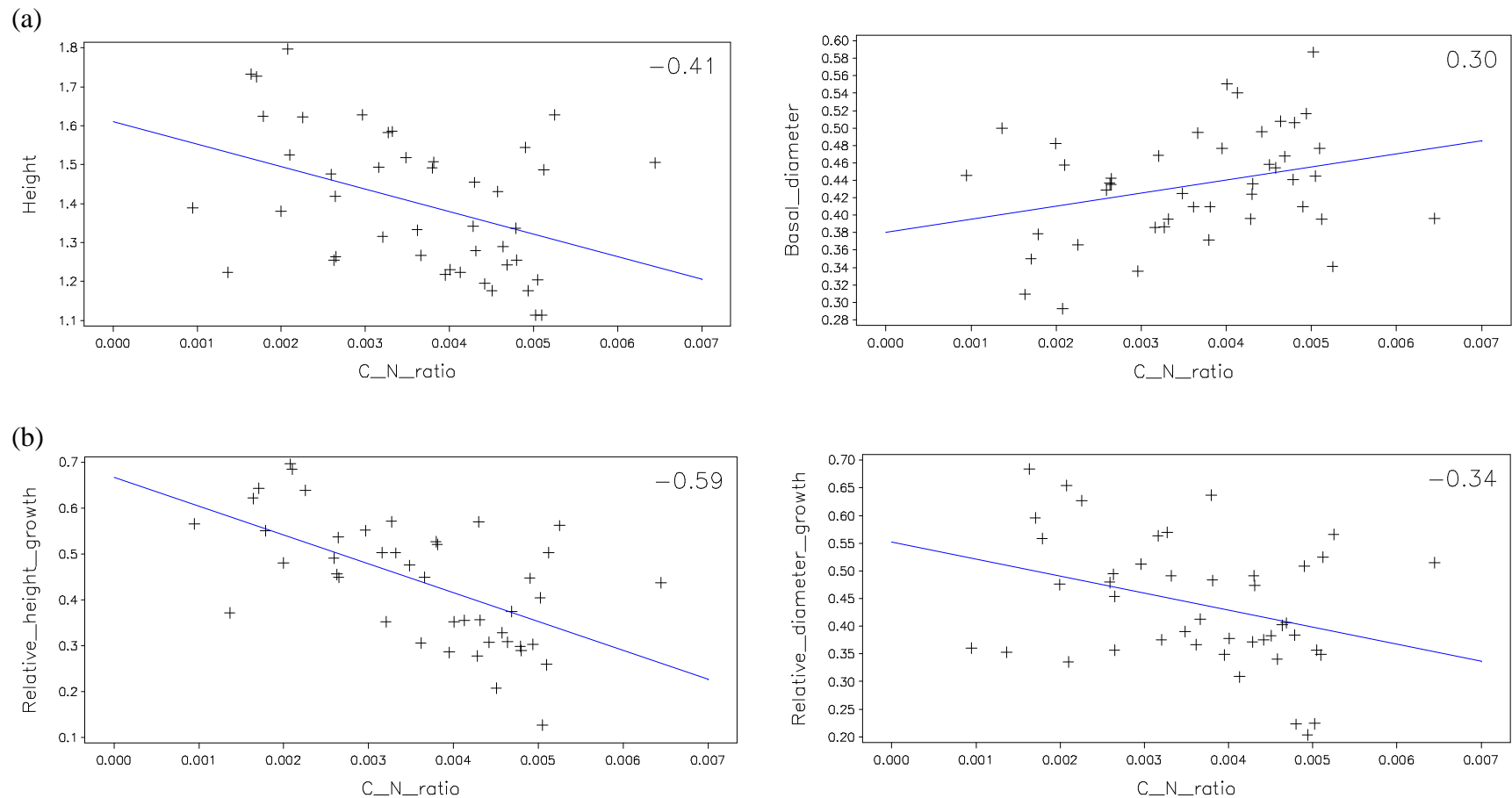


Figure 2.15. Significant correlations ($\alpha = 0.05$, $n = 44$; correlation coefficient is displayed in the upper right corner) of balsam fir seedling (a) height and basal diameter and (b) relative height growth to forest floor depth. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10). Note: All untransformed correlations were positive (data not shown). The inverse square root transformation of basal diameter in (a) changes slope direction for the transformed values.

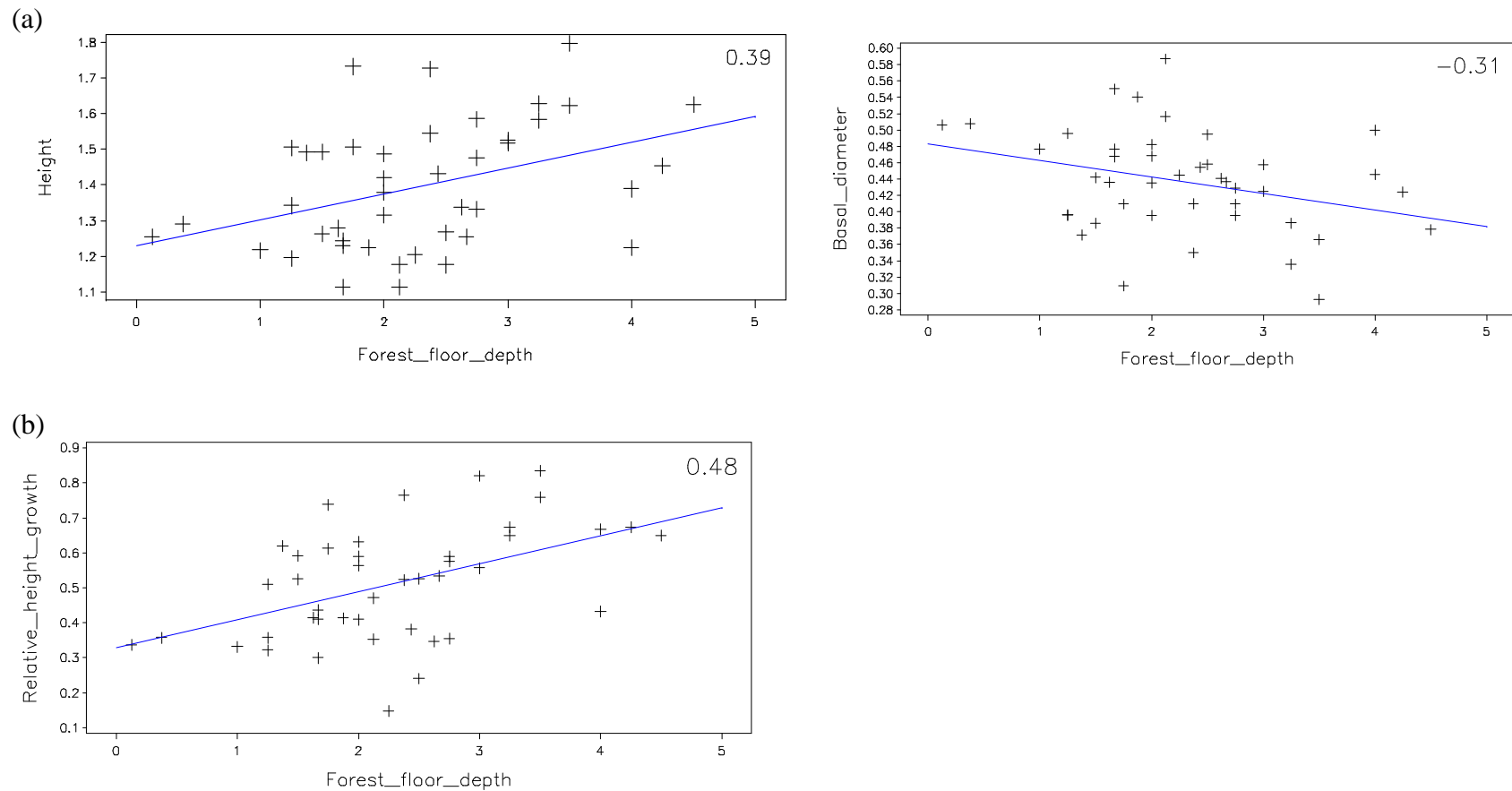
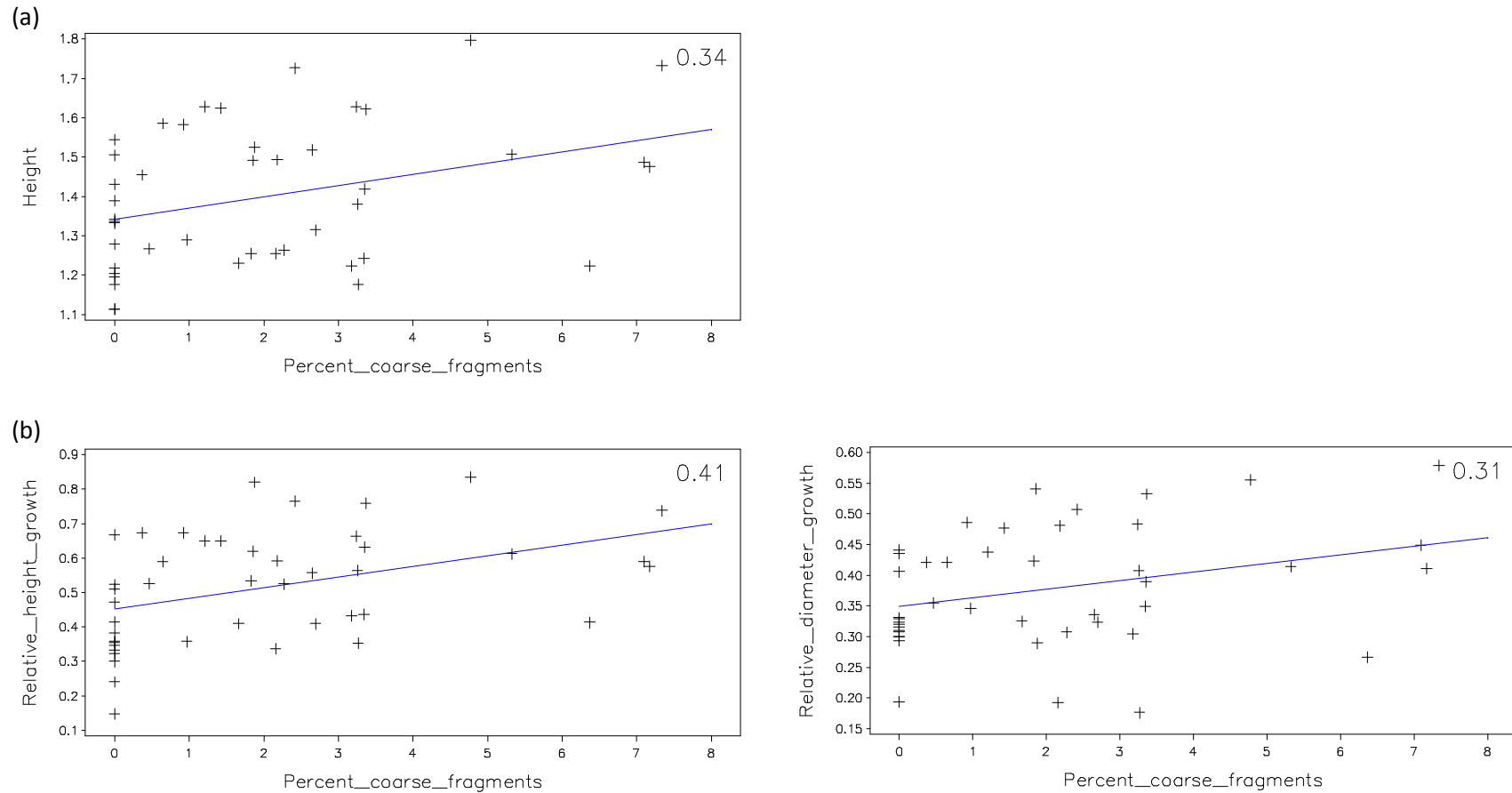


Figure 2.16. Significant correlations ($\alpha = 0.05$, $n = 44$; correlation coefficient is displayed in the upper right corner) of balsam fir seedling (a) height and (b) relative height growth and relative diameter growth to percent coarse fragments. Variables were transformed to meet assumptions of normality and variance (Tables 2.9 and 2.10).



Chapter 2 Bibliography

- Amacher, M. C., K. P. O'Neill, R. Dresbach, and C. Palmer. Forest Inventory & Analysis Manual of Soil Analysis Methods [Internet]. USDA Forest Service; 2003 [cited July 2010]. Available from: <http://nrs.fs.fed.us/fia/topics/soils/documents/FIA.P3.Soils.Lab.Manual.2003.pdf>.
- Boelter, D. H. and G. E. Close. 1974. Pipelines in forested wetlands. *Journal of Forestry* September:561-63.
- Chimner, R. A., and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Canadian Journal of Forest Research* 26:389-93.
- Clinton, B. D., and C. R. Baker. 2000. Catastrophic windthrow in the southern Appalachians: Characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management* 126(1):51-60.
- Cornett, M. W. "Conifer regeneration in mixed deciduous-evergreen forests." MS thesis, University of Minnesota, 1996.
- Cornett, M. W., P. B. Reich, and K. J. Puettmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* 4(3):353-64.
- Cornett, M. W., K. J. Puettmann, and P. B. Reich. 1998. Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. *Canadian Journal of Forest Research* 28:196-205.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000a. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000b. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. *American Journal of Botany* 87(12):1807-14.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology* 9(4):386-96.
- Davis, A., K. Puettmann, and D. Perala. 1998. *Site preparation treatments and browse protection affect establishment and growth of northern white-cedar*. Research Paper NC-330. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.

- DeLong, H. B., V. J. Lieffers, and P. V. Blenis. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27:1452-57.
- Dovčiak, M., P. B. Reich, and L. E. Frelich. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. *Canadian Journal of Forest Research* 33:1892-1904.
- Fisher, R. F., and D. Binkley. 2001. *Ecology and Management of Forest Soils*, 3rd ed. New York, NY: John Wiley & Sons, Inc.
- Forester, J. D., D. P. Anderson, and M. G. Turner. 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *American Midland Naturalist* 160:438-53.
- Fraver, S., R. G. Wagner, and M. Day. 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.
- Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, G. Johnson, and S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental Reviews* 4:238-65.
- Harper, J. L. 1977. *Population biology of plants*. San Diego, CA: Academic Press Inc., 892 p.
- Harrington, T. B., and A. A. Bluhm. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. *Forest Ecology and Management* 140:265-75.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-82.
- Heitzman, E., K. S. Pregitzer, and R. O. Miller. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Canadian Journal of Forest Research* 27:1953-61.
- Heitzman, E., K. S. Pregitzer, R. O. Miller, M. Lanasa, and M. Zuidema. 1999. Establishment and development of northern white-cedar following strip clear cutting. *Forest Ecology and Management* 123:97-104.
- Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009a. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.

Hofmeyer, P. V., R. S. Seymour, and L. S. Kenefic. 2009b. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. *Northern Journal of Applied Forestry* 26(2):68-75.

Johnston, W. F. 1972. *Balsam fir dominant species under rethinned northern white-cedar*. Research Note NC-133. St. Paul, MN: USDA Forest Service, North Central Forest Experiment station.

Johnston, W. F. 1977. *Manager's handbook for northern white cedar in the North Central States*. General Technical Report NC-35. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.

Johnston, W. F. 1990. *Thuja occidentalis* L. Northern White-Cedar. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.

Kastendick, D. N. "Riparian forest management in northern Minnesota: effects of riparian silvicultural treatments on forest biomass, structure, composition, and indices of plant available nutrients." MS thesis, University of Minnesota, 2005.

Kneeshaw, D. D., and Y. Bergeron. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79(3):783-94.

Larouche, C., L. S Kenefic, and J.-C. Ruel. 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, C., J.-C. Ruel, J.-M. Lussier, and L. Kenefic. 2006. Regeneration of *Thuja occidentalis* L. in mixedwood stands on mesic sites after partial cuts in Quebec. In: Larocque, G.R., M. Fortin, and N. Thiffault, editors: Conference handbook, 2nd ed. Forest Science across the Borders - Conference of the Eastern CANUSA; Oct. 19-21, 2006; Quebec City, Quebec, Canada. 90-94.

Logan, K. T. 1969. *Growth of tree seedlings as affected by light intensity: IV. Black spruce, white spruce, balsam fir and eastern white cedar*. Publication No.1256. Canadian Forestry Service Department of Fisheries and Forestry.

Miller, R. O. 1990. Ecology and management of northern white-cedar. In Proceedings of *Regenerating conifer cover in deer yards workshop*, 1-13. North Bay, Ontario.

Miller, R. O., M. Lanasa, D. Elsing, and M. Zuida. 1990. Northern white-cedar: stand assessment and management options. In Proceedings of *Northern white-cedar in Michigan Workshop*, 1-6. Sault Ste. Marie, MI.

Minnesota Department of Natural Resources. 2010. Minnesota's Forest Resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.

Minnesota Forest Resources Council. 2005. *Sustaining Minnesota Forest Resources: Voluntary Site-level Forest Management Guidelines for Landowners, Loggers and Resource Managers*. St. Paul, MN: Minnesota Forest Resources Council.

MNMapper [Internet]. St. Paul, MN: Department of Administration, Office of Geographical and Demographic Analysis, Land Management Information Center; [created 2009 Jul 15] Available from: www.lmic.state.mn.us/chouse.

Nelson, T. C. 1951. A reproduction study of northern white cedar. Game Division, Michigan Department of Conservation.

Nyland, R. D. 2002. *Silviculture: Concepts and Applications*, 2nd edition. New York: McGraw-Hill.

Peterson, C. J., and S. T. A. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76(3):763-74.

Pregitzer, K. S. 1990. The ecology of northern white-cedar. In *Proceedings of Northern white cedar in Michigan*, ed. D. O. Lantagne, 8-14. Research Report 512. East Lansing, MI: Michigan Agricultural Experiment Station.

Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanderklein, and C. Buschena. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* 12:327-38.

RMZ Harvest [Internet]. [updated 2008 Jul 27]. St. Paul, MN: University of Minnesota, College of Food, Agriculture and Natural Resource Sciences; [cited 2009 Jul 14]. Available from: <http://rmzharvest.cfans.umn.edu/>.

Rooney, T.P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181(1):165-76.

Roy, V., J-C. Ruel, and A. P. Plamondon. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management* 129:253-67.

SAS Institute Inc. 2003. SAS/STAT® User's Guide Version 9.1.3. Cary, NC: SAS Institute Inc.

- Schaffer, W. W. 1996. *Silvicultural guidelines for the eastern white cedar*. Technical Report TR-006, Ontario: Ontario Ministry of Natural Resources, Southern Region Science & Technology Transfer Unit.
- Scott, M. L., and P.G. Murphy. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *American Midland Naturalist* 117(1):10-16.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *Journal of Vegetation Science* 9(4):575-82.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. *Canadian Journal of Forest Research* 33:672-81.
- St. Hilaire, L. R., and D. J. Leopold. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. 1995. *Canadian Journal of Forest Research* 25:261-69.
- Stoeckeler, J. H. 1967. *Wetland road crossings: drainage problems and timber damage*. Research Note NC-27. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station. 4p.
- Verme, L. J. 1965. Swamp conifer deeryards in northern Michigan: their ecology and management. *Journal of Forestry* 63(7):523-29.
- Verme, L. J., and W. F. Johnston. 1986. Regeneration of northern white cedar deeryards in upper Michigan. *The Journal of Wildlife Management* 50(2):307-13.
- Webb, S. L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. *Canadian Journal of Forest Research* 18:1186-95.
- Weiskittel, A. R., J. A. Kershaw Jr., P. V. Hofmeyer, and R. S. Seymour. 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* 258:1695-1703.
- Weiskittel, A. R., R. S. Seymour, P. V. Hofmeyer, and J. A. Kershaw Jr. 2010. *Forest Ecology and Management* 259:1912-21.

Chapter 3

Deer Browse Effects on *Thuja occidentalis* and *Abies balsamea* Seedlings in Riparian Harvest Areas within Northern Minnesota

Chapter 3 Synopsis

Northern white-cedar (*Thuja occidentalis* L.), a long-lived conifer found within riparian forests of northeastern North America, is an important species to riparian ecosystem health and the forest products industry. Balsam fir (*Abies balsamea* (L.) Mill.) is a frequent cohort in mixed sub-boreal forests, where differing growth strategies allow both species to co-exist. Northern white-cedar is currently experiencing recruitment decline throughout much of its natural range, due primarily to herbivory by white-tailed deer (*Odocoileus virginianus*) that remove the seedling and sapling size classes. Due to preferential browse on northern white-cedar, balsam fir frequently recruits more successfully into overstory dominance. This study examines the changing interactions between these two species under the influence of herbivory. An understanding of the historical interaction is appropriate because of recent emphasis on ecosystem-based management practices that mimic natural patterns. However, management today is subject to current conditions, and herbivory presents a major barrier to the management of northern white-cedar.

A four -year study, conducted on riparian partial harvest sites located in northern Minnesota, USA, used planted 3-0 seedlings to (1) more fully understand the current dynamic between northern white-cedar and balsam fir seedlings in the presence of white-tailed deer and (2) examine partial harvest and forest floor microsite positions that might encourage northern white-cedar seedlings in the presence of deer. Fenced seedlings of both species demonstrated positive growth trends in partially harvested areas and strong potential to recruit into taller height classes. Unfenced northern white-cedar showed significant mortality and no height increase in treatments, with browse on seedlings

overwhelming the benefits of partial overstory harvests. However, seedlings demonstrated continued allocation to basal diameter growth due to their ability to re-grow browsed vegetation in the current year, as well as survival resiliency for at least four years subjected to herbivory. Balsam fir seedlings, while reduced significantly by browse, maintained growth responses to partial harvesting and showed the potential to recruit more successfully into the overstory. Species' dissimilar growth habits and architectural forms account for their different responses to browse, with northern white-cedar demonstrating greater resiliency. Recommendations to reduce herbivory on northern white-cedar seedlings are (1) increase the residual basal area of partial harvest areas to reduce woody regeneration and limit available browse; (2) alternatively, plant northern white-cedar in non-harvested areas that are less frequented by deer.

Key words: northern white-cedar, balsam fir, herbivory, browse frequency, riparian, seedling recruitment, partial overstory harvest,

Introduction

Beginning in the 1940s, forest managers across the range of northern white-cedar began to see a lack of advance regeneration and overstory recruitment. The absence of all sapling size classes from forest stands demonstrated a consistent lack of recruitment and ingrowth (Rooney et al. 2002; Forester et al. 2008). Observations of northern white-cedar stands have indicated that neither low seed production and nor low germination rates were causes of recruitment decline (Heitzman et al. 1997; Cornett et al. 2000; Forester et al. 2008). Various factors have been implicated including fire (Heinselman 1973), road construction (Stoekler 1967; Boelter and Close 1974), and loss of regeneration niches (Chimner and Hart 1996; Simard et al. 1998; Cornett et al. 2001). Slow growth rates and the ability to survive suppression for many years contribute to a delay in recruitment, which may allow species with faster growth rates to gain overstory dominance (Larouche et al. 2010). For example, balsam fir (*Abies balsamea* (L.) Mill.), a tolerant companion species of northern white-cedar in mixed forests where differing growth strategies allow them to co-exist, is reported to be capable of recruiting more successfully into the overstory under low light conditions (Johnston 1986; Schaffer 1996; Heitzman et al. 1997; Davis et al. 1998; Hofmeyer et al. 2009).

