CFRU RR 07-01

August 2007

Northern White-Cedar (*Thuja occidentalis* L.) An Annotated Bibliography

Philip V. Hofmeyer[1], Laura S. Kenefic[2], and Robert S. Seymour[1]

About the CFRU

Since 1975, the Cooperative Forestry Research Unit (CFRU) has been working to improve the stewardship of Maine's forests. This unique partnership between Maine's forest managers and the University of Maine has met a wide range of challenges. First called upon to address the devastating spruce budworm epidemic of the 1970s, CFRU has adapted to an ever-changing forest resource. As Maine's forests have evolved, the unit has kept pace by researching all aspects of forest ecosystems from the sustainability of wood supplies to the effects of forest management on wildlife habitat, water quality, and biodiversity.

With twenty seven member organizations, including private forest managers, wood processors, public agencies, and conservation organizations, the unit is continually seeking ways to help sustain Maine's tremendous forest resource. CFRU research provides both science-based information about the ecological effects of forestry practices, and tools that improve the efficiency and productivity of forest management. Under the auspices of the Center for Research on Sustainable Forests (CRSF) at the University of Maine, the CFRU continues to serve as a model of joint leadership and cooperation between the University of Maine and Maine's largest industry.

Introduction

Northern white-cedar (*Thuja occidentalis* L.) is arguably one of the least studied commercial tree species in the United States and Canada. It is an important source of wildlife habitat and forage, as well as commodities such as fence posts, shingles and siding. Much of the research on this species comes from the Lake States and Canada; few studies have been conducted in the northeastern region of the United States. A large cooperative research effort initiated and partially funded by Maibec Industries, Inc. is currently being undertaken to determine ecological and silvicultural attributes of northern white-cedar in Maine and adjacent Quebec, Canada. Collaborators and contributors include the University of Maine's Cooperative Forestry Research Unit (CFRU) and School of Forest Resources, Laval University, the U.S. Forest Service, and the Maine Bureau of Parks and Lands.

There is growing concern that recent harvesting intensities may exceed the growth capabilities of the species and that common cutting practices favor regeneration of competing species. Current U.S. Forest Service, Forest Inventory and Analysis (McWilliams et al. 2005) data show that the northern white-cedar–black spruce type occurs on approximately 1.7 million acres of forestland in Maine. Northern white-cedar live tree volumes have remained relatively stable in Maine since 1982 at approximately 2500 million cubic feet, while sawtimber volume has slightly increased to approximately 4000 million board feet.

When only growing stock cedar is considered, however, net growth in 2003 was 15,000 cubic feet while removals were approximately 25,000 cubic feet. This is a negative net change of approximately 10,000 cubic feet of commercially valuable cedar. Mortality for all species combined averaged 1.2% of live tree volume, but cedar mortality accounted for only 0.6% of live tree volume losses for that species, i.e. reduction in growing stock is not caused by excessive mortality. These data suggest that harvesting intensity is exceeding growth of merchantable stems.

Preliminary data from research suggest that northern white-cedar in northern Maine are far older than previously considered. A study of 70 sound cedar stems cut throughout northern Maine and delivered to Maibec's St. Pamphile millyard in Quebec, Canada in 2005 revealed a mean age of 190 years at stump height (12 inches) (unpublished data). None of the sampled trees were less than 100 years of age at stump height and some trees exceeded 350 years of age. A sample of 300 outwardly sound cedar 5.5 to 25.9 inches at breast height (dbh, 4.5 ft) in 60 mixed-species stands in northern Maine included many stems with 150 or

[1] School of Forest Resources, University of Maine, Orono, ME 04469;
[2] U.S. Department of Agriculture, Forest Service, Northern Research Station, Bradley, ME 04411

more years of readable rings. However, determining total age was difficult because of the high incidence of decay; approximately 80% of the sample trees were centrally decayed (Hofmeyer et al. 2006). In addition, stem analysis revealed that early height and diameter growth were slow (unpublished data), suggesting that extended periods of protection may be required for successful recruitment of cedar into the sapling and pole classes. Determining regeneration requirements, recruitment rates, growth capabilities and responses to silvicultural intervention are of utmost importance to sustaining northern white-cedar for commodity utilization.

This annotated bibliography provides a compilation of published research on northern white-cedar for use by researchers and managers. In addition to peer-reviewed journal articles, papers found in the gray literature (i.e. government documents, university publications, technical reports, and action group documents) contribute significantly to our knowledge of cedar and are included here. With this collection of citations, it is impossible to ignore the lack of fundamental silviculture studies conducted on cedar in the northeastern United States. This document is an attempt to collect past works, both to inform managers and to provide a basis for future silviculture studies.

Though many studies have included northern white-cedar, this bibliography emphasizes only research focusing on this species. Sources that include multiple species for comparison were annotated to convey the findings that pertained to northern white-cedar. Only sources in the English language are included. Units are reported in the format of the original document (i.e. no unit conversions were attempted). Papers concerning cedar in the biomedical field are not included. The citations in this document generally fall into seven broad categories:

Literature Search

Several databases and keywords were used to identify resources for this bibliography. Keywords used to identify papers focusing specifically on northern white-cedar include (either alone, or in combination): Acadian, *arborvitae*, brambant, cedar, conifer, *Cuppressaceae*, eastern, escarpment, Niagara, northern, *occidentalis*, swamp, *Thuja*, and white. Databases used to search for appropriate papers include: Agricola, CABDirect, Citation Indices, Google Scholar, Proceedings First, and World Cat. The literature cited section of each paper was reviewed for additional references. This bibliography includes papers published before April 1, 2007.