However, the foremost cause of northern white-cedar recruitment failure is herbivory from white-tailed deer (*Odocoileus virginianus*) (Alverson et al. 1988; Pregitzer 1990; Heitzman et al. 1997; Forester et al. 2008; Hofmeyer et al. 2009). Northern white-cedar foliage is the preferred winter browse for deer that exert heavy feeding pressure on all stages of tree growth. Herbivory on established seedlings and saplings serves as a major suppressor and allows less-browsed species to gain a competitive edge. Most often

cited as the species that benefits from preferential browse on northern white-cedar is balsam fir (Chimner and Hart 1996; Schaffer 1996; Van Deelen et al. 1996; Cornett et al. 2000; Davis et al. 1998; Hofmeyer et al. 2009). Other species that can benefit are white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marsh.).

Northern white-cedar introduction

Northern white-cedar (*Thuja occidentalis* L.) is a long-lived shade tolerant conifer of boreal forests. The natural range of northern white-cedar (approximately 97° W to 63°W longitude, 52°N to 43°N latitude) extends across Canada from southeastern Manitoba to the Atlantic Ocean, south into the U.S. states of Minnesota, Wisconsin, Michigan, and Maine, and occasionally appearing south to western North Carolina (Johnston 1990). Its range in Minnesota covers the northeast third of the state in what is known as the Laurentian Mixed Forest Province (MN DNR 2003). Separate populations of northern white-cedar occur in both riparian and upland forest settings, though the most common occurrence is in moist nutrient-rich sites near waterways. Here it provides ecological benefits to lake and river shore stability, water quality, and wildlife habitat. Contributions to the wood products industry include cabin logs, siding, and paneling (Johnston 1990).

Prior to European settlement in the 1800s, much of northern Minnesota forests were dominated by conifers, with disturbance-moderated patches of hardwoods (Cole 1987; Cornett 2000). Northern white-cedar comprised approximately 8% of the area covered by Minnesota's forests (Cornett 2000). Settlement brought timber harvests,

wildfires, and land development, which converted extensive conifer forests to second growth hardwoods and agricultural lands. Along with other northern conifers, northern white-cedar forest cover has declined in northern Minnesota. The northern white-cedar forest type occupies approximately 4% of Minnesota's forests today (MN DNR 2010). The majority of occurrence in Minnesota is riparian, where it occupies 8% of riparian shorelines or roughly 69, 810 hectares (172,500 acres) (MFRC 2010).

Northern white-cedar and herbivory

The white-tailed deer is a browsing ungulate of prairies and transition forests edges. The historic range of deer in Minnesota was primarily southern and central, as northern conifer forests did not offer hospitable habitat (Grigal and Ohmann 1975; Cole 1987; Cornett et al. 2000). However, land use changes that established early successional woodlands and agricultural fields provided an abundance of forage and cover for expanding deer populations (Waller and Alverson 1997; Rooney and Waller 2003; Côté et al. 2004). Removal of natural predators and initiation of modern hunting regulations in the 20th century have contributed to the increase in range and population of white-tailed deer until they now overlap the historical range of northern white-cedar (Van Deelen et al. 1996; Russell et al. 2001).

Ungulate diet varies seasonally as available plant material changes. During the summer growth season, deer prefer herbaceous and new shrubs found in open fields and along forest edges (Smith et al. 2007; Forester et al. 2008). The winter diet of deer consists primarily of the terminal ends of deciduous twigs, supplemented with arboreal lichens, forest floor litter, and conifer browse. Winter survival strategy of deer often

entails congregating in conifer stands that provide food and shelter, allowing them to conserve energy (St-Louis et al. 2000).

Beginning in the 1930s, forests were frequently managed for deer habitat. Even-aged conifer stands provided winter deer cover; timber harvests created early successional gaps with woody and herbaceous browse (Waller and Alverson 1997). Northern white-cedar deer yards were valued for their ability to provide both. However, in the ensuing decades deer populations have grown to exceed the carrying capacity of northern white-cedar deer yards. All vegetation is removed annually up to the height accessible to deer, while seedling and sapling height classes are heavily browsed. In a Wisconsin study, Forester et al. (2008) reported that the percentage of northern white-cedar seedlings and saplings browsed increased with increasing stem size. Also, small seedlings (< 7.5 cm) were the most abundant, with large saplings (> 100 cm) almost absent. This has the twofold effect of using up available forage while removing advance regeneration of northern white-cedar.

Study description

Many studies identify the loss of advance regeneration as a critical link in the presence of the northern white-cedar forest component. It is important to know more about this life stage and to examine management practices that will encourage abundance, allowing the species to compete effectively in today's managed forests. Additional study regarding the potential benefits of overstory harvests and forest floor microsites to seedling growth in deer-populated landscapes could further inform management practices.

A related study in riparian forests (Haworth 2011) examined the effects of partial overstory harvest and three microsite features (mounds, pits, and slash) on survival and growth of planted 3-0 seedlings of northern white-cedar and balsam fir in fenced deer exclosures. That study gave insight into management treatments in riparian forests that may contribute to the success of planted northern white-cedar and compared responses between the potentially competitive species of balsam fir. Results from four growing seasons in the field indicated that seedlings of both species responded similarly, with height and basal diameter increases to partial overstory harvest treatments. Further, in the absence of deer browse, balsam fir did not show a competitive advantage over northern white-cedar for up to 6.5 years from seed under any treatments.

The study reported here investigated the effects of partial overstory harvest and microsite on planted seedlings of northern white-cedar and balsam fir subjected to deer browse. Our questions were (1) how do partial harvest and microsite treatments affect the survival and growth of northern white-cedar and balsam fir seedlings in the presence of deer? and (2) how does herbivory affect the competitive relationship between northern white-cedar and balsam fir seedlings?

Materials and Methods

Site locations and characteristics

This study was conducted in the Laurentian Mixed Forest Province of northeastern Minnesota, which is characterized by mixed hardwood and conifer forests, peatlands, and lakes (MN DNR 2003). Underlying geology of the landscape is thin to deep glacial deposits over bedrock, with soils at the study sites identified as silty and sandy loams. The riparian sites used in this study were Shotley Brook (Beltrami County,

48°N, 94.5°W), Nemadji State Forest (Carlton County, 46.4°N, 92.3°W), and the East Branch Beaver River (Lake County, 47.3°N, 91.3°W) (Figure 3.1).

Sites were harvested in winter on frozen ground during the winter of 2003-2004 with conventional harvesting equipment (i.e., a tracked feller-buncher with grapple skidder). Harvests were conducted according to riparian guidelines for the state of Minnesota (MFRC 2005). The target residual basal area (RBA) for the harvest treatments was $11.6 \text{ m}^2\text{hc}^{-1}$, which is the recommended harvest level for uneven-age management of riparian forests adjacent to trout streams in Minnesota. Actual RBA differed to some extent by site. Shotley Brook post-harvest RBA was $20.1 \text{ m}^2\text{hc}^{-1}$, East Branch Beaver River RBA was $15.5 \text{ m}^2\text{hc}^{-1}$, and Nemadji state Forest RBA was $11.2 \text{ m}^2\text{hc}^{-1}$ (Kastendick 2005). Pre-harvest basal area (BA), post-harvest RBA, and forest composition were obtained from Kastendick 2005 (Table 3.1).

Experimental design and installation

The study was installed in the field in May 2004. The study design was a randomized block experiment with a $2 \times 2 \times 3 \times 2$ factorial. The study was installed in three replicates (sites) with two species (northern white-cedar and balsam fir), two overstory treatments (control and harvest), three microsite treatments (mound, pit, and slash), and two browse treatments (fenced and unfenced). Each riparian management zone (RMZ) was along one side of a waterway and contained an upstream uncut control (46 m depth x 183 m width), an unharvested buffer (61 m width), and a downstream harvest area (46 m depth x 183 m width). Upland clearcuts (137 m depth x 183 m width) were made adjacent to each RMZ; buffers and clearcuts were not part of the test areas (Figure 3.2). Three replicates of each microsite treatment were established in the control and harvest

areas (nine microsite plots per overstory treatment, 18 total plots per site), with a grand total of 54 plots at the three locations.

To control browse and to measure the impact of browsing on survival and growth, each plot was fenced and a duplicate unfenced plot established on an adjacent or nearby microsite of the same type. Polypropylene fencing 2.8 m tall with a mesh grid of 5 cm was upheld by steel fence posts and enclosed plot areas approximately 9 m². Inside and outside of each fenced plot, four northern white-cedar seedlings and four balsam fir seedlings were planted approximately 0.5 m apart, alternating individuals by species. This resulted in a total of eight northern white-cedar and eight balsam fir seedlings at each microsite plot (Figure 3.3) and a total of 432 northern white-cedar and 431 balsam fir individuals (one balsam fir was unintentionally not planted) across the three sites. Seedlings of both species were three years old when planted, grown as 3-0 nursery stock by Minnesota DNR Badoura State Forest Nursery. Seed for all seedlings used in the study was collected from the wild and conformed to MN DNR seed zone recommendations for each species when planted. Aluminum nursery tags with individual identification codes were attached loosely around the stem of each seedling.

The microsites of mound, pit, and slash, examined previously for their role in seedling growth (Haworth 2011), were examined in this study for the effects of microsite and deer browse on planted seedlings. Plot locations were selected from naturally occurring microsite features that were distributed throughout the 46 m x 183 m areas of the control and harvest RMZs.

The majority of mound microsites selected were of old tree stump origin, evidenced by the presence of large aging stump structures and the surrounding mound of

organic soil. All fit into decay class 4 (wood is mostly rotten) as described by Fraver et al. (2002). A few mounds were organic soil hummocks of unknown origin, most likely soil slumps from tree root tip-ups. Seedlings were planted on the sides and tops of mounds.

Pit microsites were distinct depressions of various origins in the forest floor. These were formed by weathered tree root tip-ups, abandoned stream channels, or dips in underlying rock substrate. Seedlings were planted around the sides and floor of pit microsites.

Slash microsites were piles of coarse and fine woody debris of different dimensions, ranging from solid boles of windthrown trees to tree-top logging debris. Seedlings were planted as close as possible along the north side of slash features to take advantage of shading and soil temperature mitigation.

Data collection and analysis

Baseline measurements of height in centimeters (ground to tip of leader) and basal diameter in millimeters (averaged from two measurements taken at right angles to each other) were taken within four weeks after planting. A standard metal tape measure was used to measure heights to the half centimeter from the seedling trunk at ground level, below litter, to the extended leader tip. Basal diameter was measured at ground level, below litter, with a dial caliper in .1 mm increments. Further height and basal diameter were collected annually in the autumn, except for the year of planting. Browse and survival data were collected each spring and autumn. Data analysis for growth and percent survival were performed on data from the final year, after four seasons in the

field. Data analysis for browse frequency was cumulative through the fourth season in the field.

Browse was calculated as “percent browse frequency” and is referred to as “browse frequency.” Data were recorded as the presence or absence (0 or 1) of seasonal browse per seedling, starting the autumn of the first growing season through autumn of the fourth growing season, for a total of seven times. Browse frequency was calculated per seedling as:

$$\text{Percent browse frequency} = \left(\frac{\text{Browse events}}{7} \right) \times 100$$

with browse events being the number of times that seasonal browse was observed at spring and autumn data collections, and 7 being the total number of times browse was monitored. Seedling data were then averaged per plot for correlation analysis; plot averages were aggregated to the treatment combination scale for GLM analysis and figure construction.

Presence or absence of browse was determined by a visual examination of each seedling and by comparing current heights with previous measurements. Ungulate (white-tailed deer) browse was recognizable by a shredded stem tip and uneven removal of foliage. Current season browse was marked by visibly light pith and fibers versus darker dried plant material of previous browse. Occasional lagomorph (eastern cottontail, *Sylvilagus floridanus* or snowshoe hare, *Lepus americanus*) or rodent (red squirrel, *Tamiasciurus hudsonicus*) browse was noted as a stem clipped with a clean, sharp 45° angle. As the incidents of lagomorph or rodent browse were few, they were combined with ungulate browse prior to analysis.

Seedling survival was scored as alive (1) if any green foliage remained and a green cambial layer was retained, or dead (0) if all foliage was removed and the seedling lacked a green cambial layer. Seedlings that died were included in the survival analysis but not in the analysis of growth data. At the end of four years in the field, percent survival was calculated per species per plot as:

$$\text{Percent survival} = \left(\frac{\# \text{ of survived seedlings}}{4} \right) \times 100$$

with 4 being the number of planted seedlings per species per plot. Plot data were used for correlation analysis and aggregated for GLM analysis and figure construction.

Associated forest floor and vegetation data, assessed in percent cover categories, were collected once during the third growing season. These categories were percent forest floor cover (forest floor area with no vegetation cover, litter may or may not be present), percent herbaceous cover (grass plus forbs), percent woody cover (shrub cover with stems < 2.5 cm diameter at breast height (DBH) and foliage height < 1.3 m), and basal area (BA). Percent forest floor and vegetation covers were compiled at each plot from four ocular estimates of one-meter quadrats, which were then averaged for a single plot value per cover. Basal area was measured at each plot by prism (factor 10) and included woody stems > 2.5 cm diameter at breast height (DBH). Stems < 2.5 cm DBH with foliage > 1.3 m height were neglected.

Different growth habits of northern white-cedar and balsam fir make direct comparisons based on height and basal diameter growth difficult. To examine growth comparisons more accurately between species, relative growth rates (RGR) were analyzed as relative height growth (RHG) and relative diameter growth (RDG). For this

study RGR is defined as the increase in logN seedling growth divided by a period of time and was calculated by species per plot as:

$$RGR = \frac{\log N \text{ final value} - \log N \text{ initial value}}{4}$$

with final value being the last measured value, initial value being the measured value at planting, and four being the length of study time in growing seasons. RGR analysis is conventionally measured in dry weight (Harper 1977) but for this study was measured in height and basal diameter to allow non-destructive sampling. RGR plot data were used for correlation analysis, and averaged to the treatment scale for GLM analysis and figure construction.

Statistical analysis was performed with SAS/STAT® software, Version 9.1.3 of the SAS System. General Linear Model (GLM) significance (Type III Sum of Squares) was based on $p \leq 0.05$. GLM was used due to imbalanced data caused by complete mortality in some pit microsites and variable species mortality. Site was used as a blocking factor ($n = 3$), allowing any differences between site conditions to be included with the error term, producing a more stringent F-test. Tukey-Kramer and Tukey's HSD pairwise tests ($\alpha = 0.05$) were used to identify which means were significantly different from one another when a significant difference was discovered by the model. The independent variables for survival and growth analyses were species (northern white-cedar and balsam fir), fence position (fenced and unfenced), overstory treatment (control and harvest), and microsite treatment (mound, pit, and slash). Interactions (referred to as 'interaction' or denoted with "x") were included in the model. The dependent variables were percent survival, percent browse frequency, height, basal diameter, RHG, and RDG.

Variable transformations were performed to meet assumptions of normality and variance, and are given beside each variable in the GLM tables presented at the end of the chapter.

Simple linear regression, performed by SAS/STAT® software Version 9.1.3, was used to examine the relationships between variables. The coefficient was calculated by Pearson product-moment correlation with the significance probability calculated for $\alpha = 0.05$ (SAS/STAT 2003). Dependent variables were browse frequency, percent survival, height, basal diameter, RHG, and RDG; independent variables were browse frequency, basal area, percent forest floor cover, percent moss cover, percent herbaceous cover, and percent woody cover. Variable transformations were performed to meet assumptions of normality and variance, and are given beside each variable in the correlation tables presented at the end of the chapter. Browse frequency was treated both as an independent variable (to examine potential correlation with species growth response) and as a dependent variable (to examine whether browse could be related to vegetation type). Percent herbaceous cover was not correlated to browse frequency as a dependent variable, because herbaceous growth was not present when most browse took place. Correlation analysis was performed at the plot mean level ($n = 54$), but due to seedling mortality in pits, $n = 46$ for northern white-cedar and $n = 43$ for balsam fir.

Results

Initial analysis was conducted between species for browse frequency, and between species and fence treatments for percent survival and relative growth rates. Separate analysis by species for percent browse frequency, percent survival, and size (height and basal diameter) gave additional information regarding seedling responses that was not demonstrated by the combined analysis.

Browse frequency

After four growing seasons in the field, GLM analysis of browse frequency between unfenced species was highly significant with northern white-cedar (37.3%) suffering higher browse frequency than balsam fir (13.2%) ($p < 0.0001$) (Table 3.2, Figure 3.4). With species pooled, overall browse frequency in overstory treatment-harvests (29.6%) was significantly higher than in controls (19.9%) ($p = 0.01$). Also browse frequency in microsite treatment-mounds (32.5%) was significantly higher than in pits (16.4%) ($p = 0.02$), but was not significantly different from slash (23.6%). Browse frequency was not significant for species x overstory, species x microsite, or species x overstory x microsite interactions.

Browse frequency on unfenced northern white-cedar seedlings was significantly higher in overstory treatment-harvest areas that were browsed at 45.1%, compared to browse in controls at 29.5% ($p = 0.003$). Browse frequency was also significantly higher on microsite-mounds (46.4%) compared to pits (31.1%) or slash (32.3%) ($p = 0.04$).

Browse frequency on unfenced balsam fir was not significant for overstory, microsite, or overstory x microsite treatments. Browse in overstory treatment-harvests was 15.8% and 10.3% in controls ($p = 0.31$). Browse was 18.6% in microsite treatment-mounds, 15.0% in slash, and 4.6% in pits ($p = 0.08$).

Percent survival

GLM analysis of percent survival overall (i.e., pooled fence positions) between species was significant, with northern white-cedar survival higher at 74.3% than balsam fir at 60.6% ($p = 0.003$) (Table 3.3, Figures 3.5a and b). With species pooled, the main effects were also significant. Survival in fenced positions (74.9%) was greater than

unfenced (60.0%) ($p = 0.002$). Survival in overstory treatment-harvests was higher (74.1%) than in controls (60.8%) ($p = 0.03$). Survival in microsite treatment-pits was lower (45.5%) than in mounds (79.4%) or slash (77.4%) ($p < 0.0001$). Species x overstory treatment, fences pooled, was the only significant interaction, with percent survival in balsam fir controls (48.0%) significantly lower than balsam fir harvests (73.2%), northern white-cedar controls (73.6%), or northern white-cedar harvests (75.0%) ($p = 0.02$).

Northern white-cedar percent survival between fence treatments returned significant differences between fenced (82.9%) and unfenced (65.7%) positions ($p = .01$). A visual review of percent survival over time illustrates the development of significant differences between fence treatments, showing stabilized seedling survival for fenced seedlings and a continuing downward trend for unfenced seedlings (Figure 3.6a). Pooled fence positions for microsite treatment were also significant with pit means (50.7%) lower than mounds (88.2%) and slash (84%) ($p = 0.0002$).

Balsam fir percent survival between fence treatments was not significantly different between fenced (67.0%) and unfenced (54.2%) positions ($p = 0.13$). A visual review of percent survival over time illustrates the similarity between fence treatments, showing stabilized seedling survival only in fenced harvest treatments and a continuing downward trend for all other seedlings (Figure 3.6b). With fence positions pooled, overstory treatment was significant with harvest treatments (73.1%) higher than controls (48.0%) ($p = 0.001$). Also microsite treatment was significant with pit means (40.3%) lower than mounds (70.6%) and slash (70.8%) ($p = 0.001$).

Relative growth rate

Overall relative height growth was significantly different between species with northern white-cedar RHG (0.09) significantly less than that of balsam fir (0.14) ($p = 0.004$) (Table 3.4, Figures 3.7a and b). With species pooled, RHG in fenced treatments (0.19) was significantly greater than in unfenced treatments (0.05) ($p = 0.001$). With species and fences pooled, RHG in overstory treatment-harvests (0.14) was significantly greater than in controls (0.09) ($p = 0.002$). Species x fence interaction was significant with northern white-cedar unfenced RHG (-0.01) significantly lower than all others, and balsam fir unfenced RHG (0.10) significantly lower than either balsam fir fenced (0.18) or northern white-cedar fenced (0.19) ($p = 0.0003$). RHG in species x overstory treatment was almost significant, with balsam fir RHG in overstory treatment-harvests (0.18) greater than controls (0.10), northern white-cedar harvests (0.10), or northern white-cedar controls (0.08) ($p = 0.06$). RHG in fence x overstory treatment with species pooled was significant at $p = 0.04$. RHG in species x fence x microsite treatment was almost significant with all values greater than northern white-cedar unfenced mounds (-0.05) ($p = 0.08$).

Overall relative diameter growth was significantly different between species with northern white-cedar RDG (0.17) significantly higher than that of balsam fir (0.13) ($p = 0.001$) (Table 3.5, Figures 3.8a and b). With species pooled, RDG in the fenced treatment (0.17) was significantly greater than in the unfenced treatment (0.12) ($p < 0.0001$). With species and fences pooled, RDG in overstory treatment-harvests (0.18) was significantly greater than in controls (0.12) ($p < 0.0001$). RDG in species x fence interaction was significantly different with northern white-cedar fenced (0.21) greater than unfenced

(0.12), balsam fir fenced (0.14), and balsam fir unfenced (0.12) ($p = 0.01$). RDG in fence x overstory treatment with species pooled was significant with fenced harvest treatments greater than all other values at $p = 0.03$.

Height and basal diameter

Analysis of northern white-cedar height was significantly greater in fenced treatments (51.2 cm) than unfenced (23.0 cm) ($p < 0.0001$) (Table 3.6a, Figure 3.9a). Height in pooled fence positions were significantly different between controls (31.8 cm) and harvests (42.4 cm) treatments ($p = .01$). Fence x overstory treatment interactions were significant for height with largest means in fenced harvest areas (62.4 cm) over fenced control (40.1 cm), unfenced control (23.6 cm), and unfenced harvest (22.4 cm) ($p = 0.002$). Fence x microsite interactions in all fenced microsites (mound = 56.3 cm, pit = 44.5 cm, slash = 52.9 cm) were significantly taller than all unfenced microsites (mound = 20.1 cm, pit = 23.6 cm, slash = 25.3 cm) ($p = 0.03$).

Similarly, basal diameter was greater in fenced treatments (6.6 mm) than unfenced (4.7 mm) ($p < 0.0001$) (Table 3.6b, Figure 3.9b). With fences pooled, basal diameter in overstory treatment-controls (4.7 mm) was significantly lower than in harvests (4.7 mm) ($p < 0.0001$). Fence x overstory interaction in fenced harvest treatments (8.0 mm) was significantly larger than fenced controls (5.2 mm), unfenced controls (4.3 mm), and unfenced harvests (5.1 mm) ($p = 0.03$).

Balsam fir height between fence positions was significantly taller in fenced treatments (27.3 cm) than unfenced (20.8 cm) ($p = 0.01$) (Table 3.7a, Figure 3.10a). Pooled fence positions resulted in significance between overstory treatments with height in harvests (30.3 cm) taller than in controls (16.3 cm) ($p < 0.0001$). Basal diameter was

significantly greater in fenced treatments (5.5 mm) than unfenced (4.7 mm) ($p = 0.03$) (Table 3.7b, Figure 3.10b). Pooled fence positions resulted in significance between overstory treatments with harvest diameters (6.1 mm) greater than controls (4.0 mm) ($p < 0.0001$).