Cliff Ecology

Bartlett, R.M. and D.W. Larson. 1990. The physiological basis for the contrasting distribution patterns of *Acer saccharum* **and** *Thuja occidentalis* **at cliff edges.** *Journal of Ecology* **78(4): 1063-1078.**

Tree seedling mortality is often high due to biological factors (e.g. herbivory) and physical factors (e.g. summer weather). There are frequently age-specific and species-specific differences in physiology that affect growth and survival. Survival of cedar and maple seedlings was evaluated in conditions equivalent to cliff and deciduous forest environments by altering light and moisture regimes. Results suggested that sugar maple seedlings were more affected by altered conditions than cedar; northern white-cedar seedlings had relatively high survival rates at low light and moisture conditions, whereas all maple seedlings died at the lowest two levels of light and moisture. Bartlett and Larson speculated that the small-seeded cedar seedlings were outcompeted in the deciduous forest by the larger-seeded sugar maple seedlings, and that sugar maple could not tolerate the extreme cliff conditions. They suggested their results are consistent with the “slow seedling” hypothesis.

Bartlett, R.M., R.J. Reader, and D.W. Larson. 1991. Multiple controls of cliff-edge distribution patterns of *Thuja occidentalis* **and** *Acer saccharum* **at the stage of seedling recruitment.** *Journal of Ecology* **79(1): 183-197.**

The mechanisms controlling the discrete distribution patterns of sugar maple and northern white-cedar on limestone cliffs in southern Ontario were investigated. Five transects consisting of five 1-m^2 seed traps were established perpendicular to the cliff face at 0, 2, 4, 8, and 16 m from the edge. Newly germinated seedlings of both species were planted in prepared plots under the existing overstory. Experimental plots were also established to test differences among plots with and without litter, caged and not caged, herbaceous understory removed and intact. Seeds of both species were found in all traps. The greatest number of cedar seedlings were found near the cliff edge and dropped off rapidly after 8 m, occurring most frequently on disturbed sites. Sugar maple seedlings were abundant at greater distances from the cliff but were sparse within 3 m of the cliff edge. After two summers, survivorship of planted cedar seedlings in the deciduous forest was nearly zero. Sugar maple seedlings had poor survivorship near the cliff edge. The authors concluded that both species' spatial and temporal distributions were affected by biotic and abiotic factors.

Buckley, B.M., R.J.S. Wilson, P.E. Kelly, D.W. Larson, and E.R. Cook. 2004. Inferred summer precipitation for southern Ontario back to AD 610, as reconstructed from ring widths of *Thuja occidentalis*. *Canadian Journal of Forest Research* **34: 2541-2553.**

Previous studies suggest correlations between northern white-cedar annual ring width and previous summer temperature (-) and precipitation (+) (e.g. Kelly et al. 1994). Buckley et al. suggested that cliff-dwelling cedar in Ontario are ideal for dendroclimatalogical research due to its advanced age and proximity to industrial sites. The authors constructed a 2787-year tree-ring chronology, with 350 years of June-July precipitation reconstruction. Though they presented a series of wet and dry periods, they conceded that their predictive power was quite low due to the complexities of tree responses; only 33% of variation in climate data was accounted for by tree-ring variation. Their chronology, however, is the longest in the eastern United States to date.

Kelly, P.E. and D.W. Larson. 1997. Dendroecological analysis of the population dynamics of an old-growth forest on cliff-faces of the Niagara Escarpment, Canada. *Journal of Ecology* **85: 467-478.**

Increment cores from northern white-cedar trees were used to reconstruct the current and past age class structure of a stand occurring on limestone cliffs in southern Ontario. The oldest living tree cored was 701 years of age at stump height, the oldest snag was 625 years, and the oldest dead stem found on the talus slope was 596 years. Shannon Stand Regularity Index values ranged between 0.75 and 0.87, calculated at 20-year intervals from the late 1700s, suggested a continual multi-aged structure. Recruitment varied through time, with distinct pulses observed in the chronology. Synchronous ring width data suggested 14 instances of growth release or suppression that affected large numbers of trees concurrently. The authors suggested that this uneven-aged, old growth forest is free from large-scale catastrophic disturbances. Mortality has exceeded recruitment during that last 140 years causing a population density decrease.

Kelly, P.E. and D.W. Larson. 1997. Effects of rock climbing on populations of presettlement eastern white cedar (*Thuja occidentalis*) on cliffs of the Niagara escarpment, Canada. *Conservation Biology* **11(5): 1125-1132.**

A virgin northern white-cedar stand on the Niagara Escarpment was evaluated for anthropogenic impacts of rock climbing on this rare forest type. The authors found significant differences between the climbed and unclimbed rock faces; though both had reverse-J diameter distributions, the numbers of very young and very old trees were greatly reduced on the climbed face. Additionally, although both populations had low stem density, the climbed portion had fewer stems and a narrower range of stand densities (2.1 to 7.8 trees per 100 m^2) than the unclimbed stands (9.1 to 21.2 trees per 100 m^2). There was also 600 to 800% more physical damage to trees on climbed faces. The authors suggested that recreation and ecological integrity are incompatible in their study area and that use should be closely monitored and adjusted, especially considering the rarity of presettlement forests on the landscape.