Northern white-cedar correlation analysis

Analysis of browse frequency of northern white-cedar as a dependent variable returned significant negative correlations to BA ($p = 0.01$, $r = -0.39$) and percent forest floor ($p < 0.0001$, $r = -0.57$) (Table 3.8). There was a close to significant but weak positive correlation to percent moss cover ($p = 0.08$, $r = 0.26$).

With height and basal diameter of northern white-cedar as dependent variables, correlations between seedling size and vegetation found in fenced treatments disappeared in unfenced treatments (Table 3.9). Fenced northern white-cedar seedling size to BA had significant negative correlations for height ($p < 0.0001$, $r = -0.64$) and basal diameter ($p < 0.001$, $r = -0.60$), while unfenced height ($p = 0.96$, $r = -0.58$) and basal diameter ($p = 0.09$, $r = -0.26$) did not. Fenced seedling size to percent forest floor cover had significant negative correlations for height ($p = 0.0001$, $r = -0.54$) and basal diameter ($p = 0.001$, $r = -0.46$), while unfenced height ($p = 0.22$, $r = 0.18$) and basal diameter ($p = 0.17$, $r = 0.21$) did not. Fenced seedling size to percent herbaceous cover had significant correlations for height ($p = 0.003$, $r = 0.42$) and basal diameter ($p = 0.01$, $r = 0.37$), while unfenced height ($p = 0.45$, $r = -0.11$) and basal diameter ($p = 0.68$, $r = -0.07$) did not. Fenced seedling size to percent woody cover had significant correlations for height ($p = 0.03$, $r = 0.31$) and basal diameter ($p = 0.01$, $r = 0.40$), while unfenced height ($p = 0.22$, $r = -0.18$) did not, although basal diameter significance remained ($p = 0.03$, $r = -0.34$). Fenced seedling size

to percent moss cover did not have significant correlations for height ($p = 0.67$, $r = -0.07$) or basal diameter ($p = 0.89$, $r = 0.02$), but unfenced height ($p = 0.06$, $r = -0.28$) and basal diameter ($p = 0.06$, $r = -0.28$) had close-to significant negative correlations.

Analysis of unfenced northern white-cedar with browse as an independent variable found a negative correlation between height and browse frequency ($p < 0.0001$, $r = -0.58$) (Table 3.9). There was not a significant correlation between basal diameter and browse frequency ($p = 0.09$, $r = -0.26$). A weak negative correlation, close to significant, was found between height and percent moss ($p = 0.06$, $r = -0.28$). No other significant correlations between seedling growth and browse frequency or associated vegetation were found.

Balsam fir correlation analysis

With browse frequency of balsam fir as a dependent variable, the only significant negative correlation found was browse to percent forest floor ($p = 0.01$, $r = -0.38$) (Table 3.8).

With height and basal diameter as dependent variables, balsam fir correlations stayed primarily the same between fence positions (Table 3.10). Fenced balsam fir seedling size to BA had significant negative correlations for height ($p = 0.0001$, $r = -0.58$) and basal diameter ($p = 0.0001$, $r = -0.55$), as did unfenced height ($p = 0.01$, $r = -0.42$) and basal diameter ($p < 0.0001$, $r = -0.56$). Neither fenced nor unfenced seedling size correlations were significant for percent forest floor cover percent or herbaceous cover. Changes in balsam fir correlations between fence positions were (a) fenced seedling height to percent woody cover was significant ($p = 0.01$, $r = 0.38$), but significance was lost in unfenced treatments ($p = 0.37$, $r = 0.14$); (b) fenced seedling size to percent moss

cover was significant with a negative correlation for height ($p = 0.02$, $r = -0.36$) but not for basal diameter ($p = 0.20$, $r = -0.21$), and significance was retained for both in unfenced treatments (height: $p = 0.01$, $r = -0.41$; basal diameter: $p = 0.03$, $r = -0.33$).

Analysis of balsam fir resulted in no significant correlations between size and browse frequency (Table 3.10). Seedling size had significant negative correlations to BA for height ($p = 0.01$, $r = -0.42$) and basal diameter ($p < 0.0001$, $r = -0.56$). Balsam fir also had negative correlations to percent moss cover for height ($p = 0.01$, $r = -0.41$) and basal diameter ($p = 0.03$, $r = -0.33$).

Discussion

Not all of the significant effects recognized by the GLM models were of interest to this study. For example, output for RHG (Table 3.4) shows the p-value for fence treatment at 0.001. This effect, pooling species as well as overstory and microsite treatments, addresses concepts that are outside of the scope of the study questions. What follows is a discussion of biologically relevant results.

Browse frequency

Data collection for this project found that herbivory on unfenced seedlings did not occur in winter because seedlings were covered with snow. The majority of browse events occurred in the spring after snowmelt but before woody budburst or emergence of herbaceous vegetation. Most browse on both species ceased after leaf emergence as deer moved on to preferred food sources. The calculation of browse frequency was based on presence/absence of herbivory viewed at a total of three spring and four fall data collections. Therefore, browse frequency percentages may appear lower than expected. In

actuality, of unfenced seedlings in the final analysis, only 16 of 142 (11%) northern white-cedar and 41 of 117 (35%) balsam fir seedlings remained unbrowsed after four field seasons.

Preferential browsing on northern white-cedar is widely reported in the literature and was also found in this study. Browse frequency across all overstory and microsite treatments was significantly higher on northern white-cedar than on balsam fir. However, significant browse between species was not found for species x overstory, species x microsite, or species x overstory x microsite interactions, suggesting that browse was evenly dispersed by species throughout overstory and microsite treatments.

While the amount of vegetation removed by browse was not measured as part of this study, field observations determined that the nature of browse differed between species. Each browse event on northern white-cedar removed most existing foliage, leaving the seedling stem. In contrast, browse on balsam fir seedlings was restricted to leaders and partial snipping of the tips of lateral branches.

Although northern white-cedar was browsed more heavily in this study, it also had better short-term recovery capabilities, while balsam fir, less browsed, recovered more slowly. However, repeated annual herbivory on northern white-cedar will continue to deplete seedling resources, leading to increased mortality. Under current browse levels northern white-cedar seedlings will eventually die, while most balsam fir seedlings will survive but grow more slowly. If browse were restricted within the first several years after planting, northern white-cedar seedling viability could be reestablished. This gives a window of several years for seedling protection to be implemented. Davis et al. (1998)

also cited recovery of height in advanced regeneration of northern white-cedar seedlings that had been previously browsed and were then protected.

Browse frequency on northern white-cedar was higher in overstory treatment-harvests than controls. This is consistent with ungulate feeding patterns, i.e., deer spend more time feeding close to forest edges where shrub forage is most available (Smith et al. 2007; Forester et al. 2008). While the amount of browse in control areas was still considerable, significantly lower browse in these areas suggests the potential for higher seedling success rates when planted in unharvested areas.

Browse frequency on northern white-cedar was also significantly greater for microsite treatment-mounds than for pits or slash. The exposed nature of mounds left seedlings particularly vulnerable to browse. Pits and slash microsites appeared to offer more protection, perhaps because (a) seedlings were less exposed by microtopography and (b) overhanging shrubs or slash afforded some degree of protection.

Although browse levels on northern white-cedar was significantly lower in slash than on mounds, considerable browse occurred in slash seedlings regardless. In most cases seedlings in this study were planted not inside slash piles but in close proximity on the north side, more as a test of shading affects than of browse protection. Planting seedlings inside slash piles may have offered more protection from browse, if seedlings were out of the reach of deer. The potential value of light slash as seedling cover from browse, often referenced in the literature (Verme and Johnston 1986; Johnston 1990; Peterson and Pickett 1995; Schaffer 1996; Davis et al. 1998), was not studied.

There was considerably less (although non-significant) browse on northern white-cedar seedlings in control x pits, where lower-forage control areas combined with low-

lying seedling placement. There was also less browse in control x slash, where some protection appeared to be provided by the lower-forage area and slash cover. It is not surprising that of all interactions, northern white-cedar harvest x mounds were the most severely browsed, combining the forage-filled harvests areas with the exposure of mounds.

After four years in the field, 76 of 117 balsam fir seedlings were browsed. It is possible that planting proximity to northern white-cedar generated incidental browse on balsam fir, inflating browse estimates to an unknown extent.

Browse frequency on balsam fir was not significant for any treatment, although pits were almost significant. Seedlings in pit microsites were less exposed and may have received some protection from overhanging shrubs. Browse on balsam fir appeared to be higher in harvest areas where shrub forage was more available, but was highly variable as evidenced by large standard errors. Deer did not target balsam fir preferentially but appeared to browse seedlings sporadically, with less vegetation removal per seedling than occurred on northern white-cedar seedlings.

Wildlife and timber management studies suggest that a population level of eight deer/km² is a standard land base carrying capacity, but ecosystem studies report that a level of one to four deer/km² is needed to avoid a detrimental impact to browse-sensitive species (Alverson et al. 1988). During the period of this study (2004-2007) fluctuating pre-fawn deer densities at the study sites were estimated to be in the these ranges: four to eight/km² at Nemadji State Forest, four to nine/km² at Shotley Brook, and one to six/km² at East Branch Beaver River (MN DNR pers. comm.; MN DNR 2007). Browse analysis from this study indicated that a population level lower than the estimates experienced at

each site would be necessary to avoid the detrimental impact of herbivory. In the bare forest floor environment following spring snowmelt, seedlings are highly vulnerable to even a few local or migrating deer.

Percent survival

After four years in the field, GLM analyses of overall (i.e., fence positions pooled) seedling percent survival between species showed northern white-cedar survival significantly higher than balsam fir. However, the observed physical condition of unfenced northern white-cedar (i.e., the amount of vegetation and twig growth removed by browse) (personal observation) was greatly compromised compared to balsam fir seedlings. Continued decline of northern white-cedar percent survival is expected, with accompanying changes in these relationships.

Fence position (with pooled species) showed significantly higher percent survival for fenced than unfenced seedlings, indicating that more seedlings survived inside fences protected from browse, regardless of species. With species and fence position pooled, harvest areas had higher survival than control areas, suggesting that regardless of species or browse effects, higher light afforded by partial harvests are better for survival than the full overstory of controls. Also microsite-pits had lower survival than mounds or slash, indicating overall seedling vulnerability to seasonal flooding.

Examined by species, survival trends are seen more clearly. Northern white-cedar percent survival became significant for fence position when survival dropped from 82.9% fenced to 65.7% unfenced, while balsam fir percent survival was not significant in spite of a drop in survival from 67.0% fenced to 54.2% unfenced. Northern white-cedar had

higher survival, despite being more severely browsed for four years in the field. Balsam fir had lower survival due to mortality in controls, but was less impacted by browse.

Lower overall survival of balsam fir was an unexpected result that was examined further by comparing the original vitality of transplant seedlings. Studies have shown that high root volume, fine root mass, and first-order lateral roots are predictive of conifer seedling success in the field (Rose et al. 1997; Davis and Jacobs 2005; Jacobs et al. 2005). Studies have also shown that higher root/shoot ratios facilitate water and nutrient uptake and storage, giving seedlings competitive survival capacity even in low light forested conditions (Greenwood et al. 2008).

In order to assess original seedling viability, biomass measurements of 50 unplanted seedlings of each species were conducted on seedlings obtained from the same nursery source. This sample returned a balsam fir mean root/shoot weight ratio of 0.66 ± 0.02 , higher than that found for 50 unplanted northern white-cedar seedlings (0.33 ± 0.03). This was also higher than that found by Greenwood et al. (2008) in naturally occurring balsam fir three to five years of age (0.45 ± 0.03). Except to show that balsam fir seedlings were well formed for outplanting, this information is inconclusive and suggests that higher balsam fir seedling mortality experienced in this study was due to unexamined parameters. It is possible that transplant seedlings grown in an open light environment may not have developed needles and root/shoot ratios that could adapt effectively to lower light levels. It may also be that growth plasticity exhibited by northern white-cedar seedlings allowed them to adapt more quickly to low-light planting environments. Though not measured, natural regeneration of varying age categories was present at all sites, indicating that conditions were suitable for balsam fir growth.

After four years in the field, percent survival of northern white-cedar seedlings was significantly higher in fenced treatments than in unfenced treatments, clearly illustrating the effect of herbivory. In unfenced treatments, no significant differences were found between overstory treatments or overstory x microsite interactions, demonstrating that even under the influence of browse, transplant seedlings were able to remain alive in the lower light environment of full overstory controls. This differs from Cornett et al. (2000) in which northern white-cedar seedlings in the Lake Superior Highlands, planted and subject to browse, were more likely to die under lower canopy openness. Seedling age at planting and length of study period were similar between studies. The difference could be due to the comparatively higher canopy density of the Cornett et al. (2000) study areas, to differences between upland and riparian conditions, or to other factors such as water stress or soil type.

Among microsite treatments of both fenced and unfenced areas, northern white-cedar percent survival in pits was significantly lower than either mounds or slash. This was most likely due to seasonal flooding. During the first two seasons in the field, pits subjected to seasonal flooding suffered almost complete mortality, while those that did not flood retained higher percent survival. Cornett (1996) found almost complete mortality of northern white-cedar germinants in pits that experienced periodic inundation. Chimner and Hart (1996) also reported very low northern white-cedar establishment in pool areas.

While 65.7% of unfenced northern white-cedar seedlings remained alive, their true physical condition was not captured by a qualitative category such as survival. In reality, after four years in the field, most unfenced northern white-cedar seedlings were in

poor condition from recurrent browsing (personal observation). Continued decline of percent survival in unfenced seedlings over the coming years is predicted, as herbivory will further deplete the resources of compromised seedlings. In a Wisconsin browse study, Davis et al. (1998) described a similar decline in browsed northern white-cedar advance regeneration. She reported browse effects after the first year, but a period of five years from plot establishment before advance regeneration was eliminated.

Comparison of survival results between fenced and unfenced balsam fir seedlings showed no significant differences between fence positions, and patterns of survival that were similar in fenced and unfenced treatments. In both fenced and unfenced treatments, percent survival was statistically higher in overstory–harvests than in controls. In a study that mimicked browsing, McLaren (1996) also reported that clipped balsam fir were more likely to die with greater than 60 percent canopy coverage, because they were unable to compensate for vegetation and leader removal. Balsam fir survival was also lowest in fenced and unfenced pit microsites, most likely due to seasonal flooding. However, with fence positions pooled, significance for both overstory and microsite were lost. This indicates that survival differences between fence positions were not strong enough to maintain statistical relevance, which is upheld by the lack of significance of survival between overall fence positions.

Higher survival for balsam fir in harvest areas, whether protected from browse or not, was an unexpected result. This result is at odds with the general description in the scientific literature of balsam fir as a shade-tolerant seedling. Indeed, in a seedling light study Logan (1969), stated that balsam fir seedling success in low light conditions (13% of full light in lath house experiments) was more the result of survival than growth,

suggesting that balsam fir can establish successfully in low light conditions but will not increase substantially in height.

Species comparison: growth

Direct comparisons between growth of northern white-cedar and balsam fir seedlings are difficult because of differences in growth form. Northern white-cedar has a leaf area distribution in the upper crown with small branch diameters; balsam fir has a leaf area distribution lower in the crown with larger branches (Weiskittel et al. 2009; Weiskittel et al. 2010). Under low light conditions, seedlings of *Thuja* species have an upright but loose frond structure with variable branching patterns (Edelstein and Ford 2003) while balsam fir commonly exhibit fixed lateral branch growth exceeding height growth, with flat shoots laterally extended (Duchesneau et al. 2001; Parent et al. 2006). These architectural and morphological differences were addressed by using relative growth rate to make comparisons between species.

Ocular field observations also determined that the nature of seedling response to browse differed between species. These differences, similar to the differences in growth form, are due to dissimilar growth habits of the two species. For northern white-cedar, the presence of new foliage at fall data collection demonstrated some degree of seasonal recovery of lost vegetation. Juvenile leaves, first-year adult leaves, and new foliage fronds were present on stems that had been browsed bare earlier in the season. Lateral shoots also expressed dominance in the same year following leader removal. In contrast, balsam fir seedlings were slower to respond to herbivory with new growth, with none occurring in the year of herbivory. Apical leader removal by browse resulted in a variety of new growth forms in balsam fir after a delay of at least one year.

The annual replacement of foliage seen on browsed northern white-cedar seedlings, though underreported in the literature, is due to physiological mechanisms that aid their growth and survival. *Thuja* species exhibit indeterminate shoot growth and rapid lateral response to leader removal (Lavender and Salim 1987; Krasowski and Owens 1991). Shoot elongation originates from apical meristems that form leaf primordia in the current year. The extent of seasonal growth is then affected by local environmental conditions (Parker and Johnson 1987; Pallardy 2008). Alternate branching architecture assists rapid transition of highest lateral branch to dominant leader upon removal of the apical bud. Krasowski and Owens (1991), studying seedling growth of western red-cedar (*Thuja plicata* Donn ex D. Don), found that a damaged terminal apex was usually replaced in the same year by the closest lateral bud.

Slower regrowth of balsam fir following herbivory is a function of determinate growth seen in the *Abies* genus in which the current year's shoot growth is restricted to preformed shoot primordia contained in apical buds formed the previous growing season (Pallardy 2008). Browsed shoot tips cannot regenerate within the same year, making recovery from browse more difficult. Whorled branch architecture slows leader replacement by lateral branches. Häslér et al. (2008), studying seven-year-old seedlings of silver fir (*Abies alba* Mill.), reported single and double leader regeneration from interwhorl or secondary whorl buds, and flagging (i.e., a lateral shoot turning upward to assume leader dominance), taking two to three years to recover lost vegetation depending on light availability. Clipped lateral branches did not affect the growth of unclipped laterals but reduced the total amount of photosynthetic leaf area available to generate new growth.

In the analysis of relative growth rates of height and basal diameter between species, species and species x fence results are of the most interest. Overall relative height growth of northern white-cedar was significantly lower than balsam fir, due to the negative growth rate seen in unfenced treatments subjected to browse. Species x fence treatments showed RHG of fenced northern white-cedar and balsam fir to be statistically similar, demonstrating positive seedling height growth for both species when protected from browse. RHG of both unfenced northern white-cedar and balsam fir was significantly lower than fenced values, showing the negative impact of browse on both species. RHG of unfenced northern white-cedar was also significantly lower than unfenced balsam fir, demonstrating the impact of preferential browse.

However, overall relative diameter growth of northern white-cedar was significantly greater than balsam fir. Species x fence treatments showed RDG of fenced northern white-cedar was significantly greater than fenced balsam fir as well, while RDG of unfenced species was statistically similar. This demonstrated that (1) when protected from herbivory, northern white-cedar seedlings were capable of faster basal diameter growth than balsam fir; and (2) even under browse pressure, northern white-cedar seedlings continued to commit resources to basal diameter growth.

The continuing basal diameter growth seen in unfenced northern white-cedar seedlings in this study may have resulted from foliage mass added during the summer: browsed seedlings could have added first foliage, then basal diameter, and then lost foliage to browse the following spring before beginning again. In this manner height growth could be negative, but diameter growth positive. This would demonstrate woody plant biomass allocation patterns, where carbon distribution first goes to photosynthetic

tissues and roots, and second to stem diameter and storage (Waring 1987), with a proportional increase between stem diameter and foliage to maintain balanced functions (Parent et al. 2006).

However, it is expected that continued browse on northern white-cedar seedlings will decrease available carbon resources, resulting in less diameter allocation, slowing diameter growth rates, and eventual increased seedling mortality.

Height and basal diameter

Height and basal diameter of fenced northern white-cedar seedlings were significantly greater than unfenced seedlings. Fenced seedling height and basal diameter were greater in overstory treatments-harvests, but unfenced seedlings showed no significant response to overstory treatments. Browse became the equalizing factor that overcame the positive effect of partial overstory removal, illustrating the damaging result on seedling growth. Cornett (2000) found similar results, reporting that browse on planted northern white-cedar seedlings was stronger than canopy influences.

While northern white-cedar seedling heights varied highly between fence positions with the exclusion of browse, the effect was not as dramatic on basal diameters, where fenced controls were similar to unfenced harvests. Basal diameter growth continued under browse pressure, though not as much as when protected.

Height and basal diameter of fenced balsam fir seedlings were significantly larger than unfenced seedlings, demonstrating that balsam fir growth was suppressed to a certain degree by browse. Cornett et al. (2000) also reported that balsam fir, though not a preferred browse species was reduced in percent cover by browsing. With fence positions pooled, overstory treatment-harvests values were greater for both height and basal

diameter. This demonstrates that growth in harvest areas, even under browse pressure, responded enough to contribute to overall significance of harvest treatments. This substantiates field observations of the lower amount of browse that occurred per balsam fir seedling per browse event – an amount not measured by this study and therefore not captured.

Correlation analysis

Correlations between fenced and unfenced seedling size and independent variables differed between species. While northern white-cedar correlations seen in fenced treatments disappeared in unfenced treatments, balsam fir correlations stayed primarily the same between fence positions. This illustrated the effect of herbivory on unprotected northern white-cedar seedlings that overwhelmed environmental correlations.

Northern white-cedar correlations

Browse frequency on northern white-cedar as a dependent variable was negatively correlated to BA and percent forest floor cover. These features are often associated in the forest. Higher basal area produces heavier shade and suppresses woody and herbaceous understory plant growth, resulting in more exposed forest floor. Because deer select areas with woody shrubs to feed, seedlings planted in harvested areas with lower basal area may experience more browse (as was established by GLM analysis). However, it should be noted that a correlation was not found between browse frequency and percent woody cover. This may be the result of inadequate woody cover measurements that did not completely capture this variable.

As expected, there was a negative correlation between northern white-cedar height and browse frequency as the independent variable. This illustrates the impact of

browse on seedling height and suggests that browse overrode any other potential correlations. There was not a significant correlation between basal diameter and browse frequency, demonstrating that even with substantial herbivory, seedlings continued to commit carbohydrates to basal diameter growth.

Northern white-cedar height and basal diameter in fenced treatments had strong negative correlations to BA, implying that seedling size increased with partial overstory removal. This correlation disappeared in unfenced treatments where seedlings were subjected to herbivory that overwhelmed growth responses. A negative correlation also existed in fenced seedlings to percent forest floor cover, but disappeared in unfenced treatments under the influence of browse. These correlations are different measures of the same mechanism, because forest floor lacking vegetation increases with the environment of lower available light associated with higher overstory, and thus they commonly occur together.

Fenced northern white-cedar seedling height and basal diameter had positive correlations to both percent herbaceous cover and percent woody cover, which disappeared in unfenced seedlings (except for basal diameter to percent woody cover). In fenced treatments, seedlings responded in growth in a similar fashion as surrounding herbaceous and woody vegetation – but in unfenced treatments this response was lost, due to the effects of browse on unprotected seedlings.

Northern white-cedar height and basal diameter of unfenced seedlings had very close to significant negative correlations to percent moss cover, but fenced seedlings did not. This may reflect the greater exposure of seedlings in plots with higher moss cover and consequent vulnerability to browse. The absence of a correlation between fenced

seedlings and moss cover further supports this suggestion. Another possibility is that the greater presence of moss reflects a higher soil acidity that adversely affected unfenced seedlings already compromised by herbivory.

Balsam fir correlations

Analysis of unfenced balsam fir found no significant correlations for growth to browse frequency. However, GLM analysis of height and basal diameter was significantly different between fence positions. This suggests that browse on balsam fir was significant enough to make an overall difference in growth between fenced and unfenced seedlings, but the incidence of browse was not significant enough to be detected by correlation analysis.

Fenced and unfenced balsam fir had significant negative correlations between height and basal diameter as dependent variables and BA. A negative correlation to BA implies lower growth under higher canopy cover, which was also found significant by GLM analysis in both fenced and unfenced seedlings. Fenced height to percent woody cover was positively correlated but this was lost in unfenced areas. This could be a reflection of the amount of browse on unfenced seedlings. Fenced height to percent moss cover was negative and significant, and this continued in unfenced height and basal diameter. The negative correlation to percent moss could imply a pattern of higher herbivory on seedlings planted on exposed mossy surfaces; however, browse frequency did not show a relationship to any balsam fir growth response. Since correlation of percent moss to fenced growth was also negative and significant, there may be an untested factor (such as soil pH) involved with these results.

Summary

This study investigated the combined effects of partial overstory harvest, microsite, and herbivory by white-tailed deer on survival and growth of planted seedlings of northern white-cedar and balsam fir in riparian areas within northern Minnesota. The questions addressed treatment options that might benefit northern white-cedar, giving insight into the competitive relationship between northern white-cedar and balsam fir seedlings under the influence of herbivory.

After four years in the field, comparisons between fenced and unfenced planted northern white-cedar seedlings demonstrated that fenced partial harvests resulted in greater height and basal diameter than controls, but that browse overcame the potential overstory benefits in unfenced treatments, significantly reducing survival and growth. Northern white-cedar seedlings continued to allocate resource to basal diameter even under the influence of herbivory, though at a lower rate. Northern white-cedar relative diameter growth overall was greater than balsam fir. Companion plantings of balsam fir demonstrated that fenced partial harvests resulted in greater height and basal diameter than controls. This was also found for seedlings in unfenced treatments, although with lower values. Balsam fir relative height growth was greater overall than northern white-cedar. Balsam fir did not show significant differences between survival in fenced and unfenced plantings, although survival was lower in unharvested controls of both fence treatments. Some microsite effects were found for both species, specifically higher browse on exposed mounds and lower survival in seasonally flooded pits.

Analysis of growth rates led to the conclusion that planted seedlings of northern white-cedar were competitive with balsam fir seedlings of the same age for up to four

years in the field. Continued monitoring of seedlings would determine any future changes in growth rate that could alter this dynamic. The reputation of balsam fir as a fast-growing species, coupled with northern white-cedar's reputation as slow-growing, may exhibit itself at some point in the future.

Browse on northern white-cedar seedlings was strongly correlated to a reduction in height growth. Browse was not correlated to basal diameter, demonstrating that even when browsed, northern white-cedar continued for four years to commit resources to basal diameter growth. Browse on northern white-cedar was statistically lower in unharvested control areas and in pit and slash microsites. However, neither percent survival nor growth reflected a significant benefit from this lower browse, with the result that these treatments offered no substantive protection. Browse on balsam fir was not correlated to growth, nor was it significantly different in any treatments, demonstrating a high level of preferential browse on northern white-cedar. Browse analysis indicated that a population level less than the number of deer present at study sites would be necessary to avoid the detrimental impact of herbivory on northern white-cedar.

Results further indicated that in the face of current herbivory levels (1) planted northern white-cedar seedlings continue to expend biological resources by replacing lost vegetation despite negative height growth and positive basal diameter growth, and (2) planted balsam fir seedlings experience positive growth rates for both height and basal diameter. This dynamic suggests that at current herbivory levels, northern white-cedar seedlings will expend their carbohydrate reserves and eventually die, while balsam fir seedlings are likely to survive and grow to maturity. This scenario illustrates the failure

of sapling recruitment that characterizes northern white-cedar in the presence of deer populations.

Observations of annual re-growth of removed vegetation suggest that if browse were restricted within the first few years of planting, this trend could be stopped. Northern white-cedar seedlings exhibit a strong ability to restore browsed vegetation annually and to commit resources to basal diameter growth even under the influence of browse. It has been demonstrated that this can continue for several years, which could provide a window of opportunity for protection critical for seedling survival.

Northern white-cedar is well suited to planting in riparian areas, if sites that experience a high incidence of seasonal flooding are avoided. Planted seedlings have the potential to re-establish advance regeneration lost to herbivory, and are appropriate for reforestation and restoration in both harvested and unharvested riparian areas.

Further research

Continued research into the performance of planted northern white-cedar seedlings (from this established study and in new plantings) will help us develop management strategies that encourage this valuable riparian forest species. The following topics are of interest:

(1) Ongoing observation of existing plantings would provide information about (a) changing growth rates of both northern white-cedar and balsam fir as they progress into the sapling stage and (b) long-term implications for interspecies competition and potential overstory recruitment under this target harvest scenario ($11.6 \text{ m}^2\text{hc}^{-1}$ RBA).

(2) Closer examination of the soil environment and surrounding vegetation, with correlation to height and basal diameter growth, would reveal specific seedling nutrient and light requirements that could be helpful in identifying optimal planting sites.

(3) Additional study of biomass allocation to root, shoot, and vegetation growth would help us further understand seedling growth mechanisms and their response to stress.

(4) Examination of site level differences (such as topography, slope, depth to groundwater, soil type, width of flood zone) and their contribution to long-term seedling performance could increase our understanding of the requirements for northern white-cedar forest stands.

(5) Research into herbivory repellents and deer exclusion treatments are needed, such as foliar sprays, bud-capping, and slash barriers. This study did not fully examine slash configurations as long-term seedling cover. Protection of a subset of browsed seedlings could provide information about the potential for recovery from browse.

(6) Further study of different harvest designs (such as uneven or increased RMZ widths and low or no-harvest uplands) and densities (other than $11.6 \text{ m}^2 \text{ hc}^{-1}$ RBA) and their effects on deer movement and consequent herbivory would develop alternative harvest scenarios that could optimize protection of planted northern white-cedar seedlings.

Chapter 3 Tables

Table 3.1. Study site locations and local site information. Data is from Kastendick 2005 and author field data (*).

Site name	Latitude Longitude	County	Waterbody width (m)	Soil Type*	Relief (m)*		Primary pre- harvest timber species present	Mean (\pm SE) pre- harvest RMZ basal area (m ² hc ⁻¹)	Mean (\pm SE) post- harvest RMZ basal area (m ² hc ⁻¹)
					Control	Harvest			
Shotley Brook	N 48.05958 W 94.55176	Beltrami	4.6	Deep sandy loam	0-2	0-2	Northern hardwoods, aspen, lowland hardwoods	33.6 (4.9)	20.1 (3.7)
Nemadji State Forest	N 46.42021 W 92.31652	Carlton	1	Sandy loam, sandy clay loam	0-20	0-4	Northern hardwoods and aspen	20.8 (5.4)	11.2 (4.3)
East Branch Beaver River	N 47.33702 W 91.36048	Lake	5.5	Shallow sandy loam, shallow clay loam	0-10	0-25	Birch, aspen, lowland hardwoods, balsam fir	22.7 (3.1)	15.5 (2.8)

Table 3.2. General linear model output for browse frequency between unfenced species (Spp: northern white-cedar and balsam fir seedlings, four years in the field) in overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformation: $\sqrt{\sin^2}$ = arcsine square root.

Browse frequency $\sqrt{\sin^2}$ ($r^2 = 0.81$)

<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.0955	NR	NR
Species	1	0.8456	47.90	<.0001*
Microsite	2	0.1677	4.75	0.0212*
Overstory	1	0.1348	7.64	0.0124*
Spp x Ms	2	0.0579	1.64	0.2201
Spp x Os	1	0.0193	1.09	0.3087
Ms x Os	2	0.0034	0.10	0.9094
Spp x Ms x Os	2	0.0439	1.24	0.3106
Model	13	1.4090	6.14	0.0002*
Error	19	0.3354		
Corrected Total	32	1.7444		

Table 3.3. General linear model output for percent survival between species (Spp: northern white-cedar and balsam fir seedlings, four years in the field) in fence positions (F: fenced, unfenced), overstory treatments (Os: control, harvest), and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformation: $\sqrt{\arcsin}$ = arcsine square root.

Percent Survival $\sqrt{\arcsin}$ ($r^2 = 0.76$)

<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	5.1887	NR	NR
Species	1	0.8133	9.58	0.0034*
Fence	1	0.9110	10.73	0.0020*
Overstory	1	0.4341	5.11	0.0286*
Microsite	2	3.9508	23.26	<.0001*
Spp x F	1	0.1311	1.54	0.2204
Spp x Os	1	0.5070	5.97	0.0185*
Spp x Ms	2	0.0614	0.36	0.6986
F x Os	1	0.0420	0.49	0.4854
F x Ms	2	0.3478	2.05	0.1407
Os x Ms	2	0.0391	0.23	0.7951
Spp x F x Os	1	0.0071	0.08	0.7739
Spp x F x Ms	2	0.0030	0.02	0.9825
Spp x Os x Ms	2	0.0393	0.23	0.7945
F x Os x Ms	2	0.0835	0.49	0.6148
Spp x F x Os x Ms	2	0.0243	0.14	0.8669
Model	25	12.5836	5.93	<.0001*
Error	46	3.9072		
Corrected Total	71	16.4908		

Table 3.4. General linear model output for relative height growth between species (Spp: northern white-cedar and balsam fir seedlings, four years in the field) in fence positions (F: fenced, unfenced), overstory treatments (Os: control, harvest), and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformation: $\sqrt{\arcsin}$ = arcsine square root.

Relative Height Growth $\sqrt{\arcsin}$ ($r^2 = 0.72$)

<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.1563	NR	NR
Species	1	0.0529	9.21	0.0043*
Fence	1	0.0710	12.37	0.0011*
Overstory	1	0.0616	10.72	0.0022*
Microsite	2	0.0117	1.02	0.3700
Spp x F	1	0.0885	15.41	0.0003*
Spp x Os	1	0.0221	3.86	0.0567
Spp x Ms	2	0.0034	0.29	0.7482
F x Os	1	0.0261	4.54	0.0394*
F x Ms	2	0.0043	0.38	0.6876
Os x Ms	2	0.0054	0.47	0.6261
Spp x F x Os	1	0.0034	0.59	0.4455
Spp x F x Ms	2	0.0308	2.68	0.0813
Spp x Os x Ms	2	0.0177	1.54	0.2274
F x Os x Ms	2	0.0079	0.69	0.5097
Spp x F x Os x Ms	2	0.0023	0.21	0.8147
Model	25	0.5725	3.99	<.0001*
Error	39	0.2240		
Corrected Total	64	0.7965		

Table 3.5. General linear model output for relative diameter growth between species (Spp: northern white-cedar and balsam fir seedlings, four years in the field) in fence positions (F: fenced, unfenced), overstory treatments (Os: control, harvest), and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformation: UT = untransformed.

Relative Diameter Growth^{UT} ($r^2 = 0.71$)

<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.0290	NR	NR
Species	1	0.0253	11.80	0.0014*
Fence	1	0.0466	21.70	<.0001*
Overstory	1	0.0506	23.59	<.0001*
Microsite	2	0.0033	0.76	0.4739
Spp x F	1	0.0146	6.78	0.0130*
Spp x Os	1	0.0030	1.40	0.2443
Spp x Ms	2	0.0028	0.65	0.5264
F x Os	1	0.0104	4.85	0.0337*
F x Ms	2	0.0028	0.66	0.5229
Os x Ms	2	0.0030	0.69	0.5073
Spp x F x Os	1	0.0001	0.02	0.8896
Spp x F x Ms	2	0.0064	1.50	0.2357
Spp x Os x Ms	2	0.0002	0.05	0.9469
F x Os x Ms	2	0.0035	0.82	0.4468
Spp x F x Os x Ms	2	0.0007	0.17	0.8417
Model	25	0.2066	3.85	<.0001*
Error	39	0.0837		
Corrected Total	64	0.2903		

Table 3.6. General linear model output for (a) height and (b) basal diameter of northern white-cedar seedlings (four years in the field) by fence position (F: fenced, unfenced), overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformations: $\Phi = \log$.

(a)					(b)				
<u>Height Φ ($r^2 = 0.92$)</u>					<u>Basal diameter Φ ($r^2 = 0.85$)</u>				
<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.0799	NR	NR	Site	2	0.1012	NR	NR
Overstory	1	0.8772	8.57	0.0090*	Overstory	1	0.1161	27.92	<.0001*
Microsite	2	0.0120	1.02	0.3820	Microsite	2	0.0082	0.99	0.3914
Fence	1	0.0506	148.69	<.0001*	Fence	1	0.1439	34.62	<.0001*
Os x Ms	2	0.0488	0.07	0.9301	Os x Ms	2	0.0023	0.28	0.7595
Os x F	1	0.0803	13.62	0.0017*	Os x F	1	0.0222	5.33	0.0331*
Ms x F	2	0.0009	4.13	0.0334*	Ms x F	2	0.0133	1.60	0.2300
Os x Ms x F	2	0.0089	0.75	0.4865	Os x Ms x F	2	0.0066	0.80	0.4666
Model	13	1.2455	16.24	<.0001*	Model	13	0.4367	8.08	<.0001*
Error	18	0.1062			Error	18	0.0748		
Corrected Total	31	1.3517			Corrected Total	31	0.5115		

Table 3.7. General linear model output for (a) height and (b) basal diameter of balsam fir seedlings (four years in the field) in fence position (F: fenced, unfenced), overstory treatments (Os: control, harvest) and microsite treatments (Ms: mound, pit, slash). N = 3 sites; NR = not reported because Site was used as the blocking factor. Reported r^2 value is for the model. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformations: $\Phi = \log$.

(a)					(b)				
<u>Height</u> Φ ($r^2 = 0.78$)					<u>Basal diameter</u> Φ ($r^2 = 0.75$)				
<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>	<u>Source</u>	<u>DF</u>	<u>Type III SS</u>	<u>F-stat</u>	<u>P-value</u>
Site	2	0.1635	NR	NR	Site	2	0.0349	NR	NR
Overstory	1	0.4551	42.34	<.0001*	Overstory	1	0.2302	38.36	<.0001*
Microsite	2	0.0233	1.08	0.3583	Microsite	2	0.0350	2.91	0.0788
Fence	1	0.0928	8.63	0.0084*	Fence	1	0.0342	5.70	0.0275*
Os x Ms	2	0.0466	2.17	0.1418	Os x Ms	2	0.0170	1.41	0.2678
Os x F	1	0.0099	0.92	0.3491	Os x F	1	0.0113	1.88	0.1866
Ms x F	2	0.0225	1.05	0.3707	Ms x F	2	0.0114	0.95	0.4029
Os x Ms x F	2	0.0030	0.14	0.8722	Os x Ms x F	2	0.0060	0.50	0.6135
Model	13	0.7198	5.15	0.0007*	Model	13	0.3382	4.33	0.0020*
Error	19	0.2042			Error	19	0.1140		
Corrected Total	32	0.9240			Corrected Total	32	0.4522		

Table 3.8. Correlations between percent browse frequency on unfenced seedlings (four years in the field) and independent variables of surrounding vegetation; see *Data collection and analysis* section for an explanation of variables. (-) indicates a negative correlation. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformations: Φ = log, Θ = square root, Ψ = arcsine square root.

Independent variable	Northern white-cedar %Browse frequency Ψ (n = 46)		Balsam fir %Browse frequency Ψ (n = 43)	
	P value	r	P value	r
Basal area Φ, Θ	0.01*	- 0.39	0.14	- 0.23
% Forest floor cover Ψ	< .0001*	- 0.57	0.01*	- 0.38
% Moss cover Φ	0.08	0.26	0.74	0.05
% Woody cover Ψ	0.19	0.20	0.44	0.12

Table 3.9. Correlations between height and basal diameter of northern white-cedar seedlings (four years in the field) and independent variables of surrounding vegetation and browse frequency; see *Data collection and analysis section* for explanation of variables. (-) indicates a negative correlation. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformations: Θ = square root, \bullet = inverse square root, Φ = log, UT = untransformed, Ψ = arcsine square root.

FENCED Northern white-cedar					UNFENCED Northern white-cedar				
Independent variable	Height Θ (n = 46)		Basal diameter \bullet		Independent variable	Height Θ (n = 46)		Basal diameter UT	
	P value	r	P value	r		P value	r	P value	r
					% Browse frequency Ψ	<.0001*	- 0.58	0.09	- 0.26
Basal area Φ	< .0001*	- 0.64	< .0001*	- 0.60	Basal area Φ	0.96	0.01	0.71	- 0.06
% Forest floor cover Θ	0.0001*	- 0.54	0.001*	- 0.46	% Forest floor cover Ψ	0.22	0.18	0.17	0.21
% Moss cover Θ	0.67	- 0.07	0.89	0.02	% Moss cover Φ	0.06	- 0.28	0.06	- 0.28
% Herbaceous cover UT	0.003*	0.42	0.01*	0.37	% Herbaceous cover Θ	0.45	- 0.11	0.68	- 0.07
% Woody cover Θ	0.03*	0.31	0.01*	0.40	% Woody cover Ψ	0.22	- 0.18	0.03*	- 0.34

Table 3.10. Correlations between height and basal diameter of balsam fir seedlings (four years in the field) and independent variables of surrounding vegetation and browse frequency; see *Data collection and analysis* section for explanation of variables.(-) indicates a negative correlation. Asterisk (*) indicates significant p-values at $\alpha = 0.05$. Transformations: Φ = log, \bullet = inverse square root, Θ = square root, UT = untransformed, Ψ = arcsine square root.

FENCED Balsam fir					UNFENCED Balsam fir				
Independent variable	Height Φ (n = 44)		Basal diameter \bullet		Independent variable	Height Φ (n = 43)		Basal diameter Φ	
	P value	r	P value	r		P value	r	P value	r
					% Browse frequency Ψ	0.16	- 0.22	0.77	0.05
Basal area Φ	0.0001*	- 0.58	0.0001*	- 0.55	Basal area Φ	0.01*	- 0.42	<.0001*	- 0.56
% Forest floor cover Θ	0.42	- 0.13	0.17	- 0.21	% Forest floor cover Ψ	0.21	- 0.20	0.06	- 0.29
% Moss cover Θ	0.02*	- 0.36	0.20	- 0.21	% Moss cover Φ	0.01*	- 0.41	0.03*	- 0.33
% Herbaceous cover ^{UT}	0.78	0.04	0.41	0.13	% Herbaceous cover Θ	0.83	0.03	0.37	0.14
% Woody cover Θ	0.01*	0.38	0.16	0.21	% Woody cover Ψ	0.37	0.14	0.20	0.20

Chapter 3 Figures

Figure 3.1. Location of study sites in Minnesota. 1 = Shotley Brook, Beltrami County; 2 = Nemadji State Forest, Carlton County; 3 = East Branch Beaver River, Lake County. (MNMapper Jul 2009).

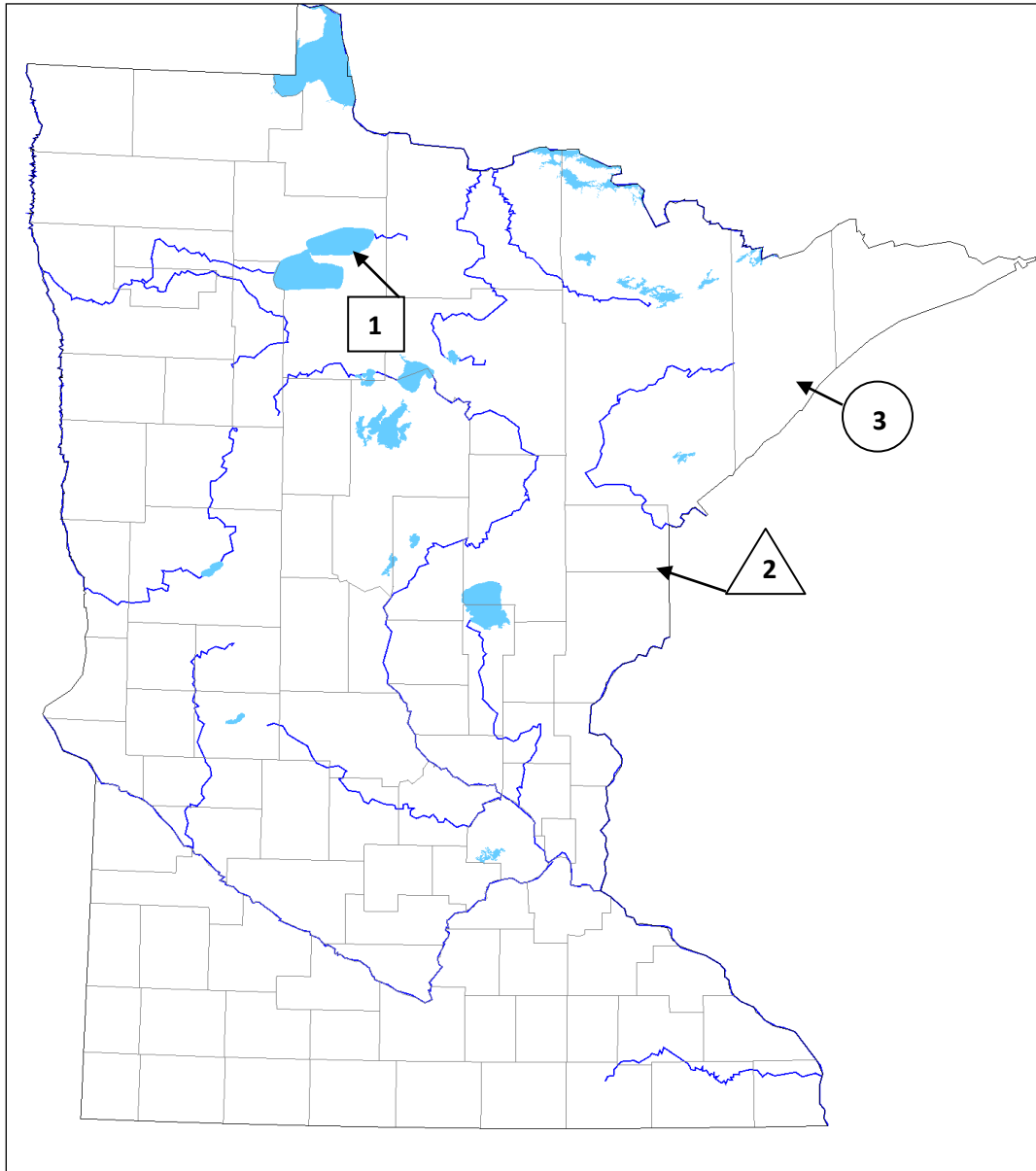


Figure 3.2. Conceptual model of experimental design at each of three study sites. M = mound microsite, P = pit microsite, S = slash microsite. Control and partial harvest areas measure 46 m deep by 183 m wide; unharvested buffer areas measure 46 m deep by 61 m wide. Illustration is not to scale.