Kelly, P.E., E.R. Cook, and D.W. Larson. 1992. Constrained growth, cambial mortality, and dendrochronology of ancient *Thuja occidentalis* on cliffs of the Niagara Escarpment: an eastern version of bristlecone pine? *International Journal of Plant Sciences* **153: 117-127.**

Arguably the most extensive old-growth forest in eastern North America occurs on the limestone cliff faces of the Niagara Escarpment in southern Ontario. The authors discovered northern white-cedar in excess of 1030 years of age, contrary to earlier beliefs that cedar is a short-lived tree species. They compared growth and morphological characteristics of 1860 cedar trees to those of bristlecone pine and discovered that cedar architecture is highly variable and distorted, with growth rates in some individuals less than 0.1mm yr-1. Cambial mortality did not seem to negatively impact long-term survival; all mature trees had some cambial dieback. All trees older than 500 years had live crown restricted to a single branch. The authors suggested that undisturbed snags can persist approximately 600 years and fallen logs 3000 years, making this species valuable for dendrochronology studies.

Kelly, P.E., E.R. Cook, and D.W. Larson. 1994. A 1397-year tree-ring chronology of *Thuja occidentalis* from cliff faces of the Niagara Escarpment, southern Ontario, Canada. *Canadian Journal of Forest Research* **24(5): 1049-1057.**

Tree ring chronologies of 142 living and dead cedar trees were used to make a dendrochronological study of diameter growth and climate. This chronology spanned a period from 594 to 1990 and is the longest in Canada to date of their publication. Northern white-cedar radial increment was negatively correlated with the previous year's maximum summer temperature; extremely hot weather negatively affected growth the following year. The authors suggested that cedar would be a good choice for future regional climate analyses because of the longevity of suppressed populations.

Larson, D.W. 1990. Effects of disturbance on old-growth ***Thuja occidentalis*** **at cliff edges.** *Canadian Journal of Botany* **68(5): 1147-1155.**

Along the limestone cliffs of the Niagara Escarpment in southern Ontario, northern white-cedar can be a long-lived tree species with individuals exceeding 1000 years of age. However, cedar abundance declines rapidly away from the cliff edge. Because recreation uses greatly impact this forest type, the author studied the relationships between disturbance and forest structure with a sample of 441 cedar trees in both disturbed and undisturbed cliff sections. Disturbed areas were nearly devoid of cedar regeneration, while there were wide ranges of true ages and sizes in undisturbed stands. Disturbed stands showed significant increases in stem mass and annual productivity as distance from cliff edge increased. Given the age of many of the individuals and the lack of recruitment, the author suggested that disturbed populations are not self-sustaining and that active management of human use is important.

Larson, D.W. 2001. The paradox of great longevity in a short-lived tree species. *Experimental Gerentology* **36(4): 651-673.**

According to the author, much of the literature on northern white-cedar suggests that it is a short-lived tree with a normal life span of 80 years and a maximum lifespan of 400 years. Ancient cedar found on xeric cliffs along the Niagara Escarpment in southern Ontario have several unique attributes that allow them to live to ages exceeding 1000 years. The author discovered that cliff-dwelling cedar have internal sectoring that allows portions of the hydraulic architecture to be disrupted without causing the entire tree to die, similar to some junipers and bristlecone pine. This attribute commonly leads to partial shoot mortality. In addition, stunted cedar have stronger wood that is more dense (has a higher specific gravity) with higher crushing strengths than "normal" cedar. The author argued that though cedar is commonly considered a pioneer species, it can also be considered a climax species on xeric sites.

Larson, D.W. and P.E. Kelly. 1991. The extent of old-growth ***Thuja occidentalis*** **on cliffs of the Niagara Escarpment.** *Canadian Journal of Botany* **69: 1628-1636.**

Nine sites in an extensive cedar forest on the limestone cliffs of the Niagara Escarpment were sampled for age characteristics, fire disturbance, and anthropogenic disturbances. The authors found that nearly the entire limestone community sampled was old-growth due to high densities of old trees, uneven age structure, and lack of human disturbance. Much of this age structure was similar throughout the range sampled. Tree ages in excess of 1000 years were discovered in what the authors report to be the most extensive old-growth forest in eastern North America.

Larson, D.W. and Melville, L. 1996. Stability of wood anatomy of living and Holocene ***Thuja occidentalis*** **L. derived from exposed and submerged portions of the Niagara Escarpment. Quaternary Research 45: 210-215.**

Northern white-cedar is commonly used for dendrochronology research due to its sensitivity to moisture and temperature fluctuations, and long life span along the Niagara Escarpment in southern Ontario. The authors compared wood anatomy of living, subfossil exposed dead, and submerged dead northern white-cedar tissues. Exposed dead trees were living from 3500 to 1600 yr B.P.; submerged dead trees dated to more than 8000 yr B.P. Under low magnification, cells retained their roughly rectangular shape regardless of location. Higher magnification revealed distinctly flattened latewood cells in living and exposed subfossil samples. Earlywood was nearly identical in living and exposed samples, while submerged earlywood tracheid cells were slightly rounded. Because subfossil samples were taken from environments conducive to high rates of deterioration, the relatively insignificant structural changes found were surprising to the authors. The slight changes observed will not negatively impact the use of subfossil cedar in future dendrochronological studies.