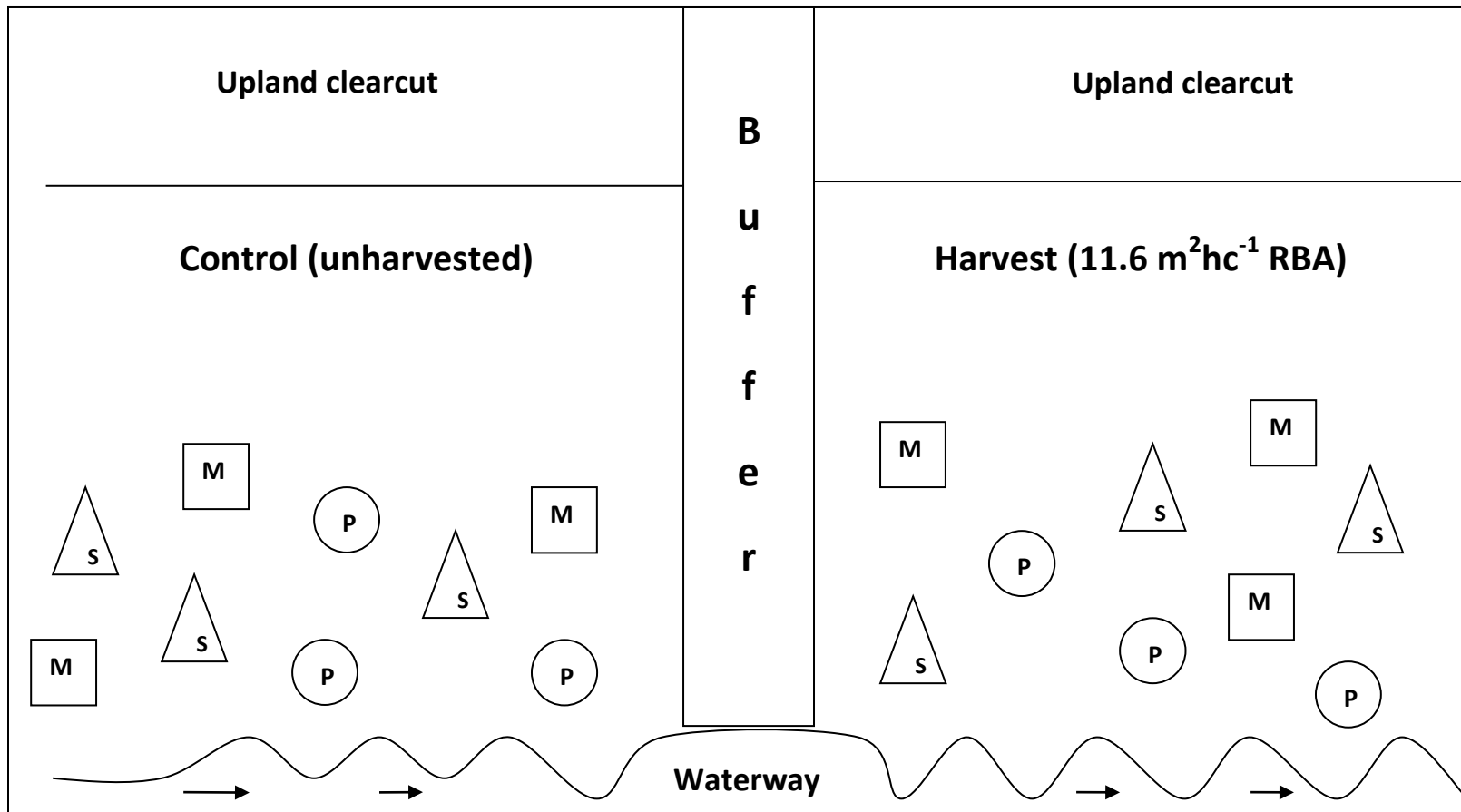


Figure 3.3. Idealized microsite plot with planted seedlings. Squares (N) represent northern white-cedar seedlings, circles (B) represent balsam fir seedlings.

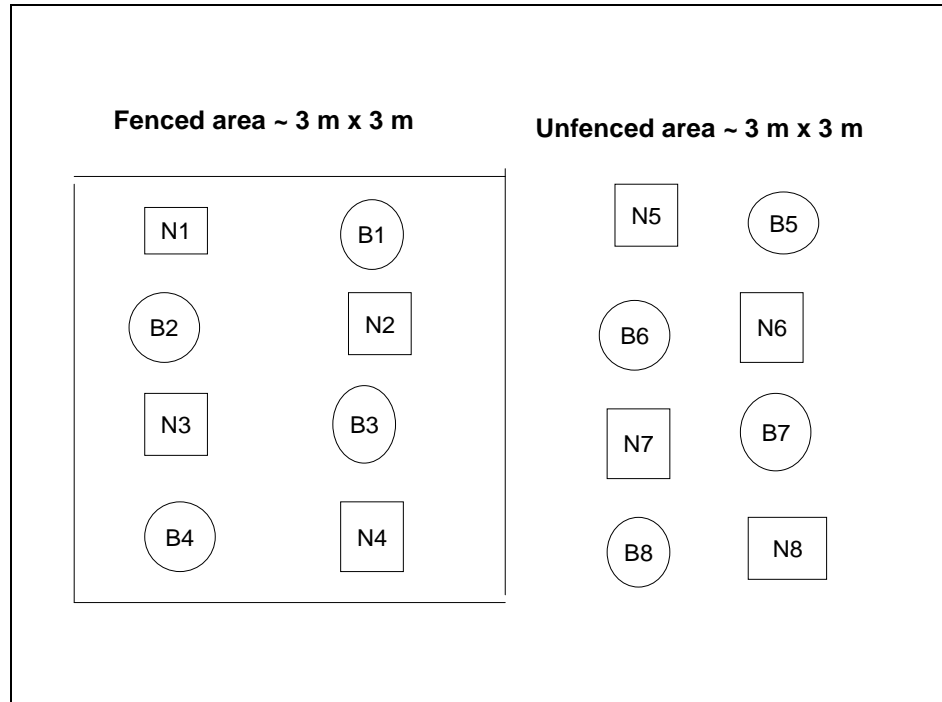


Figure 3.4. Percent browse frequency after four years in the field on unfenced northern white-cedar and balsam fir seedlings by overstory and microsite treatments. Column bars show standard errors for $n = 3$ ($n = 2$ in pits due to mortality). Tukey-Kramer means with the same letter are not significantly different at $\alpha = 0.05$. Browse between species (A,B), overstory treatments (a,b), and microsites (mounds > pits, data not shown) were all significant.

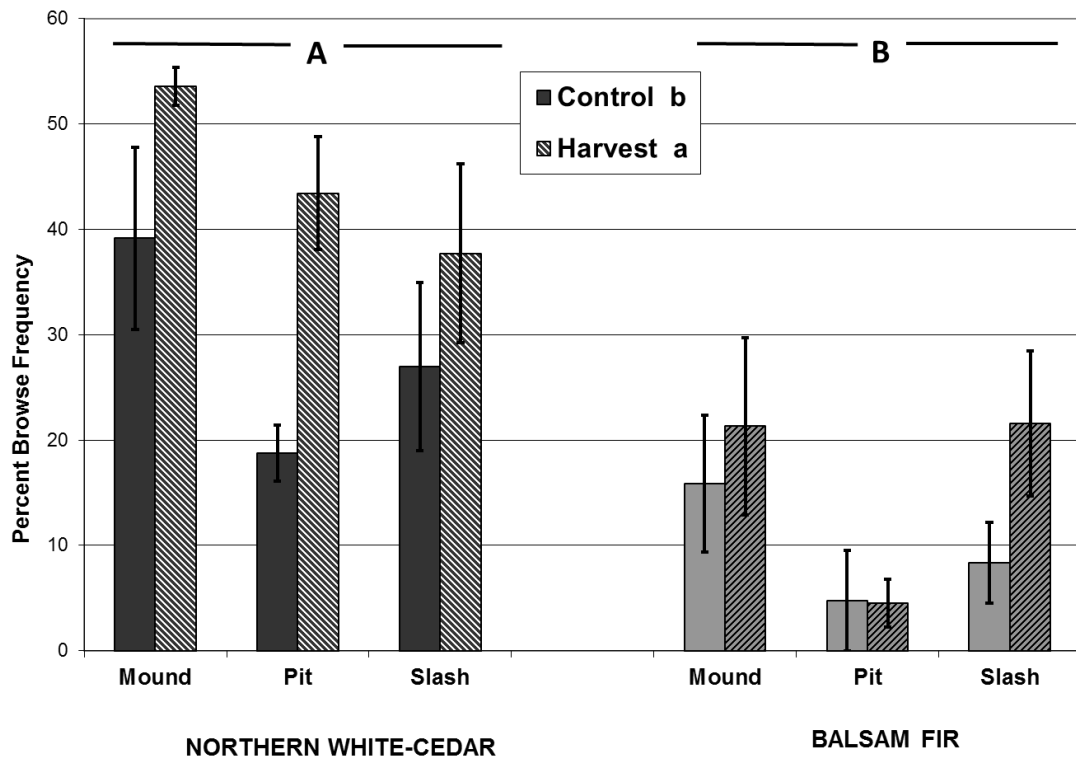


Figure 3.5. Percent survival for northern white-cedar and balsam fir seedlings after four years in the field by fence, overstory, and microsite treatments. Column bars show standard errors for n = 3 (n = 2 in pits due to mortality). Significant differences are shown between fence treatment (A,B) and species x fence treatment (a,b). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey-Kramer's test.

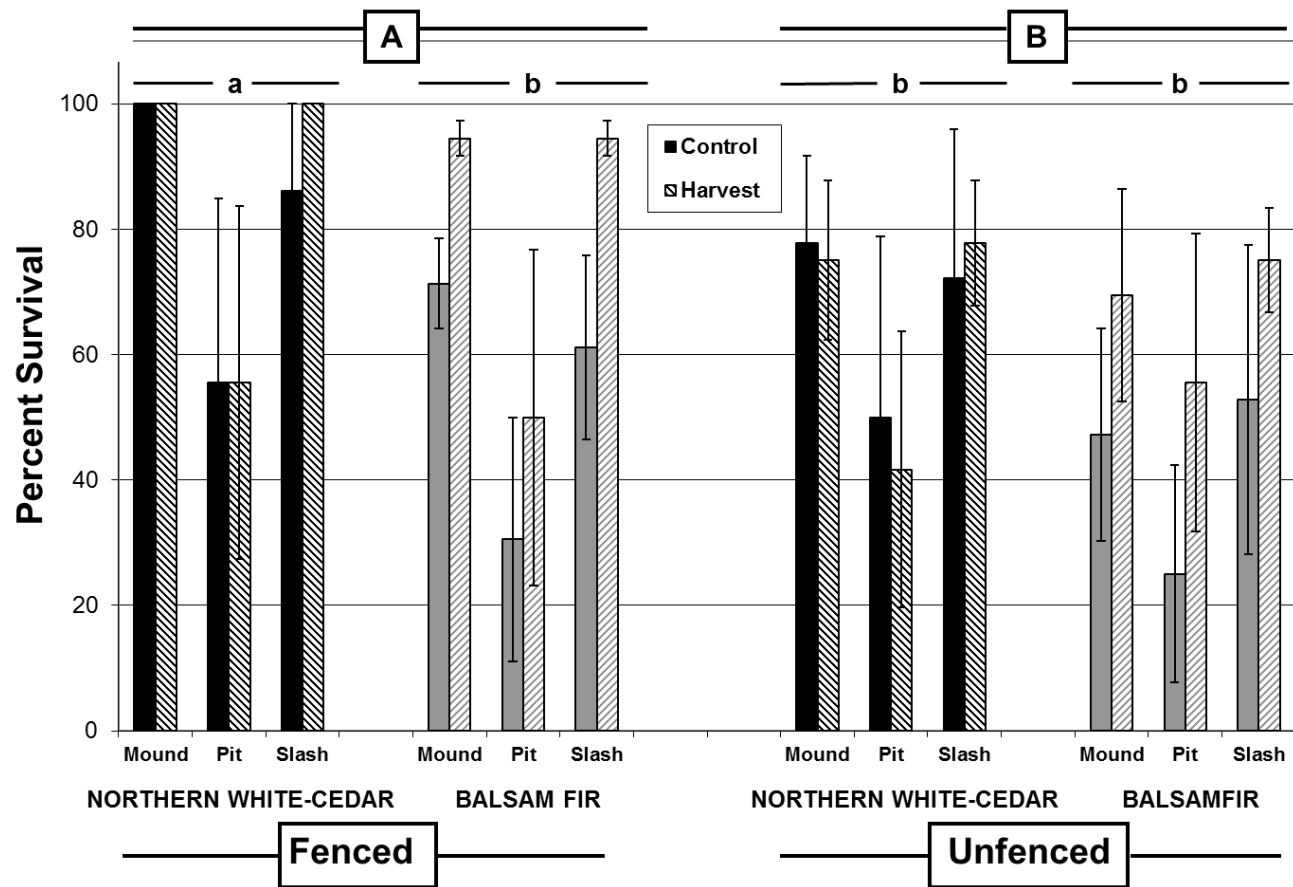
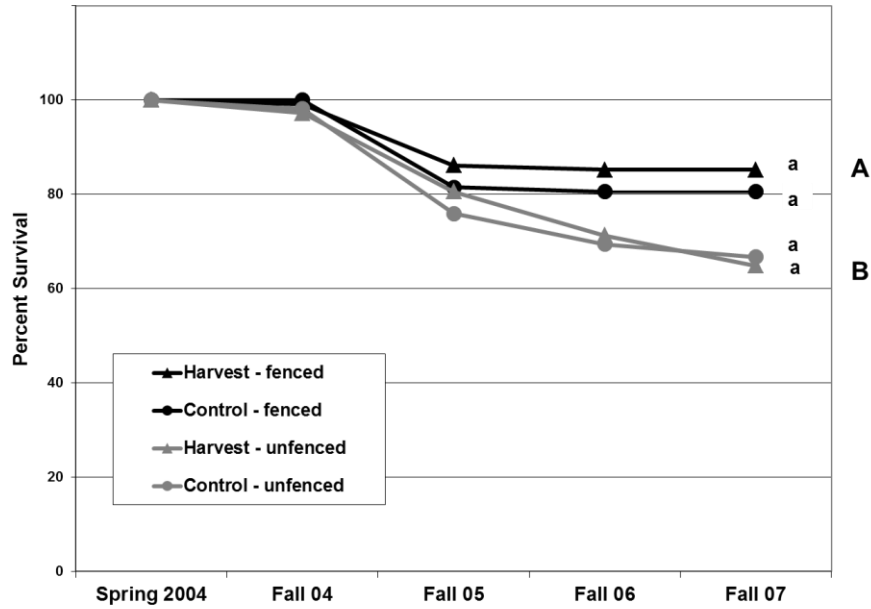


Figure 3.6. Percent survival over time for (a) northern white-cedar and (b) balsam fir. Significance is shown within species for fence treatment (A,B) and overstory treatment (a,b). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's HSD test.

(a) Northern white-cedar



(b) Balsam fir

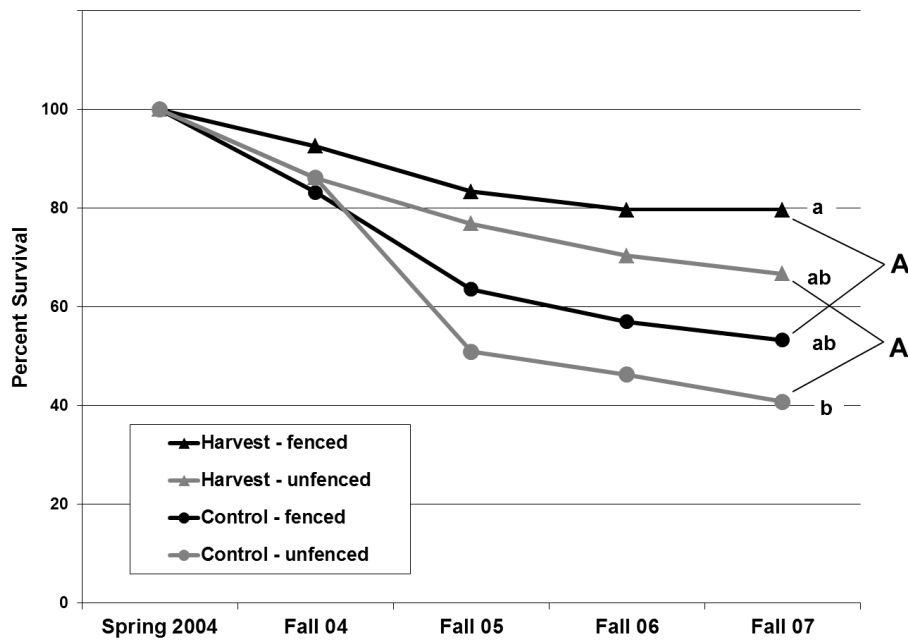


Figure 3.7. Relative height growth (RHG) of northern white-cedar and balsam fir seedlings after four years in the field by fence, overstory, and microsite treatments. Column bars show standard errors for n = 3 (n = 2 in pits due to mortality). Significant differences are shown between fence treatments (A,B) and species x fence treatment (a,b,c). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey-Kramer's test.

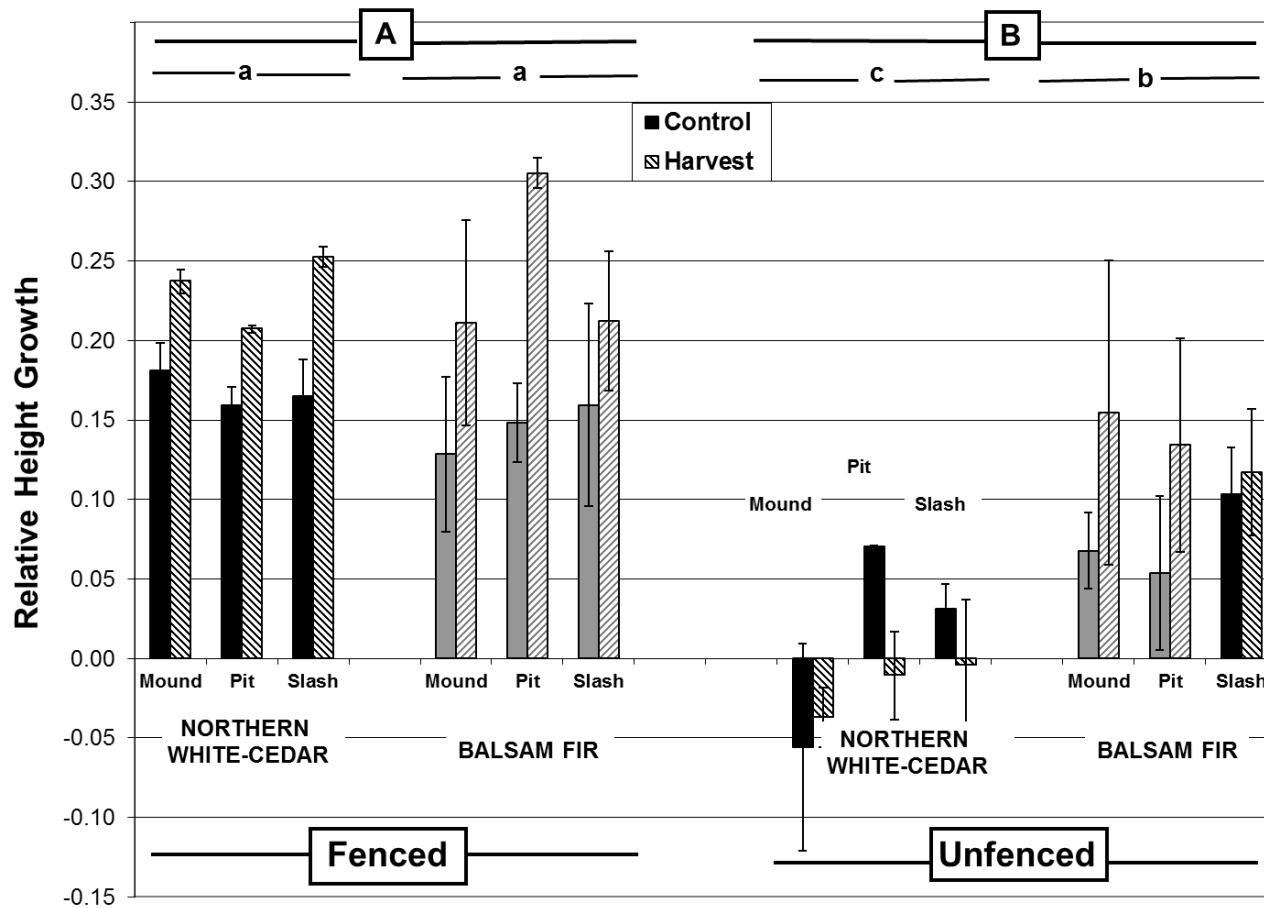


Figure 3.8. Relative diameter growth (RDG) of northern white-cedar and balsam fir seedlings after four years in the field by fence, overstory, and microsite treatments. Column bars show standard errors for n = 3 (n = 2 in pits due to mortality). Significant differences are shown between fence treatment (A,B) and species x fence treatment (a,b). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey-Kramer's test.

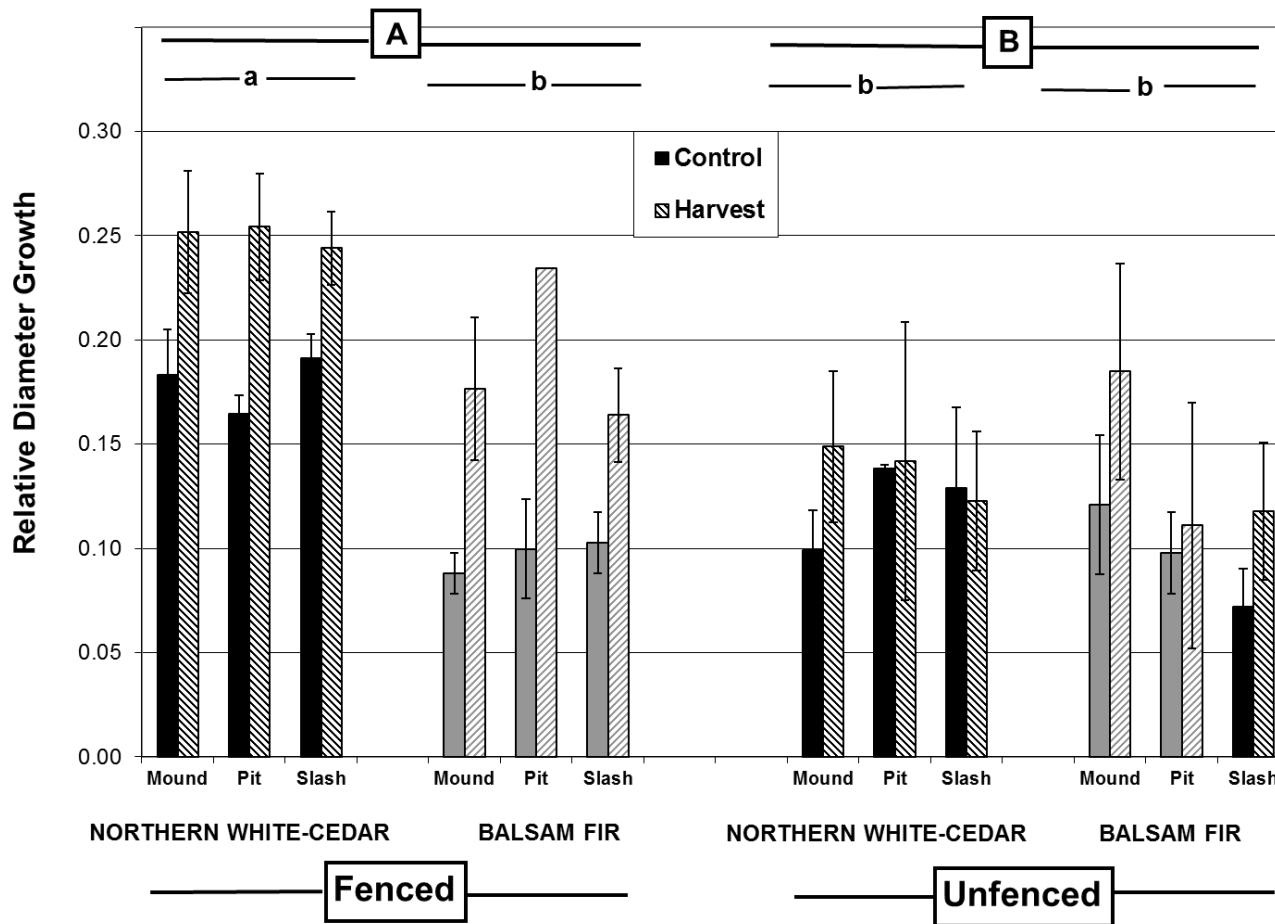
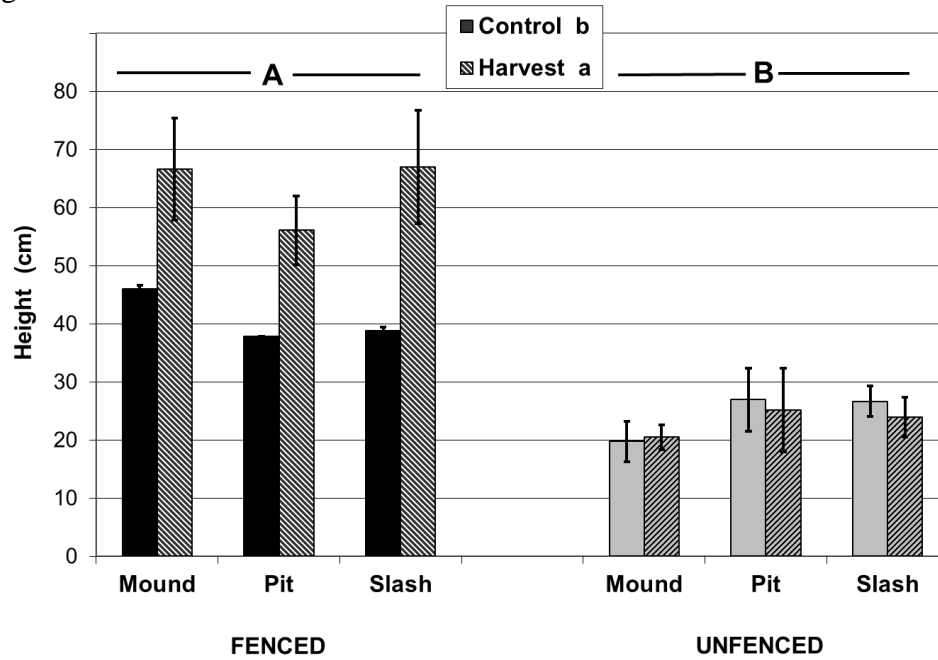


Figure 3.9. Size of northern white-cedar seedlings after four years in the field by fence, overstory and microsite treatments for (a) height and (b) basal diameter. Column bars show standard errors for $n = 3$ ($n = 2$ in pits due to mortality). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey-Kramer's test. Significant differences exist between fence treatments (A,B) and between overstory treatments pooled across fence positions (a,b).

(a) Height



(b) Basal diameter

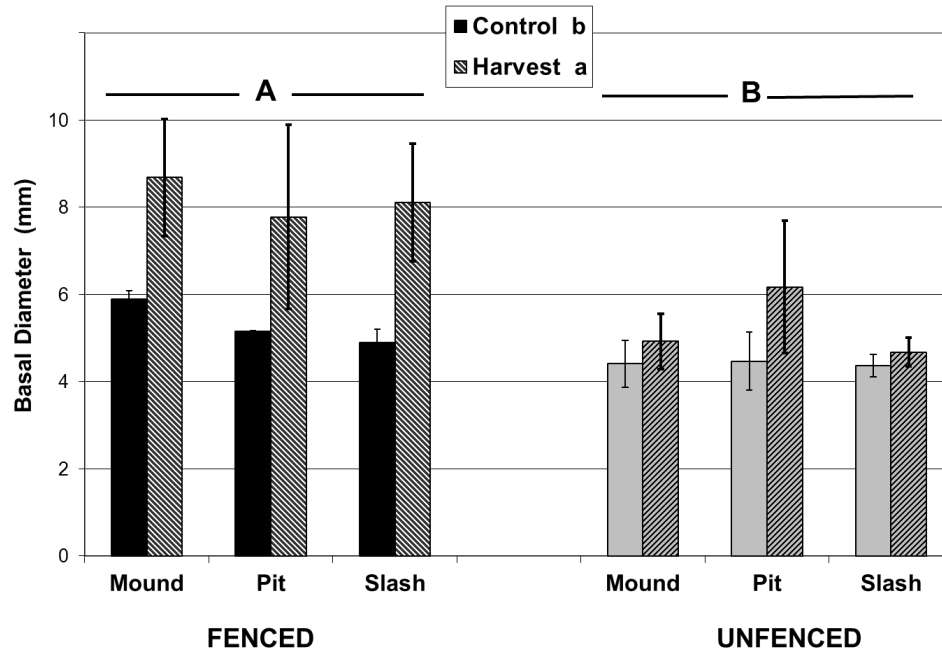
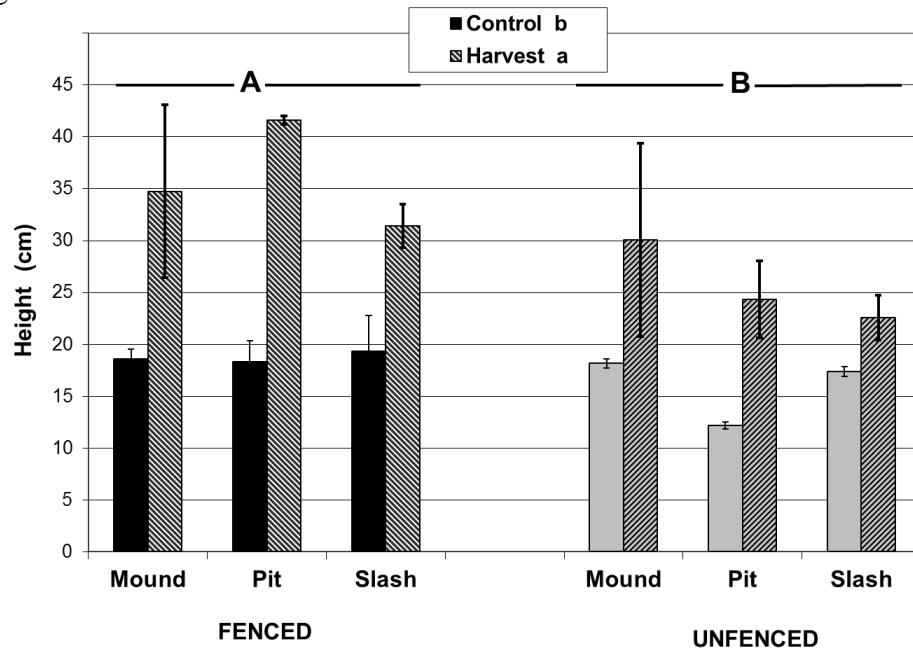
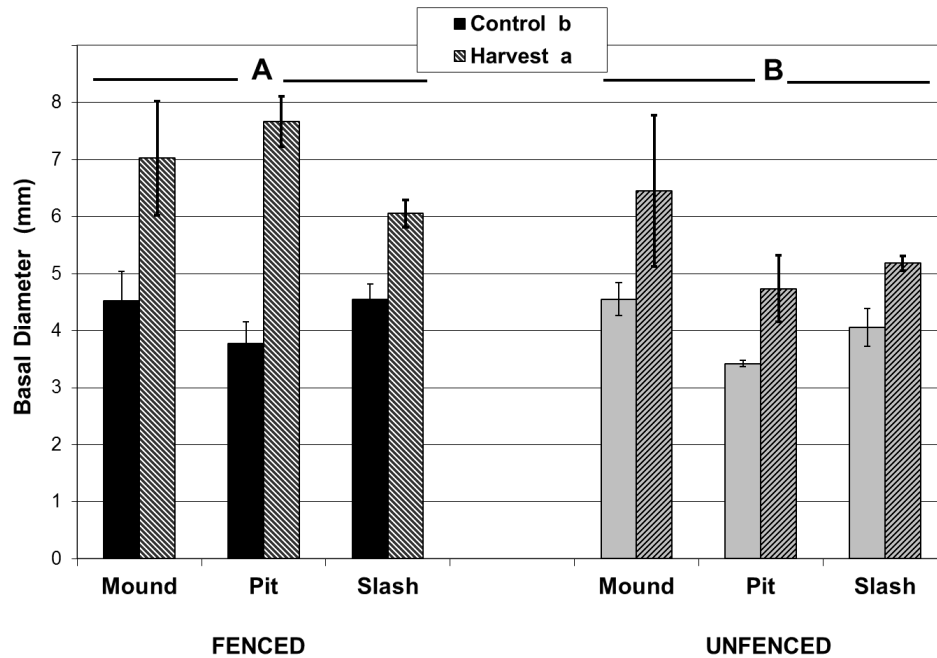


Figure 3.10. Size of balsam fir seedlings after four years in the field by fence, overstory and microsite treatments for (a) height and (b) basal diameter. Column bars show standard errors for $n = 3$ ($n = 2$ in pits due to mortality). Treatment means with the same letter are not significantly different at $\alpha = 0.05$ by Tukey-Kramer's test. Significant differences exist between fence treatments (A,B) and between overstory treatments pooled across fence positions (a,b).

(a) Height



(b) Basal diameter



Chapter 3 Bibliography

- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2(4):348-58.
- Boelter, D. H., and G. E. Close. 1974. Pipelines in forested wetlands. *Journal of Forestry* September:561-63.
- Chimner, R. A., and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Canadian Journal of Forest Research* 26:389-93.
- Cole, G. F. 1987. Changes in interacting species with disturbance. *Environmental Management* 11(2):257-64.
- Cornett, M. W. "Conifer regeneration in mixed deciduous-evergreen forests." MS thesis, University of Minnesota, 1996.
- Cornett, M. W. "Ecological restoration of upland northern white cedar forests on the Lake Superior highlands." Ph.D. diss., University of Minnesota, 2000.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology* 9(4):386-96.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.
- Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics* 35:113-47.
- Davis, A. S., and D. F. Jacobs. 2005. Quantifying root system quality of nursery seedlings and relationship to outplanting performance. *New Forests* 30:295-311.
- Davis, A., K. Puettmann, and D. Perala. 1998. *Site preparation treatments and browse protection affect establishment and growth of northern white-cedar*. Research Paper NC-330. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- Duchesneau, R., I. Lesage, I. Robin, C. Messier, and H. Morin. 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management* 140:215-25.
- Edelstein, Z. R., and E. D. Ford. 2003. Branch and foliage morphological plasticity in old-growth *Thuja plicata*. *Tree Physiology* 23:649-62.

- Forester, J. D., D. P. Anderson, and M. G. Turner. 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *American Midland Naturalist* 160:438-53.
- Fraver, S., R. G. Wagner, and M. Day. 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.
- Greenwood, M. S., C. L. O'Brien, J. D. Schatz, C. A. Diggins, M. E. Day, G. L. Jacobson, A.S. White, and R. G. Wagner. 2008. Is early life cycle success a determinant of the abundance of red spruce and balsam fir? *Canadian Journal of Forest Research* 38:2295-2305.
- Grigal, D. F., and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecological Monographs* 45:389-407.
- Habeck, J. R. 1958. White cedar ecotypes in Wisconsin. *Ecology* 39(3):457-63.
- Harper, J. L. 1977. *Population Biology of Plants*. San Diego, CA: Academic Press, Inc.
- Häsler, H., J. Senn, and P. J. Edwards. 2008. Light-dependent growth responses of young *Abies alba* to simulated ungulate browsing. *Functional Ecology* 22:48-57.
- Haworth, B. K. "A comparison of *Thuja occidentalis* and *Abies balsamea* seedling response to partial harvest and microsite in northern Minnesota riparian forests." Ch. 2 of MS thesis, University of Minnesota, 2011.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-82.
- Heitzman, E., K. S. Pregitzer, and R. O. Miller. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Canadian Journal of Forest Research* 27:1953-61.
- Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.
- Jacobs, D. F., K. F. Salifu, J. R. Seifert. 2005. Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. *New Forests* 30:235-51.
- Johnston, W. F. 1986. *Manager's handbook for balsam fir in the North Central States*. General Technical Report NC-111. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.

- Johnston, W. F. 1990. *Thuja occidentalis* L. Northern white-cedar. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.
- Kastendick, D. N. "Riparian forest management in northern Minnesota: Effects of riparian silvicultural treatments on forest biomass, structure, composition, and indices of plant available nutrients." MS thesis, University of Minnesota, 2005.
- Krasowski, M. J., and J. N. Owens. 1991. Growth and morphology of western red cedar seedlings as affected by photoperiod and moisture stress. *Canadian Journal of Forest Research* 21:340-52.
- Larouche, C., L. S. Kenefic, and J.-C. Ruel. 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.
- Lavender, D. P., and S. N. Salim. 1987. The role of plant growth regulators in dormancy in forest trees. *Plant Growth Regulation* 6:171-91.
- Logan, K. T. 1969. *Growth of tree seedlings as affected by light intensity: IV. Black spruce, white spruce, balsam fir and eastern white cedar*. Publication No.1256. Canadian Forestry Service Department of Fisheries and Forestry.
- McLaren, B. E. 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. *Ecology* 77(1):228-35.
- Minnesota Department of Natural Resources. 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR St. Paul, MN.
- Minnesota Department of Natural Resources. 2010. Minnesota's forest resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.
- Minnesota Department of Natural Resources. 2007. [Internet]. Pre-fawn deer density from deer population model. [cited 2010 Dec 12] Available from: http://files.dnr.state.mn.us/recreation/hunting/deer/deer_density_prefawn_2007.pdf.
- Minnesota Forest Resource Council. 2010. [Internet]. Economic analysis of potential changes to the riparian forest management guidelines, SL-0110; prepared by C. Hibbard and R. Slesak. [cited 2010 Sep 12]. Available from: http://www.frc.state.mn.us/documents/council/site-level/MFRC_RSTC_econ_report_2010-01-15.pdf.
- Minnesota Forest Resources Council. 2005. *Sustaining Minnesota Forest Resources: Voluntary Site-level Forest Management Guidelines for Landowners, Loggers and Resource Managers*. St. Paul, MN: Minnesota Forest Resources Council.

MNMapper [Internet]. St. Paul, MN: Department of Administration, Office of Geographical and Demographic Analysis, Land Management Information Center; [created 2009 Jul 15] Available from: www.lmic.state.mn.us/chouse.

Pallardy, S. G. 2008. *Physiology of Woody Plants*, 3rd ed. Burlington, MA: Academic Press.

Parent, S., H. Morin, C. Messier, and M-J. Simard. 2006. Growth, biomass allocation, and adventitious roots of balsam fir seedlings growing in closed-canopy stands. *Ecoscience* 13(1):89-94.

Parker, T., and F. D. Johnson. 1987. Branching and terminal growth of western redcedar. *Northwest Science* 61(1):7-12.

Peterson, C. J., and S. T. A. Pickett. 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. *Ecology* 76(3):763-74.

Pregitzer, K. S. 1990. The ecology of northern white-cedar. In *Proceedings of Northern white cedar in Michigan*, ed. D. O. Lantagne, 8-14. Research Report 512. East Lansing, MI: Michigan Agricultural Experiment Station.

Rooney, T.P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165-76.

Rose, R., D. L. Haase, F. Kroihner, and T. Sabin. 1997. Root volume and growth of ponderosa pine and douglas-fir seedlings: A summary of eight growing seasons. *Western Journal of Applied Forestry* 12(3):69-73.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. *American Midland Naturalist* 146(1): 1-26.

SAS Institute, Inc. 2003. SAS/STAT® Software Version 9.1.3. Cary, NC: SAS Institute Inc.

Schaffer, W. W. 1996. *Silvicultural guidelines for the eastern white cedar*. Technical Report TR-006, Ontario: Ontario Ministry of Natural Resources, Southern Region Science & Technology Transfer Unit.

Simard, M.-J., Y. Bergeron, and L. Sirois. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: The importance of substrate. *Journal of Vegetation Science* 9(4):575-82.

- Smith, J. R., R. A. Sweitzer, and W. F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. *Journal of Wildlife Management* 71(8):2719-26.
- St-Louis, A., J.-P. Ouellet, M. Crête, J. Maltais, and J. Huot. 2000. Effects of partial cutting in winter on white-tailed deer. *Canadian Journal of Forest Research* 30:655-661.
- Stoeckeler, J. H. 1967. *Wetland road crossings: Drainage problems and timber damage*. Research Note NC-27. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. *American Midland Naturalist* 135(2):181-94.
- Verme, L. J., and W. F. Johnston. 1986. Regeneration of northern white cedar deeryards in upper Michigan. *The Journal of Wildlife Management* 50(2):307-13.
- Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: A keystone herbivore. *Wildlife Society Bulletin* 25(2):217-26.
- Waring, R. H. 1987. Characteristics of trees predisposed to die: Stress causes distinctive changes in photosynthates allocation. *BioScience* 37(8):569-74.
- Weiskittel, A. R., J. A. Kershaw Jr., P. V. Hofmeyer, and R. S. Seymour. 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* 258:1695-1703.
- Weiskittel, A. R., R. S. Seymour, P. V. Hofmeyer, and J. A. Kershaw Jr. 2010. *Forest Ecology and Management* 259:1912-21.

Chapter 4

Recommendations for Management of Planted Northern White-cedar Seedlings in Riparian Forests within Northern Minnesota

Chapter 4 Synopsis

Northern white-cedar (*Thuja occidentalis* L.), a long-lived conifer of riparian forests of northeastern North America, is an important species to riparian ecosystem health and to the forest products industry. The species is currently experiencing recruitment decline throughout much of its natural range, owing primarily to herbivory by white-tailed deer (*Odocoileus virginianus*) that remove seedling and sapling size classes. Due to preferential browse on northern white-cedar, balsam fir (*Abies balsamea* Mill.), a frequent cohort in mixed sub-boreal forests, often recruits more successfully into older age classes, further displacing the northern white-cedar component.

A four-year study, conducted on riparian harvest sites located in northern Minnesota, USA, was designed to (a) examine partial harvest and microsite effects on planted northern white-cedar seedling growth and (b) more fully understand the current dynamic between northern white-cedar and balsam fir seedlings in the presence of white-tailed deer. Results indicated that protected from herbivory, partial harvest of the overstory contributed to significant seedling growth with both species demonstrating potential to recruit into taller height classes. Microsites of mound, pit, and slash (important to seedling germination and establishment) did not contribute significantly to growth. Due to seasonal flooding, pits had a significant negative effect on survival.

Unfenced northern white-cedar showed significant mortality and no height increase in any treatments, with browse on seedlings overwhelming the benefits of overstory harvests. However, seedlings continued carbon allocation to basal diameter due to their ability to replace browsed foliage in the current year. In addition, northern white-cedar displayed survival resiliency for the four years when subjected to herbivory. Balsam fir seedlings were affected to a lesser degree by browse, maintained growth responses to harvest treatments, and did not experience significant mortality. Balsam fir exhibited the potential to recruit successfully into the overstory even under browse pressure, while northern white-cedar did not. Management activities that increase light availability while retaining some overstory structure and selection of planting sites that limit or exclude browse will result in the best chance for northern white-cedar seedlings to recruit into the sapling stage.

Background

The northern white-cedar forest type in Minnesota occurs primarily as a lowland conifer in the northeastern third of the state, occupying approximately 231,885 of 659,638 hectares (573,000 acres of 1.63 million acres) of riparian forests (MN DNR 2010; MFRC 2010), in addition to its common presence in mixed species stands. In riparian areas it provides ecological services to lake and river shore stability, water quality, wildlife habitat, and forest diversity. Accounting for 4% of total state timberland acreage, northern white-cedar has a rotation age of 70 to 140 years (with a potential life-span over 400 years), and offers economic products to the wood products industry including cabin logs, siding, and paneling (MN DNR 2010). Today's northern white-cedar stands likely originated after clear-cut harvests and subsequent wildfires (Pregitzer 1990; Heitzman et al. 1997).

Since the mid-twentieth century a decline in northern white-cedar recruitment has been documented throughout its range in the US. Contributing factors include fire (Heinselman 1973), impeded drainage (Boelter and Close 1974), competition (Heitzman et al. 1997), loss of decayed woody regeneration niches (Cornett et al. 2001), and slow growth rates (Larouche et al. 2010). However, the foremost cause of recruitment failure is herbivory from white-tailed deer (*Odocoileus virginianus*) (Cornett et al. 2000; Rooney et al. 2002; Hofmeyer et al. 2009). The ranges of northern white-cedar and white-tailed deer in Minnesota, once primarily separate now overlap. This allows deer to exert heavy feeding pressure on seedling and sapling size classes, effectively removing advance regeneration from the forest (Cornett et al. 1997; Heitzman et al. 1999). Balsam fir (*Abies*

balsamea Mill.) a less-browsed companion species in mixed sub-boreal forests, often recruits more successfully into taller height classes, further suppressing the northern white-cedar component (Hofmeyer et al. 2009).

Loss of advance regeneration has resulted in an aging northern white-cedar resource in Minnesota, where 45% of the northern white-cedar cover type (occupying 104,409 hectares or 258,000 acres) is older than 100 years and 2.5% (occupying less than 6,070 hectares or 15,000 acres) is younger than 30 years (MN DNR 2010) (Figure 4.1).