Larson, D.W., U. Matthes-Sears, and P.E. Kelly. 1993. Cambial dieback and partial shoot mortality in cliff-face ***Thuja occidentalis*****: evidence for sectored radial architecture.** *International Journal of Plant Sciences* **154: 496-505.**

Stress-tolerant conifers growing in harsh conditions commonly have slow growth rates and reach old age, suffering from partial cambial mortality and distorted growth morphology. Twelve trees were sampled from limestone cliffs in southern Ontario by serial-sectioning the main stem to determine exact dates of root and shoot mortality events, allowing the authors to reconstruct architectural development. Root mortality events were paired with shoot mortality events that occurred within two years of one another. In every tree sampled, root death corresponded to death of a specific region of the shoot system, as well as a portion of the cambium. On average, small- and large-scale mortality episodes occurred every 71 and 107 years, respectively, with a mortality event of any size occurring every 42 years. Results of this study suggested that specific portions of the root system are linked to specific portions of the shoot system. The authors argue that this may allow cedar to exist in harsh environments where rockfall events and water stress are common.

Matthes-Sears, U. and D.W. Larson. 1990. Environmental controls of carbon uptake in two woody species with contrasting distributions at the edge of cliffs. *Canadian Journal of Botany* **68(11): 2371-2380.**

The Niagara escarpment in southern Ontario is characterized by northern white-cedar and other stress-tolerant plants on the cliff faces, with species-rich, sugar maple-dominated woodlands farther from the cliff edge. The authors hypothesized that sugar maple was constrained at the cliff edges by a decrease in moisture availability and an increase in temperature, while cedar was restricted to the cliffs due to a decrease in temperature and photosynthetically active radiation as distance from the cliff edge increases. The authors discovered that cedar expressed drought avoidance similar to mesic hardwoods, evident in depressed net photosynthetic rates in both cliff and mesic environments during drought. Their findings suggested that sugar maple has higher light use efficiency than northern white-cedar, potentially allowing sugar maple to remain dominant on the mesic sites. This finding is contrary to Habeck (1958) and Musselman et al. (1975), who suggested that ecotypic variation of cedar exists among sites.

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.**

Cliff and swamp populations of northern white-cedar were tested for ecotypic differences in growth and tree physiology. No discernable patterns of productivity, nutrient levels, shading, or light saturation were observed among sites; the authors report that no ecotypic differentiation was evident. They suggested that a lack of water in cliff sites limits productivity, while excess water limits productivity in swamp sites. The authors concluded that cedar growth factors are site-, not habitat-, specific.

Matthes-Sears, U. and D.W. Larson. 1995. Rooting characteristics of trees in rock: a study of *Thuja occidentalis* on cliff faces. *International Journal of Plant Sciences* **156(5): 679-686.**

The authors argued that cliff-dwelling trees often have several distinct traits; they tend to be small, stunted and morphologically deformed with slow growth rates and the potential to reach very old ages. Sixty-two rock-face northern white-cedar from four rooting substrates (roots occurring in only solid rock, rock and small soil pockets, soil accumulations over exposed rock, and only soil) were excavated to determine if rooting characteristics were correlated with growth attributes. When corrected for age, biomass differences were not attributable to soil impacts; root:shoot ratios were not significantly different across rooting substrates. No differences in growth rate were observed. The authors suggested that cedar trees possess plastic root systems, allowing individuals to compete on a wide range of sites. The authors found that the limestone rock surface held more moisture than soil pockets along the cliff face. They also suggested that nutrient availability from subsurface bacteria could explain for the lack of difference among rooting substrates.

Matthes-Sears, U. and D.W. Larson. 1999. Limitations to seedling growth and survival by the quantity and quality of rooting space: implications for the establishment of *Thuja occidentalis* on cliff faces. *International Journal of Plant Sciences* **160(1): 122-128.**

Cedar trees have leaf morphology that is very different from other Acadian forest conifers.

First and second year growth and survival of northern white-cedar seedlings were examined using 9 treatment combinations of 3 nutrient levels (Hoagland's solution at half-strength, one-tenth strength, and no nutrient) and 3 pot sizes (1, 10, and 100 ml). High nutrient levels resulted in higher growth rates than low and no nutrient levels. Pot size had inconsistent effects on seedling growth; seedlings in small pots had greatest main axis elongation but no difference in branch elongation as compared to other pot sizes. Seedlings in large pots had the highest survivorship, regardless of nutrient treatment. Increasing nutrient availability increased growth rates, but had no effect on survivorship. Increasing available rooting material had little effect on growth and a small effect on survival. Only three seedlings were alive after the second growing season, all in large pots.