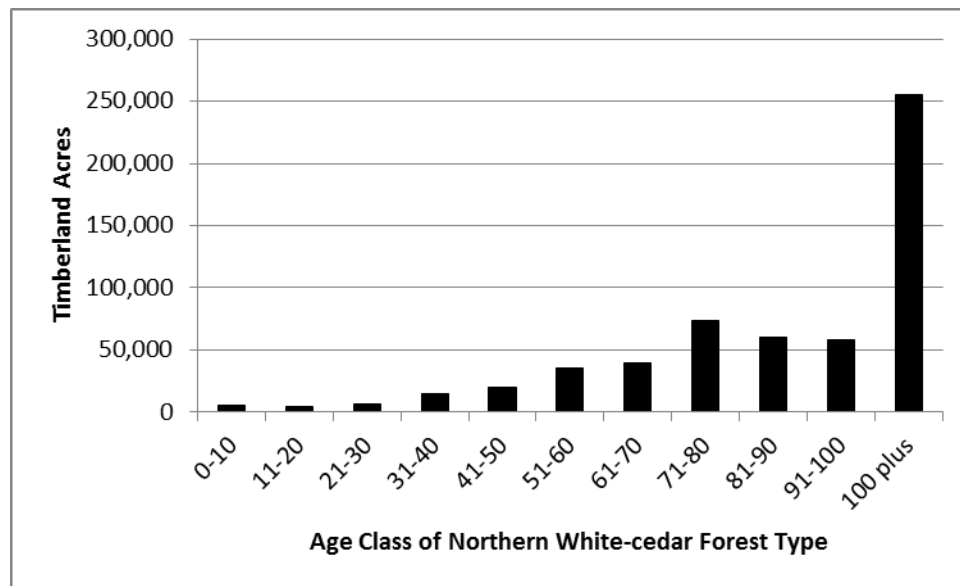


Figure 4.1. Timberland acres of the northern white-cedar forest type by age class in the state of Minnesota, all ownerships combined. There were 573,000 total acres in this forest type. (Data from MN DNR 2010).

By 1990 state and federal agencies in the Lake States had enforced limited cutting of northern white-cedar in response to diminished seedling recruitment (Miller et al. 1990). Currently federal and state land managers in Minnesota practice no cutting and leave tree policies (MN DNR, Superior National Forest, Chippewa National Forest pers. comm.).

Today the absence of sapling and pole size classes within both pure and mixed stands indicates that recruitment into existing stands may be insufficient to maintain viable populations in the future.

Riparian harvest, microsite and deer exclosure study

More information is needed on the recruitment requirements of northern white-cedar seedlings that are almost absent from Minnesota's productive riparian forests. Studies indicate that seed germination and establishment are aided by specialized forest microsites such as soil and stump mounds, decayed logs, pits, and slash piles (Johnston 1990; Cornett et al. 2001), but little is known about the advantages these microsites provide for the seedling to sapling stage. A study was conducted in the riparian management zones (RMZs) of three northern Minnesota harvest operations located in Beltrami, Carlton and Lake Counties. Artificial regeneration, a common reforestation practice, was used to establish planted seedlings of white-cedar and balsam fir. The purposes of the study were (a) to evaluate the benefits of combined harvest and microsite features to planted northern white-cedar seedlings and (b) to more fully understand the current dynamic between northern white-cedar and balsam fir seedlings in the presence of white-tailed deer.

Percent survival, height and basal diameter growth, and growth rate of planted 3-0 seedlings of white-cedar and balsam fir were examined in a factorial experiment that assessed combinations of fence position (fenced and unfenced), overstory treatment (control and harvest), and three microsite features commonly found in riparian forest landscapes (mound, pit, and slash).

The target residual basal area (RBA) for the harvest treatments was $11.6 \text{ m}^2\text{hc}^{-1}$ ($50 \text{ ft}^2\text{ac}^{-1}$), although actual RBA differed to some extent by site from 11.2 to $20.1 \text{ m}^2\text{hc}^{-1}$ ($48 \text{ to } 88 \text{ ft}^2\text{ac}^{-1}$) RBA. RMZs were 45 m (150 ft) deep from the water's edge per the recommendations for even-age management of trout streams in Minnesota (MFRC 2005).

Study results and management applications

Seedling Percent Survival

After four years in the field, fenced seedlings of northern white-cedar had high survival (82.0%) that was not different between overstory treatments. However, pit microsites subject to seasonal flooding had low survival (55.6%), even with short-term inundation. Outside of exclosures white-cedar was heavily browsed, with significantly lower survival (65.7%). Even though browse frequency was higher in partial harvest treatments than in control areas, overstory treatment was still not significant for survival. If protected from herbivory, planted northern white-cedar seedlings show good survival potential, regardless of overstory treatment, but pit microsites should be avoided in flood-prone areas. Mound and slash microsites resulted in good survival and should be selected for planting sites wherever they are available.

Graphing percent survival over time revealed stabilized mortality inside fences but a continuing downward trend outside of fences (Figure 4.2). It should be noted that despite their survival after four field seasons the observed physical condition of northern white-cedar seedlings subjected to deer browse (i.e., the amount of vegetation and twig growth removed by browse) was severely compromised. An increasing rate of mortality

is expected in unfenced northern white-cedar in the future as seedlings continue to suffer from herbivory.

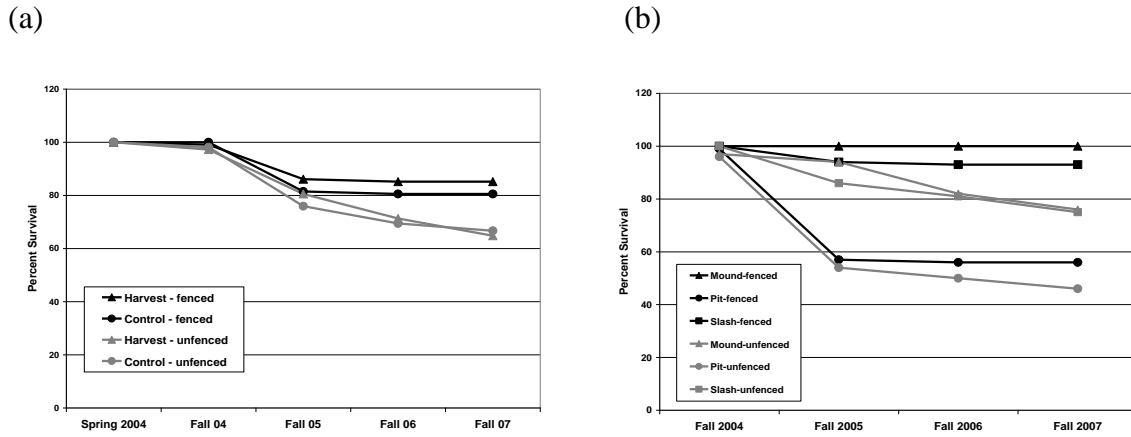


Figure 4.2. Annual seedling percent survival for northern white-cedar showing trends over time in (a) fence x overstory treatments and (b) fence x microsite treatments.

Seedling Growth

For fenced northern white-cedar seedlings, partial overstory removal was the primary factor benefiting growth. Seedling height, basal diameter, and growth rate were significantly greater in harvested areas compared to unharvested controls (Figures 4.3 and 4.4). However, the growth seen inside fences in both harvested and unharvested areas demonstrated the potential for planted northern white-cedar seedlings to recruit into sapling size categories in varied light conditions, with higher growth rates in harvested areas. Fenced seedling growth responded statistically the same to the variety of microsite and overstory x microsite combinations in which they were planted. This demonstrated the versatility of planted seedlings at this life stage in adapting to various soil and light conditions. The specific microsite requirements needed for seed germination and seedling establishment phases are no longer restricting elements.

Outside exclosures, browse overwhelmed the benefits of harvest treatments for white-cedar height growth (Figure 4.3a), reducing heights below their initial measurements and creating a negative relative growth rate (Figure 4.4a). Basal diameter was also lower under the influence of herbivory than when protected (Figure 4.3b). However, relative diameter growth was still positive, showing that even after four years subjected to herbivory, white-cedar seedlings continued to commit resources to basal diameter growth (Figure 4.4b).

Artificial regeneration of northern white-cedar in areas of varying basal area retention (tested in this study at 11 to 34 m²hc⁻¹ (50 to 145 ft²ac⁻¹)) will result in positive growth rates that can be expected to increase with lower BA. Mound (providing richer soil and higher moisture retention) and slash (providing partial shade and cooler soil temperature) microsites also supply benefits to growth and should be selected for planting sites if they are available. Pits that are not subject to seasonal flooding are also appropriate for planting.

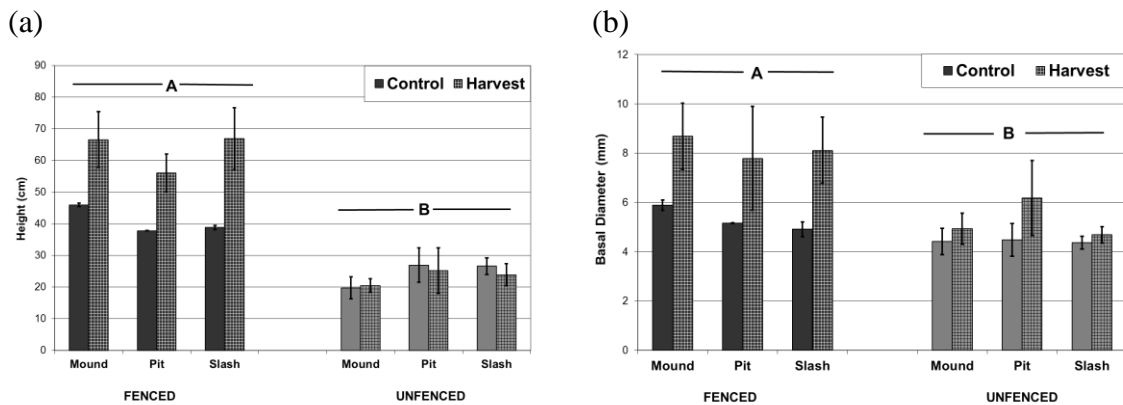


Figure 4.3. Growth of fenced and unfenced northern white-cedar seedlings after four years in the field for (a) height and (b) basal diameter. Growth of fenced and unfenced seedlings are statistically different from each other, denoted by A,B. With fence treatments pooled, overstory treatment-harvests are greater than controls for both (a) and (b).

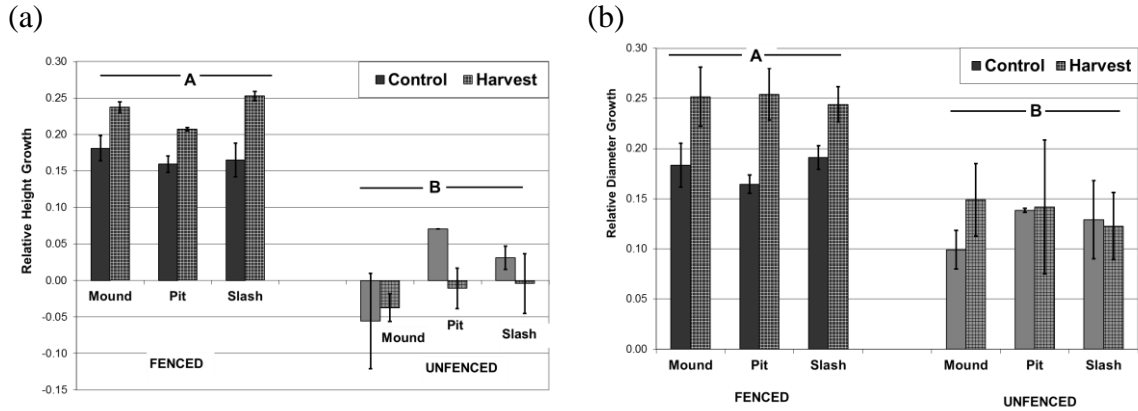


Figure 4.4. Relative growth rate (RGR) of fenced and unfenced northern white-cedar seedlings after four years in the field for (a) relative height growth and (b) relative diameter growth. RGR growth of fenced and unfenced seedlings are statistically different from each other, denoted by A,B.

Competition

At residual basal levels of 11.2 to 20.1 m^2hc^{-1} (48 to 88 $\text{ft}^2\text{ac}^{-1}$), fenced northern white-cedar seedlings did not appear to suffer competitive suppression from herbaceous vegetation and woody shrubs. In control areas understory vegetation was inhibited by denser overstory, while in harvest areas the seedlings grew in both height and basal diameter indicating that they could effectively compete for resources. Further study would be necessary to determine if results differ with greater overstory removal, making some control of surrounding vegetation advisable.

Fenced seedlings of northern white-cedar and balsam fir responded in height and basal diameter growth in a similar manner to the treatments. This indicates that, in the absence of deer browse and for up to four years in the field, balsam fir seedlings of the same age do not have a competitive advantage over northern white-cedar seedlings. However, species-specific growth rates are reported to vary over time (Logan 1969),

which may change this relationship in the future. Also, native balsam fir seedlings may be better adapted to lower light environments than open-grown planting stock of northern white-cedar. Therefore, if native balsam fir are present in a planting area, it would be advisable to avoid proximity or to remove neighboring individuals to avoid potential competition.

Effect of Herbivory

The calculation of browse frequency was based on presence/absence of herbivory viewed at a total of seven spring and fall data collections. Outside fenced exclosures, only 16 of 142 northern white-cedar and 41 of 117 balsam fir seedlings remained unbrowsed throughout the course of four years in the field.

In unfenced plots, browse frequency on northern white-cedar was significantly higher in partial harvests areas (45.1%) than in control areas (29.5%). This is consistent with knowledge of ungulate feeding patterns, i.e., they spend more time feeding on new growth at forest edges and clearings where shrub forage is most available (Smith et al. 2007; Forester et al. 2008). Browse was also higher on mound microsites (46.4%) than in pits (31.1%) and slash (32.3%), most likely because (a) seedlings were more exposed by mound microtopography and (b) overhanging shrubs or woody debris afforded some degree of protection in pit and slash microsites. However, neither percent survival nor growth reflected a significant benefit from this lower browse, with the result that these treatments offered no substantive protection. Lower percent survival outside fences was the result of four years of herbivory.

Herbivory on seedlings in this study did not occur in winter because seedlings were covered with snow. The majority of browse events occurred in the spring after snowmelt and before other vegetation flushed. Most browse on northern white-cedar and balsam fir stopped after leaf emergence as deer moved on to preferred food sources.

Both the amount and the nature of browse differed between species. Browse frequency was higher on northern white-cedar (37.3%) than on balsam fir (13.2%) (Figure 4.5). Each browse event on northern white-cedar removed most existing foliage, leaving the seedling stem. In contrast, browse on balsam fir seedlings was restricted to leaders and partial snipping of the tips of lateral branches. For the four years of this study, many browsed white-cedar seedlings were able to survive even if all foliage was stripped from the stem.

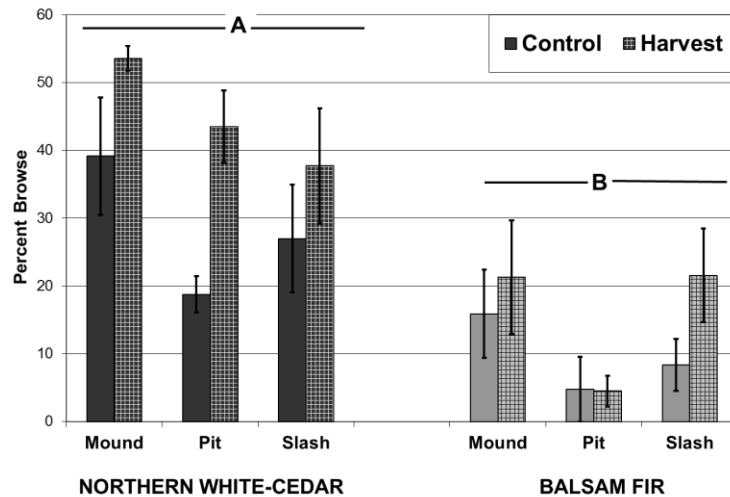


Figure 4.5. Browse frequency on unfenced northern white-cedar and balsam fir seedlings. Browse frequency was statistically higher on northern white-cedar (denoted by A,B), and with species pooled was highest in overstory treatment-harvest and in microsite treatment-mounds.

Field observations also determined that the nature of seedling response to browse differed between species, and can be explained by the dissimilar growth habits of the two species. For northern white-cedar, the presence of new foliage at fall data collection (the result of indeterminate shoot growth and current year leaf formation) demonstrated some degree of seasonal recovery of vegetation lost to browsing. Balsam fir (with determinate shoot growth and previous year leaf bud formation) did not exhibit new growth in the same year.

Northern white-cedar, browsed more heavily in both frequency and amount, has short-term recovery capabilities; balsam fir, less-browsed, recovers more slowly. Under continuing browse, northern white-cedar seedlings will eventually die while less-browsed balsam fir seedlings will survive but grow more slowly. However, if browse were restricted within the first several years after planting, white-cedar seedling health could be restored. This gives a window of several years for the implementation of seedling protection.

Wildlife and forest timber management studies suggest that a maximum population level of 8 deer/km² (20 deer/mi²) is necessary to avoid detrimental impact to browse-sensitive vegetation. However, ecosystem studies find that a population level closer to 1-4 deer/km² (2-8 deer/mi²) is needed (Alverson et al. 1988). During the period of this study (2004-2007) fluctuating pre-fawn deer densities at the study sites were estimated to be 4-9/km² (8-23 deer/mi²) at Shotley Brook, 4-8/km² (8-21 deer/mi²) at Nemadji State Forest, and 1-6/km² (2-15 deer/mi²) at East Branch Beaver River (MN DNR pers. comm.; MN DNR 2007). Browse frequency on seedlings did not vary

according to estimated deer populations levels at each site. Analysis from this study indicated that a population level less than the lowest estimate of 4 deer/km² (2 deer/mi²) would be necessary to avoid the impact of herbivory on planted northern white-cedar seedlings. In the bare forest floor environment of spring snowmelt, seedlings are highly vulnerable to even a few local or migrating deer.

Site Effects

Northern white-cedar performance in this study indicates that it is a good candidate for planting in a variety of riparian landscapes in northern Minnesota. Soils varied from shallow to deep, sandy loam to silty and clay sandy loams; topographical relief varied from 0 – 25 m (0 – 82 ft), water body width ranged from 1 – 5.5 m (3 – 18 ft), and depth to water table differed (seasonally and by site) from the soil surface to below the rooting zone.

When protected from herbivory, seedlings at all sites increased in size and had high survival rates. However there were non-significant differences seen between growth at the various sites that may forecast larger differences in the future. For example, mean growth for northern white-cedar at Site 1-Harvest located in a floodplain was 49.6 cm height, 6.3 mm basal diameter; mean growth at Site 3-Harvest located on a terrace above a steep river bank was 75.1 cm height, 10.1 mm basal diameter. Landscape site differences may have greater influences in successive life stages of northern white-cedar. Examination of site level differences (such as topography, slope, depth to groundwater, soil type, width of flood zone) and their contribution to long-term seedling performance

could increase our understanding of the requirements for northern white-cedar forest stands.

Summary of northern white-cedar treatment means

The following summary presents treatment means (by fence, overstory, and microsite treatments) of northern white-cedar seedling survival and size after four years in the field. Stated differences between the means were found to be statistically significant.

Survival

- Percent survival of fenced northern white-cedar was greater than unfenced

Fenced 82.9% > Unfenced 65.7%

- Percent survival within fence positions was not different between overstory treatments

Fenced: control 80.6% \approx harvest 85.2%

Unfenced: control 66.7% \approx harvest 64.8%

- Percent survival of fenced and unfenced NWC was lower in pits than mounds or slash

Fenced: pit 55.6% < mound 100% or slash 93.1%

Unfenced: pit 45.6% < mound 76.4% or slash 75%

Browse

- Browse frequency on unfenced northern white-cedar was different between overstory treatments

Unfenced: harvest 45.1% > control 29.5%

- Browse frequency on unfenced NWC was different among microsites

Unfenced: mound 46.4% > pit 31.1% or slash 32.3%

Growth

- Fenced height and basal diameter of northern white-cedar were larger than unfenced

Fenced height 51.2cm > Unfenced height 23.0cm

Fenced basal diameter 6.6mm > Unfenced basal diameter 4.7mm

- Fenced height and basal diameter were larger in harvested areas than in controls

Height in harvest 63.2cm > control 40.9cm

Basal diameter in harvest 8.9mm > control 5.3mm

- Unfenced height and basal diameter were not different between overstory treatments

Height in harvest 23.2cm \approx control 24.5cm

Basal diameter in harvest 5.3mm \approx control 4.4mm

- Northern white-cedar height was

Greatest in fenced-harvest areas 63.2cm

Lowest in unfenced-harvest areas 23.2cm

- Northern white-cedar basal diameter was

Greatest in fenced-harvest areas 8.2mm

Lowest in unfenced control areas 4.4mm

Planting recommendations for northern white-cedar seedlings

1) When planting in riparian areas, select sites with topographical gradients that encourage drainage. In low-relief riparian areas, select raised and mound microsites that may be above flood levels. Avoid planting in pit microsites subject to seasonal inundation.

2) Select decayed stump and soil mounds that provide nutrients and moisture retention benefitting seedling growth. This is especially effective in areas of higher basal area where seedlings have slower growth rates. However, seedlings in mounds experience higher herbivory because of exposure.

3) Seedlings planted in areas of partial harvest that afford more light will grow faster than those planted in unharvested areas, although seedling survival has been shown to be good in both. Planting in unharvested areas that support lower growth rates is consistent with growth patterns seen in natural regeneration, where northern white-cedar seedlings are capable of many years of suppression in the understory until natural disturbance offers release.

4) The presence of native balsam fir of equal or larger size may create competition for light and soil resources. Avoid planting in the proximity of this species, or remove prior to planting northern white-cedar.

5) Browse from white-tailed deer occurs less in unharvested areas. Deer are attracted to newly harvested sites with fresh slash and to previously harvested sites that support new woody and herbaceous growth. When possible, do not plant in the proximity of heavily harvested areas where seasonal deer populations are likely to be higher.

6) Long-term protection from herbivory can be attained by planting within deer-proof exclosures. Logging slash can also provide barriers to deer movement and reduce browse frequency. Additional protection methods at time of planting, of varying efficacy, include foliar sprays, bud-capping, and slash barriers.

Management recommendations for northern white-cedar seedlings

1) Overstory harvests to approximately $11.6 \text{ m}^2\text{hc}^{-1}$ ($50 \text{ ft}^2\text{ac}^{-1}$) residual basal area (RBA) give sufficient light for a strong growth response by planted northern white-cedar seedlings.

2) Harvests to approximately $11.6 \text{ m}^2\text{hc}^{-1}$ ($50 \text{ ft}^2\text{ac}^{-1}$) RBA do not require control of herbaceous or woody vegetation for planted seedling growth. Seedlings planted in higher harvest areas may benefit from control of overtopping grasses and shrubs.

3) As herbivory is lowest in unharvested woodlands, consider these management strategies in proximity to areas where northern white-cedar is planted:

(a) low or no-harvest in uplands above plantings

(b) low or no-harvest in RMZs with plantings

(c) in the presence of harvested uplands, widen RMZs with plantings

4) Control continued deer herbivory by activities such as local population control, construction of low-cost exclosures, piling slash for protected plantings, foliar sprays, and bud-capping.

Chapter 4 Bibliography

- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2(4):348-58.
- Boelter, D. H., and G. E. Close. 1974. Pipelines in forested wetlands. *Journal of Forestry* September:561-63.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology* 9(4):386-96.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.
- Cornett, M. W., P. B. Reich, and K. J. Puettmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* 4(3):353-64.
- Forester, J. D., D. P. Anderson, and M. G. Turner. 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *American Midland Naturalist* 160:438-53.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-82.
- Heitzman, E., K. S. Pregitzer, and R. O. Miller. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Canadian Journal of Forest Research* 27:1953-61.
- Heitzman, E., K. S. Pregitzer, R. O. Miller, M. Lanasa, and M. Zuidema. 1999. Establishment and development of northern white-cedar following strip clear cutting. *Forest Ecology and Management* 123:97-104.
- Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.
- Johnston, W. F. 1990. *Thuja occidentalis* L. Northern white-cedar. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.

- Larouche, C., L. S. Kenefic, and J.-C. Ruel. 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.
- Logan, K. T. 1969. *Growth of tree seedlings as affected by light intensity: IV. Black spruce, white spruce, balsam fir and eastern white cedar*. Publication No.1256. Canadian Forestry Service Department of Fisheries and Forestry.
- Miller, R. O., M. Lanasa, D. Elsing, and M. Zuیدا. 1990. Northern white-cedar: Stand assessment and management options. In *Proceedings of Northern white-cedar in Michigan Workshop*, 1-6. Sault Ste. Marie, MI.
- Minnesota Department of Natural Resources. 2010. Minnesota's forest resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.
- Minnesota Department of Natural Resources. 2007. [Internet]. Pre-fawn deer density from deer population model. [cited 2010 Dec 12] Available from: http://files.dnr.state.mn.us/recreation/hunting/deer/deer_density_prefawn_2007.pdf.
- Minnesota Forest Resource Council. 2010. [Internet]. Economic analysis of potential changes to the riparian forest management guidelines, SL-0110; prepared by C. Hibbard and R. Slesak. [cited 2010 Sep 12]. Available from: http://www.frc.state.mn.us/documents/council/site-level/MFRC_RSTC_econ_report_2010-01-15.pdf.
- Minnesota Forest Resources Council. 2005. *Sustaining Minnesota Forest Resources: Voluntary Site-level Forest Management Guidelines for Landowners, Loggers and Resource Managers*. St. Paul, MN: Minnesota Forest Resources Council.
- Pregitzer, K. S. 1990. The ecology of northern white-cedar. In *Proceedings of northern white cedar in Michigan*, ed. D. O. Lantagne, 8-14. Research Report 512. East Lansing, MI: Michigan Agricultural Experiment Station.
- Rooney, T.P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.
- Smith, J. R., R. A. Sweitzer, and W. F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. *Journal of Wildlife Management* 71(8):2719-26.

Cumulative Bibliography

- Aldous, S. E. 1944. A deer browse survey method. *Journal of Mammalogy* 25(2):130-36.
- Aldous, S. E. 1952. Deer browse clipping study in the lake states region. *Journal of Wildlife Management* 16(4):401-09.
- Aldous, S. E. 1941. Deer management suggestions for northern white cedar types. *Journal of Wildlife Management* 5(1):90-94.
- Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: Edge effects in northern Wisconsin. *Conservation Biology* 2(4):348-58.
- Amacher, M. C., K. P. O'Neill, R. Dresbach, and C. Palmer. Forest Inventory & Analysis Manual of Soil Analysis Methods [Internet]. USDA Forest Service; 2003 [cited July 2010]. Available from: <http://nrs.fs.fed.us/fia/topics/soils/documents/FIA.P3.Soils.Lab.Manual.2003.pdf>.
- Bakuzis, E. V., and H. L. Hansen. 1965. *Balsam fir – a Monographic Review*. Minneapolis, MN: University of Minnesota Press.
- Batzer, H. O., and M. P. Popp. 1985. Forest succession following a spruce budworm outbreak in Minnesota. *Forestry Chronicle* 61(2):75-80.
- Blais, J. R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13:539-47.
- Boelter, D. H. and G. E. Close. 1974. Pipelines in forested wetlands. *Journal of Forestry* September: 561-63.
- Bouchard, M., D. Kneeshaw, and Y. Bergeron. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology* 87(9):2319-29.
- Briand, C. H., U. Posluszny, and D. W. Larson. 1992. Comparative seed morphology of *Thuja occidentalis* (eastern white cedar) from upland and lowland sites. *Canadian Journal of Botany* 70(2):434-38.
- Chimner, R. A., and J. B. Hart. 1996. Hydrology and microtopography effects on northern white-cedar regeneration in Michigan's Upper Peninsula. *Canadian Journal of Forest Research* 26:389-93.

- Chojnacky, D. C., R. A. Mickler, L. S. Heath, C. W. Woodall. 2004. Estimates of down woody materials in eastern US forests. *Environmental Management* 33: Supplement 1: S44-55.
- Chouinard, A., and L. Filion. 2001. Detrimental effects of white-tailed deer browsing on balsam fir growth and recruitment in a second-growth stand on Anticosti Island, Québec. *Ecoscience* 8(2):199-210.
- Clinton, B. D., and C. R. Baker. 2000. Catastrophic windthrow in the southern Appalachians: Characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management* 126(1):51-60.
- Cole, G. F. 1987. Changes in interacting species with disturbance. *Environmental Management* 11(2):257-64.
- Cornett, M. W. "Conifer regeneration in mixed deciduous-evergreen forests." MS thesis, University of Minnesota, 1996.
- Cornett, M. W. "Ecological restoration of upland northern white cedar forests on the Lake Superior highlands." Ph.D. diss., University of Minnesota, 2000.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. *Restoration Ecology* 9(4):386-96.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests. *Biological Conservation* 93:359-69.
- Cornett, M. W., L. E. Frelich, K. J. Puettmann, and P. B. Reich. 2000. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. *American Journal of Botany* 87(12):1807-14.
- Cornett, M. W., K. J. Puettmann, and P. B. Reich. 1998. Canopy type, forest floor, predation, and competition influence conifer seedling emergence and early survival in two Minnesota conifer-deciduous forests. *Canadian Journal of Forest Research* 28:196-205.
- Cornett, M. W., P. B. Reich, and K. J. Puettmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* 4(3):353-64.

- Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics* 35:113-47.
- Crow, T. R., M. E. Baker, and B. V. Barnes. 2000. Diversity in riparian landscapes. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 43-65. Boca Raton, FL: Lewis Publishers.
- Curtis, J. D. 1946. Preliminary observations on northern white cedar in Maine. *Ecology* 27(1):23-36.
- Davis, A. S., and D. F. Jacobs. 2005. Quantifying root system quality of nursery seedlings and relationship to outplanting performance. *New Forests* 30:295-311.
- Davis, A., K. Puettmann, and D. Perala. 1998. *Site preparation treatments and browse protection affect establishment and growth of northern white-cedar*. Research Paper NC-330. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.
- DeLong, H. B., V. J. Lieffers, and P. V. Blenis. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 2:1452-57.
- Ditchkoff, S. S., and F. A. Servello. 1998. Litterfall: An overlooked food source for wintering white-tailed deer. *Journal of Wildlife Management* 62(1):250-55.
- Dovčiak, M., P. B. Reich, and L. E. Frelich. 2003. Seed rain, safe sites, competing vegetation, and soil resources spatially structure white pine regeneration and recruitment. *Canadian Journal of Forest Research* 33:1892-1904.
- Duchesneau, R., I. Lesage, I. Robin, C. Messier, and H. Morin. 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management* 140:215-25.
- Edelstein, Z. R., and E. D. Ford. 2003. Branch and foliage morphological plasticity in old-growth *Thuja plicata*. *Tree Physiology* 23:649-62.
- Eyre, F. H., ed. 1980. *Forest Cover Types of the United States and Canada*. Washington, D.C.: Society of American Foresters.
- Fieberg, J., D. W. Kuehn, and G. D. DelGiudice. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. *Journal of Mammalogy* 89(6):1529-39.
- Fisher, R. F., and D. Binkley. 2001. *Ecology and Management of Forest Soils*, 3rd ed. New York, NY: John Wiley & Sons, Inc.

Forester, J. D., D. P. Anderson, and M. G. Turner. 2008. Landscape and local factors affecting northern white cedar (*Thuja occidentalis*) recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.). *American Midland Naturalist* 160:438-53.

Frank, R. M. 1990. *Abies balsamea* (L.) Mill. Balsam fir. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.

Fraver, S., R. G. Wagner, and M. Day. 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.

Freedman, B., V. Zelazny, D. Beaudette, T. Fleming, S. Flemming, G. Forbes, G. Johnson, and S. Woodley. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environmental Reviews* 4: 238-265.

Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Horin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29:824-39.

Greenwood, M. S., C. L. O'Brien, J. D. Schatz, C. A. Diggins, M. E. Day, G. L. Jacobson, A.S. White, and R. G. Wagner. 2008. Is early life cycle success a determinant of the abundance of red spruce and balsam fir? *Canadian Journal of Forest Research* 38:2295-2305.

Goebel, P. C., K. S. Pregitzer, and B. J. Palik. 2006. Landscape hierarchies influence riparian ground-flora communities in Wisconsin, USA. *Forest Ecology and Management* 230:43-54.

Grigal, D. F., and L. F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota wilderness area. *Ecological Monographs* 45:389-407.

Habeck, J. R. 1958. White cedar ecotypes in Wisconsin. *Ecology* 39(3):457-63.

Habeck, J. R. 1960. Winter deer activity in the white cedar swamps of northern Wisconsin. *Ecology* 41(2):327-33.

Hardwood and Conifer Swamps – White Cedar Swamp [Internet]. [updated 2008 May 29]. St. Paul, MN: University of Minnesota, College of Biological Sciences, Cedar Creek Ecosystem Science Reserve; [cited 2009 Apr 1]. Available from: <http://www.cedarcreek.umn.edu/conservation/habitats/swamp/>.

- Harper, J. L. 1977. *Population Biology of Plants*. San Diego, CA: Academic Press, Inc.
- Harrington, T. B., and A. A. Bluhm. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. *Forest Ecology and Management* 140:265-75.
- Häsler, H., J. Senn, and P. J. Edwards. 2008. Light-dependent growth responses of young *Abies alba* to simulated ungulate browsing. *Functional Ecology* 22:48-57.
- Haworth, B. K. "A comparison of *Thuja occidentalis* and *Abies balsamea* seedling response to partial harvest and microsite in northern Minnesota riparian forests." Ch. 2 of MS thesis, University of Minnesota, 2011.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-82.
- Heitzman, E., K. S. Pregitzer, and R. O. Miller. 1997. Origin and early development of northern white-cedar stands in northern Michigan. *Canadian Journal of Forest Research* 27:1953-61.
- Heitzman, E., K. S. Pregitzer, R. O. Miller, M. Lanasa, and M. Zuidema. 1999. Establishment and development of northern white-cedar following strip clear cutting. *Forest Ecology and Management* 123:97-104.
- Hofmeyer, P. V., L. S. Kenefic, and R. S. Seymour. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. *Northern Journal of Applied Forestry* 26(1):21-27.
- Hofmeyer, P. V., R. S. Seymour, and L. S. Kenefic. 2009. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. *Northern Journal of Applied Forestry* 26(2):68-75.
- Holcombe, J. W. 1976. The bryophyte flora of *Thuja* seedbed logs in a northern white-cedar swamp. *The Michigan Botanist* 15:173-81.
- Ilhardt, B. L., E. S. Verry, and B. J. Palik. 2000. Defining riparian areas. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 23-41. Boca Raton, FL: Lewis Publishers.
- Jacobs, D. F., K. F. Salifu, and J. R. Seifert. 2005. Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. *New Forests* 30:235-51.

Johnston, W. F. 1972. *Balsam fir dominant species under rethinned northern white-cedar*. Research Note NC-133. St. Paul, MN: USDA Forest Service, North Central Forest Experiment station.

Johnston, W. F. 1986. *Manager's handbook for balsam fir in the North Central States*. General Technical Report NC-111. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.

Johnston, W. F. 1977. *Manager's handbook for northern white cedar in the North Central States*. General Technical Report NC-35. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station.

Johnston, W. F. 1990. *Thuja occidentalis* L. Northern white-cedar. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Tech. cords. R. M. Burns and B. H. Honkala. Handbook 654. Washington, D.C.: USDA Forest Service.

Kastendick, D. N. "Riparian forest management in northern Minnesota: effects of riparian silvicultural treatments on forest biomass, structure, composition, and indices of plant available nutrients." MS thesis, University of Minnesota, 2005.

Kneeshaw, D. D., and Y. Bergeron. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*: 79(3):783-94.

Krasowski, M. J., and J. N. Owens. 1991. Growth and morphology of western red cedar seedlings as affected by photoperiod and moisture stress. *Canadian Journal of Forest Research* 21:340-52.

Larouche, C., L. S. Kenefic, and J.-C. Ruel. 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, C., J.-C. Ruel, J.-M. Lussier, and L. Kenefic. 2006. Regeneration of *Thuja occidentalis* L. in mixedwood stands on mesic sites after partial cuts in Quebec. In: Larocque, G.R., M. Fortin, and N. Thiffault, editors: Conference handbook, 2nd ed. Forest Science across the Borders - Conference of the Eastern CANUSA; Oct. 19-21, 2006; Quebec City, Quebec, Canada. 90-94.

Lavender, D. P and S. N. Salim. 1987. The role of plant growth regulators in dormancy in forest trees. *Plant Growth Regulation* 6:171-91.

Lefort, S., J. P. Tremblay, F. Fournier, F. Potvin, and J. Huot. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of their distribution range. *Ecoscience* 14(1):109-16.

Logan, K. T. 1969. *Growth of tree seedlings as affected by light intensity: IV. Black spruce, white spruce, balsam fir and eastern white cedar*. Publication No.1256. Canadian Forestry Service Department of Fisheries and Forestry.

Matthes-Sears, U., and D. W. Larson. 1991. Growth and physiology of *Thuja occidentalis* L. from cliffs and swamps: Is variation habitat or site specific? *Botanical Gazette* 152(4):500-508.

Matthes-Sears, U., S. C. Stewart, and D. W. Larson. 1991. Sources of allozymic variation in *Thuja occidentalis* in southern Ontario, Canada. *Silvae Genetica* 40(3-4):100-105.

McLaren, B. E. 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. *Ecology* 77(1):228-35.

Miles, P. D., and G. J. Brand. 2007. *Minnesota's forest resources in 2005*. Resource Bulletin NRS-6. Newton Square, PA: USDA Forest Service, Northern Research Station. 33 p.

Miller, R. O. 1990. Ecology and management of northern white-cedar. In *Proceedings of Regenerating conifer cover in deer yards workshop*, 1-13. North Bay, Ontario.

Miller, R. O., M. Lanasa, D. Elsing, and M. Zuida. 1990. Northern white-cedar: stand assessment and management options. In *Proceedings of Northern white-cedar in Michigan Workshop*, 1-6. Sault Ste. Marie, MI.

Minnesota Department of Natural Resources. 2003. Field guide to the native plant communities of Minnesota: The Laurentian Mixed Forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. MNDNR, St. Paul, MN.

Minnesota Department of Natural Resources. 2010. Minnesota's forest resources 2009. St. Paul, MN: Minnesota DNR Forestry Division Utilization & Marketing Program.

Minnesota Department of Natural Resources. 2007. [Internet]. Pre-fawn deer density from deer population model. [cited 2010 Dec 12] Available from: http://files.dnr.state.mn.us/recreation/hunting/deer/deer_density_prefawn_2007.pdf.

Minnesota Forest Resource Council. 2010. [Internet]. Economic analysis of potential changes to the riparian forest management guidelines, SL-0110; prepared by C. Hibbard and R. Slesak. [cited 2010 Sep 12]. Available from: http://www.frc.state.mn.us/documents/council/site-level/MFRC_RSTC_econ_report_2010-01-15.pdf.

- Minnesota Forest Resources Council. 2005. *Sustaining Minnesota Forest Resources: Voluntary Site-level Forest Management Guidelines for Landowners, Loggers and Resource Managers*. St. Paul, MN: Minnesota Forest Resources Council.
- MNMapper [Internet]. St. Paul, MN: Department of Administration, Office of Geographical and Demographic Analysis, Land Management Information Center; [created 2009 Jul 15] Available from: www.lmic.state.mn.us/chouse.
- Musselman, R. C., D. T. Lester, and M. S. Adams. 1975. Localized ecotypes of *Thuja occidentalis* L. in Wisconsin. *Ecology* 56:647-55.
- Nelson, T. C. 1951. A Reproduction study of Northern White Cedar. Game Division, Michigan Department of Conservation.
- Nyland, R. D. 2002. *Silviculture: Concepts and Applications*, 2nd edition. New York: McGraw-Hill.
- Palik, B., S. M. Tang, and Q. Chavez. 2004. *Estimating riparian area extent and land use in the Midwest*. Gen. Tech. Rep. NC-248. St. Paul, MN: USDA Forest Service, North Central Research Station.
- Palik, B., J. Zasada, and C. W. Hedman. 2000. Ecological principles for riparian silviculture. In *Riparian management in forests of the continental eastern United States*, eds. Verry, E. S., J. W. Hornbeck, and C. A. Dolloff, 233-54. Boca Raton, FL: Lewis Publishers.
- Pallardy, S. G. 2008. *Physiology of Woody Plants*, 3rd ed. Burlington, MA: Academic Press.
- Parent, S., H. Morin, C. Messier, and M-J. Simard. 2006. Growth, biomass allocation, and adventitious roots of balsam fir seedlings growing in closed-canopy stands. *Ecoscience* 13(1):89-94.
- Parent, S., M.-J. Simard, H. Morin, and C. Messier. 2003. Establishment and dynamics of balsam fir seedling bank in old forests in northeastern Quebec. *Canadian Journal of Forest Research* 33:597-603.
- Parker, T., and F. D. Johnson. 1987. Branching and terminal growth of western redcedar. *Northwest Science* 61(1):7-12.
- Peterson, C. J. and S. T. A. Pickett. 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. *Ecology* 76(3):763-74.

- Pregitzer, K. S. 1990. The ecology of northern white-cedar. In *Proceedings of Northern white cedar in Michigan*, ed. D. O. Lantagne, 8-14. Research Report 512. East Lansing, MI: Michigan Agricultural Experiment Station.
- Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanderklein, and C. Buschena. 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* 12:327-38.
- RMZ Harvest [Internet]. [updated 2008 Jul 27]. St. Paul, MN: University of Minnesota, College of Food, Agriculture and Natural Resource Sciences; [cited 2009 Jul 14]. Available from: <http://rmzharvest.cfans.umn.edu/>.
- Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* 74(3):201-08.
- Rooney, T.P., S. L. Solheim, and D. M. Waller. 2002. Factors affecting the regeneration of northern white-cedar in lowland forests of the Upper Great Lakes region, USA. *Forest Ecology and Management* 163:119-30.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181(1):165-76.
- Rose, R., D. L. Haase, F. Kroihner, and T. Sabin. 1997. Root volume and growth of ponderosa pine and douglas-fir seedlings: A summary of eight growing seasons. *Western Journal of Applied Forestry* 12(3):69-73.
- Roy, V., J-C. Ruel, and A. P. Plamondon. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management* 129:253-67.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. *American Midland Naturalist* 146(1): 1-26.
- SAS Institute, Inc. 2003. SAS/STAT® Software Version 9.1.3. Cary, NC: SAS Institute Inc.
- SAS Institute Inc. 2003. SAS/STAT® User's Guide Version 9.1.3. Cary, NC: SAS Institute Inc.
- Schaffer, W. W. 1996. *Silvicultural guidelines for the eastern white cedar*. Technical Report TR-006, Ontario: Ontario Ministry of Natural Resources, Southern Region Science & Technology Transfer Unit.

- Schmitz, O. J. 1990. Management implications of foraging theory: Evaluating deer supplemental feeding. *Journal of Wildlife Management* 54(4):522-32.
- Scott, M. L., and P.G. Murphy. 1987. Regeneration patterns of northern white cedar, an old-growth forest dominant. *American Midland Naturalist* 117(1):10-16.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: The importance of substrate. *Journal of Vegetation Science* 9(4):575-82.
- Simard, M.-J., Y. Bergeron, and L. Sirois. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. *Canadian Journal of Forest Research* 33:672-81.
- Smith, J. R., R. A. Sweitzer, and W. F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. *Journal of Wildlife Management* 71(8):2719-26.
- Stewart, G. 1925. Forest types of the northern swamps. *Journal of Forestry* 23:160-72.
- St. Hilaire, L. R., and D. J. Leopold. 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. 1995. *Canadian Journal of Forest Research* 25:261-69.
- St-Louis, A., J.-P. Ouellet, M. Crête, J. Maltais, and J. Huot. 2000. Effects of partial cutting in winter on white-tailed deer. *Canadian Journal of Forest Research* 30:655-61.
- Stoekeler, J. H. 1967. *Wetland road crossings: Drainage problems and timber damage*. Research Note NC-27. St. Paul, MN: USDA Forest Service, North Central Forest Experiment Station. 4p.
- Stroh, N., C. Baltzinger, and J-L. Martin. 2008. Deer prevent western redcedar (*Thuja plicata*) regeneration in old-growth forests of Haida Gwaii: Is there a potential for recovery? *Forest Ecology and Management* 255:3973-79.
- Stromayer, K. A., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25(2):227-34.
- Taylor, S. L., and D. A. MacLean. 2005. Rate and cause of decline of mature and overmature balsam fir and spruce stands in New Brunswick, Canada. *Canadian Journal of Forest Research* 35: 2479-90.

- Tremblay, J.-P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2007. Long-term decline in white-tailed deer browse supply: Can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology* 83:1087-96.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, B. E. Brent, and K. E. Kemp. 1968. Digestibility of cedar and balsam fir browse for the white-tailed deer. *Journal of Wildlife Management* 32:162-71.
- Ullrey, D. E., W. G. Youatt, H. E. Johnson, P. K. Ku, and L. D. Fay. 1964. Digestibility of cedar and aspen browse for the white-tailed deer. *Journal of Wildlife Management* 28(4):791-97.
- Van Deelen, T. R., K. S. Pregitzer, and J. B. Haufler. 1996. A Comparison of presettlement and present-day forests in two northern Michigan deer yards. *American Midland Naturalist* 135(2):181-94.
- Verme, L. J. 1965. Swamp conifer deeryards in northern Michigan: their ecology and management. *Journal of Forestry* 63(7):523-29.
- Verme, L. J., and W. F. Johnston. 1986. Regeneration of northern white cedar deeryards in upper Michigan. *The Journal of Wildlife Management* 50(2):307-13.
- Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25(2):217-26.
- Waring, R. H. 1987. Characteristics of trees predisposed to die: Stress causes distinctive changes in photosynthates allocation. *BioScience* 37(8):569-74.
- Webb, S. L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. *Canadian Journal of Forest Research* 18:1186-95.
- Weiskittel, A. R., J. A. Kershaw Jr., P. V. Hofmeyer, and R. S. Seymour. 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* 258:1695-1703.
- Weiskittel, A. R., R. S. Seymour, P. V. Hofmeyer, and J. A. Kershaw Jr. 2010. *Forest Ecology and Management* 259:1912-21.
- Zenner, E. K., and J. E. Peck. 2009. Maintaining a pine legacy in Itasca State Park. *Natural Areas Journal* 29(2):157-66.