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.**

Allozyme patterns among cliff and swamp cedar stands in southern Ontario were examined for ecotypic variation. Shoot samples were collected from 162 trees in 3 swamp and 3 cliff stands. Little genetic diversity was present among the sites tested. Only 1.9% of genetic variability distinguished stands within habitat types, and only 1.2% detected differences between swamps and cliffs. These data suggested that all trees studied were members of a larger homogeneous population, regardless of habitat type. The authors questioned conclusions from previous research which argued that northern white-cedar has ecotypic subpopulations (e.g. Habeck 1958, Musselman et al. 1975).

Matthes-Sears, U., C. Neeser, and D.W. Larson. 1992. Mycorrhizal colonization and macronutrient status of cliff-edge *Thuja occidentalis* **and** *Acer saccharum***.** *Ecography* **15(3): 262-266.**

The authors observed vesicular-arbuscular mycorrhizal (VAM) colonization in forest, cliff edge, and cliff face northern white-cedar stands. All cedar types had abundant VAM colonization, though higher levels of association were observed in forest and cliff face stands than cliff edge stands. VAM colonization was more abundant in sugar maple than in cedar, with no observed site effects. Cedar foliar macronutrient concentration was largely unaffected by site. Swamp cedar shoots had a lower Mg concentration than other locations. Cliff-edge cedar had higher N/K ratios than swamp trees, however the differences were minimal. The authors suggested that the level of mycorrhizal colonization was not a limiting factor for either species among the habitats investigated.

Macronutrient levels in all site types were within optimal levels, leading to the conclusion that nutrient level is unrelated to the stunted morphology of cliff-dwelling cedar.

Matthes-Sears, U, C.H. Nash, and D.W. Larson. 1995. Constrained growth of trees in a hostile environment: the role of water and nutrient availability for *Thuja occidentalis* on cliff faces. *International Journal of Plant Sciences* **156(3): 311-319.**

Moisture and nutrient limitations on cedar sapling productivity were investigated along the Niagara Escarpment limestone cliffs. Sixty saplings were placed into one of three treatment groups: watered, fertilized or untreated control. Treatments were applied in-situ and each sapling was given a rooting medium rating from 1 to 4 (1 = no soil, 4 = more than half the root system in soil). Shoot elongation was no different in watered and control saplings, but was higher in fertilized plants. Leaf area growth was higher in fertilized than watered saplings, while the controls did not differ from either. Leaf area growth was also higher in the largest and youngest individuals. No ring width differences were detected after one year of treatment; however, fertilized saplings had wider rings than the other treatments after two years. Leaf tissue concentrations of N, K and Mg did not vary among treatments. P was higher and Ca was lower in the fertilized treatment than the others. The authors concluded that stunted cliff-dwelling cedar are no more nutrient deprived than fast-growing individuals, and that additional environmental constraints are likely limiting growth responses.

Matthes-Sears, U., P.E. Kelly, C.E. Ryan, and D.W. Larson. 2002. The formation and possible ecological function of stem strips in *Thuja occidentalis*. *International Journal of Plant Sciences* **163(6): 949-958.**

Seven sites along the Niagara Escarpment in southern Ontario were used to examine development and function of stem strips in 842 cliff-dwelling cedar trees. Sampled trees ranged from 1-810 years of age, of which 21% had stem stripping. Tree age was the most significant predictor of stem stripping; alternating vertical strips of dead and exposed wood with strips of live cambium and bark. Stem stripping is likely a result of permanent cavitation in sections of trees with hydraulic sectoring. The authors suggested that old trees are predisposed to cavitation events due to the formation of large pits. Forty-five of 66 old trees and 25 of 392 young trees sampled exhibited stem stripping. They argued that cedar stem stripping is a survival mechanism in harsh environments that have variable moisture regimes.

General Ecology

Abrams, M.D. and M.L. Scott. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. *Forest Science* **35(1): 42-49.**

The authors suggested that logging disturbances accelerate the shift from cedar-dominated old-growth stands to climax sugar maple-dominated communities. They argued that northern white-cedar can be an early successional species on some sites, and that it may be displaced without concerted efforts to protect and establish regeneration during logging.

Archambault, S. and Y. Bergeron. 1992. Discovery of a living 900-year-old northern white cedar, ***Thuja occidentalis*****, in northwestern Quebec.** *Canadian Field Naturalist* **106(2): 192-195.**

The authors discovered thirty 500 to 900 year-old northern white-cedar growing on xeric sites in Quebec, seven of which exceeded 700 years. The oldest of the trees sampled had 869 readable rings with time since germination estimated to exceed 900 years. Northern white-cedar was at one time considered a short-lived species of wet sites, however, this discovery and other recent work in Ontario suggest otherwise (e.g. Larson and Kelly 1991). The authors created an 802-year chronology using 38 cedar stems. Radial growth was reported to be correlated with the previous year's summer temperatures and precipitation.

Beals, E.W. 1965. An anomalous white cedar–black spruce swamp in northern Wisconsin. *American Midland Naturalist* **74(1): 244.**

Beals suggested that past research has indicated that stands intermediate between northern white-cedar and black spruce are rare in northern Wisconsin. A lowland cedar–fir–black spruce stand was discovered on muck soils with a pH of 4.0. The author suggested that northern white-cedar is generally associated with woody peat swamps while black spruce is more commonly associated with sphagnum peat soils. The particular swamp sampled had woody peat soil and was dominated in the overstory by northern white-cedar. Retrogressive succession was occurring as black spruce began invading the understory due to flooding from beaver activities. The author reported that this successional shift is more pronounced in the lower strata of the stand.

Bentley, P.A. and E.C. Smith. 1960. A study of northern white cedar and jack pine in Nova Scotia. *Proceedings of the Nova Scotian Institute of Science* **24: 376-398.**

Eight cedar and eight jack pine stands were investigated throughout Nova Scotia to determine ecological attributes of each stand type. Cedar was common on old-pasture sites and lake-side or swamp sites. The authors observed that the lake-side sites contained old trees and seedlings, but few saplings. The old-pasture sites tended to be younger and relatively even-aged. Lake-side trees were reported to have slower growth rates and poorer form than those associated with old-pasture sites. The authors found a mean soil pH of 5.0 (range 4.1 to 5.7), mean exchangeable calcium in milli equivalents per 100 grams of soil of 1.71 (range 0.12 to 7.26) in the A2 horizon and 1.45 (range 0.30 to 6.03) in the B horizon. Drainage on cedar and jack pine stands varied from good to poor, however, cedar tended to occur on the poorer sites while jack pine was most predominant on the better sites. Soil acidity was high for both stand types though cedar tended to occur in the less acidic sites with higher exchangeable calcium values. The authors concluded that cedar is a climax community on the lake shores and a pioneer community on the abandoned pasture sites, noting that soil drainage had a greater impact on cedar distribution than soil chemical properties.

Bhatt, G.C. 1970. The soil microfungi of white cedar forests in Ontario. *Canadian Journal of Botany* **48(2): 333-339.**

Northern white-cedar is commonly associated with neutral to slightly alkaline, deep, organic soils. Bhatt discovered 184 fungal species, but suggested this was an underestimate due to limited isolation techniques. A high number of wood saprophytes were found, attributed to the high organic content of cedar soils. Few basidiomycetes were isolated, though they were found fruiting within the stand. The author suggested that a more extensive study with improved isolation techniques would reveal more fungi in these communities.

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): 434-438.**

Northern white-cedar was noted to have bimodal site distribution patterns, occupying dry upland sites and wet lowland sites. The authors determined that within-site seed morphology variability was extremely high and did not detect differences among sites. Unlike Habeck (1958) and Musselman et al. (1975), the authors suggested that there is no genetic ecotypic difference between wetland and upland cedar. For most measured attributes, within-stand variability was high enough to offset detectable differences found among stands. The authors suggested that this variability may allow cedar to establish across a wide range of environmental conditions.

Collingwood, G.H. 1940. Northern white cedar. *American Forests* **12: 558-559.**

The authors described northern white-cedar as a small-stature tree that can occasionally reach heights of 70 feet with a maximum diameter of 3 to 6 feet. It is reported to be a slow growing tree reaching ages of 250 to 300 years. The stem is often lobed or buttressed, commonly divided into two or more secondary stems, and frequently distorted or twisted. Dry weight of the wood is reported as 19 pounds per cubic foot. This species is commonly afflicted with "ring shake" or "wind shake" which separates annual growth rings from one another.

Collins, S.L., J.L. Vankat, and J.V. Perino. 1979. Potential tree species dynamics in the arbor vitae association of Cedar Bog, a west-central Ohio fen. Bulletin of the Torrey Botanical Club 106(4): 290-298.

The authors reported that earlier works suggested that cedar communities in bogs are either climax communities or early-successional pioneer communities that are being displaced. Though both cedar and hardwood species were present in this study, neither seemed to be displacing the other. Using Cole's Index of Association, the authors determined that this Ohio bog community was stable due to continual vegetative regeneration, unlike other cedar-hardwood communities.

Curtis, J.D. 1941. Report of northern white cedar research in Maine. Unpublished manuscript. Orono, ME. 23 p.

Cedar was reported to grow most commonly on wet sites with some drainage and on dry, thin-soiled, rocky ledges. The author claimed that growth is best on moist upland sites (2 to 3 times the growth rate of lowland sites). "Pistol butted" stems are reported to be more common in lowland than upland sites as a result of shallow rooting, partial windthrow and snow loading. The author noted that there was a scarcity of stems ranging between 6 inches and 10 feet tall, though germinants and small seedlings were common. Vegetative reproduction, including layering, tip-ups, and fracturing was reported as a dominat regeneration mechanism. The author suggested that cedar has poor form (e.g. pistol butting, spiral grains, and poor apical control leading to forking) across many habitat types. Heart rot was reported to be problematic in older stems; *Fomes roseus* and *Polyporous schweinitzii* were said to be common decay fungi afflicting cedar.

Curtis, J.D. 1944. Northern white cedar on upland soils in Maine. *Journal of Forestry* **42: 756-759.**

Curtis suggested that northern white-cedar is an early successional forest type that colonizes upland well-drained old fields and pasture lands. Upland cedar often grow in dense stands with high stocking (>320 square feet of basal area per acre) capable of growing 0.5 cords per acre per year. Yield tables for differing sites are presented. Crown and selection thinning methods were applied to a 50-year-old stand to investigate cedar responses to silviculture in future research; trees with poor form and vigor were targeted for removal.

Curtis, J.D. 1946. Preliminary observations on northern white cedar in Maine. *Ecology* **27(1): 23-36.**

This report described general characteristics and ecology of northern white-cedar based on a five-year study in Maine. The author suggested that cedar requires a pH of 5.5 to 6.7 for optimal growth. Vegetative reproduction was reported to be common and vigorous; northern white-cedar has the ability to send out roots from any portion of the stem or branches in optimal conditions. The author noted that cedar tends to have a spiral grain pattern, but that upland cedar commonly have higher volume growth and better stem form. Observed sapwood radius was small, seldom exceeding three inches and commonly much narrower. Shade-tolerance was noted to be difficult to discern; it seemed to range from very shade-tolerant (slightly less than balsam fir) to moderately shade-tolerant (less than eastern white pine). The author stressed concern for future stands because seedlings were abundant but few were recruited to saplings.

de Blois, S. and A. Bouchard. 1995. Dynamics of ***Thuja occidentalis*** **in an agricultural landscape of southern Quebec.** *Journal of Vegetation Sciences* **6(4): 531-542.**

The authors argued that cedar in southern Quebec persist as dense, isolated populations that resist invasion from competing species. Land use practices that modify soil and vegetation competition allow cedar to colonize mesic sites. In this study, 95% of the sites that had a grazing history were colonized by cedar and 68% of the cedar stands that were associated with pasture had moderate drainage. The authors suggested that this is because cattle preferentially browse other species, and cedar is resistant to trampling. Multivariate analysis suggested that environmental variables accounted for

29% of the species variation among sites, whereas land use history accounted for a much higher percentage (value not reported).

Fernald, M.L. 1919. Lithological factors limiting the ranges of *Pinus banksiana* and *Thuja occidentalis*. *Rhodora* 21: 41-67.

The author argued that jack pine is confined to acidic soils while northern white-cedar is restricted to basic soils. While it is noted that cedar can occur on more acidic soils, the author stresses that the best growth and form can only occur on calcareous sites. Anecdotal evidence from several sites were provided to support his argument that cedar stands are associated with pockets with calcareous soils in a matrix of more acidic soils.

Godman, R.M. 1958. Silvical characteristics of northern white-cedar (*Thuja occidentalis*). Department of Agriculture, United States Forest Service Lake States Forest Research Experiment Station Paper Number 67. 17p.

This report presented an overview of cedar in Maine, Michigan and Wisconsin. The author reported that cedar grow primarily on swamps and uplands, but does not proliferate on extremely wet or dry conditions. In lowlands, cedar quality was reported to improve as the depth of peat increases and the internal drainage improves. The author suggested that growth rate and form was superior on old field sites than lowlands. Though cedar was found on acidic soils, it was reported to do best on neutral or alkaline soils. Cedar was noted to be the only northeastern conifer that does not have mycorrhizal fungi associated with its roots. Conventional silvicultural methods were reported to have inconsistent results, often with poor regeneration post-cutting. Data suggested 80 to 100 years are required to grow a 6-inch tree, though upland trees may grow faster. Cedar was generally considered a longer-lived species, reaching ages of 400 years in lowland types. Cedar wood was reported to be light, relatively free from warping when dried and have low shrinkage.

Habeck, 1958. White cedar ecotypes in Wisconsin. *Ecology* 39: 457-463.

Seeds were collected from upland and lowland cedar and transplanted to study ecotypic variation in cedar from different sites. Cedar seedlings were found to have higher survival rates and more plastic root development from upland sites than lowland cedar seedlings. Based on significant differences between the populations, the author concluded that genetic ecotypic variation exists in northern white-cedar. This is consistent with findings from Musselman et al. (1975), although several authors later refuted ecotypic variation in this species (e.g. Matthes-Sears and Larson 1991, Briand et al. 1991, 1992, and Edwards and Dixon 1995a, 1995b).

Harlow, W.M. 1927. The effect of site on the structure and growth of white cedar *Thuja occidentalis* L. *Ecology* 8(4): 453-470.

This study compared growth and wood properties of northern white-cedar trees growing in a bog to those of three trees on calcareous (limestone outcrop) soils in New York. Three of the five wood properties examined had greater variation within than among sites (fiber length, tracheid number per mm, and ray volume). Specific gravity was higher in the limestone outcrop sample than in the bog sample (0.365 and 0.322, respectively). Crushing strength was also greater in the limestone community than in the bog (966 pounds/cm^2 and 803 pounds/cm^2, respectively), however these differences were negligible once specific gravity was accounted for. Harlow found no correlation between specific gravity and number of rings per cm, suggesting that wood density and strength are not related to growth rate in this species. A total of 80 trees were cored to test growth differences among sites, with an average diameter growth of 1.55 mm/yr in the bog community and 3.10 mm/year in the limestone community. These differences were attributed in part to the fact that the limestone community was a more open grown, second-growth forest. The author noted that both communities had remarkable "evenness" in yearly growth.

Hofstra, G. and R. Hall. 1971. Injury on roadside trees: leaf injury on pine and white cedar in relation to foliar levels of sodium and chloride. ***Canadian Journal of Botany*** **49: 613-622.**

Northern white-cedar and several pine species were examined for injury resulting from salt spray due to nearby highway traffic. Cedar stands on the leeward side of the road tended to be smaller, and showed considerable loss and browning compared to those found on the windward side of the road. Elevated levels of sodium, chloride, and foliar injury were found in the leeward stands. Levels of chloride were lower in cedar foliage than in most pine species, and injury was far less in cedar for a given level of chloride and sodium. Injury was greatest for all species near the highway and reduced as distance from the road increased.

Johnston, W.F. 1990. *Thuja occidentalis* L. – northern white-cedar. In: Silvics of North America. Vol. 1. Conifers. U.S. Department of Agriculture Agricultural Handbook 654: 1189-1209.

Phil Hofmeyer takes an increment core to determine the age of a spruce tree.

This handbook reports the general silvics of northern white-cedar including habitat range, climate, site, and life history characteristics. Cedar occurs on cool, moist, nutrient-rich, calcareous sites with moving groundwater; upland seepage areas and abandoned farm lands are also commonly colonized by cedar. Johnston reported that better stem quality is associated with upland sites. This species was noted to have high genetic variability, however, there are no known subspecies or races. Sexual reproduction occurs most readily on disturbed, moist sites with slow seedling height growth (8 cm/year). Vegetative growth (layering) occurs most commonly on the lowland sites, resulting in more robust and shade-tolerant progeny than seedling reproduction. Upland cedar stands tend to be very stable, whereas lowland stands are subject to frequent blowdown. Though cedar is affected by few insect pests, it is commonly afflicted with fungal butt rot. The author noted that cedar has many unique attributes that make expectations of shade-tolerance and seral stage difficult.

Johnston, W.F. and M.J. Hyvarinen. 1979. Northern white-cedar: An American wood. U.S. Department of Agriculture Forest Service Miscellaneous Research Report FS-227. 4 p.

Northern white-cedar has the lightest wood of any commercial species in the United States. Cedar heartwood resists decay and termites but has poor bending strength and nail-holding properties. Cedar sawtimber often has low yields because of knotty, crooked, sweeping, or hollow stems. The authors suggested that pure cedar stands often perpetuate themselves, while cedar growing in mixed-species associations are often replaced by competing species. They note that cedar trees grow best on alkaline, well-drained soils. Tall trees are vulnerable to windthrow due to shallow and weak roots. Cedar was reported to reach ages exceeding 400 years, but it is known to be slow-growing in relation to competing species.

Jokela, J.J. and C.L. Cyr. 1977. Performance of northern white-cedar in central Illinois. In Proceedings of the 13th Lake States Forest Tree Improvement Conference. General Technical Report NC-50. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. p. 100-106.

Seeds were collected from 32 stands throughout the botanical range of cedar in 1964. Seedlings (2-0 stock) were planted as windbreaks in Illinois in 1967. At 12 years, there were no survival differences among provenances. Growth rate and susceptibility to winter foliage damage differed among provenances, however, no geographic pattern was observed. The authors speculated this could be a reflection of localized lowland and upland ecotypes, as described by Habeck (1958).

Kangas, P. 1989. Comparison of two northern white cedar (*Thuja*) forests. *The Michigan Botanist* **28(2): 59-66.**

A cedar stand in Ohio was compared to a cedar stand in Michigan using a complexity index based on structure and composition. Similar cedar importance and complexity index values were found on these sites, and suggested that site similarities override climatic differences for these stands. The author however, predicted that future stand compositions will likely be dissimilar. The Ohio stand, which may have been disturbed recently, was more stable in terms of cedar regeneration, whereas the undisturbed Michigan stand was increasing in balsam fir importance. The author pointed out that cedar can be shade-tolerant and slow-growing but likely requires disturbance to regenerate.

Moore, B. and N. Taylor. 1921. Plant composition and soil acidity of a Maine bog. *Ecology* **2(4): 258-261.**

A sedge bog on Mount Desert Island, Maine had a mixture of black spruce and northern white-cedar on the margin, all less than 10 feet in height. The bog itself had a pH of 6.0, though the rooting soil of the cedar trees had a pH of 4.5. This was the lowest soil pH that the author had ever seen associated with cedar trees.

Musselman, R.C., D.T. Lester, and M.S. Adams. 1975. Localized ecotypes of ***Thuja occidentalis*** **L. in Wisconsin.** *Ecology* **56: 647-655.**

Northern white-cedar was reported to have a bimodal site distribution, with populations occurring most frequently on either hydric or xeric sites. Significant differences in root development were found among the studied habitat types. Root structures changed from tap roots with few laterals to no tap root but many laterals as soil moisture levels increased. This led the authors to conclude that a genetic ecotypic variation exists among sites. This is in contrast to later reporting of Matthes-Sears and Larson (1991), Briand et al. (1991, 1992), and Edwards and Dixon (1995a, b), but consistent with Habeck (1958).

Pregitzer, K.S. 1990. The ecology of northern white cedar. Northern White Cedar in Michigan Workshop. D.O. Lantagne, Ed. Michigan State University Agricultural Experiment Station Research Report 512: 7-12.

This paper addressed northern white-cedar ecology, including life history differences on lowland and upland sites and reproduction and regeneration dynamics. The author discussed the difficulty of categorizing cedar into a specific seral stage and attempted to explain why cedar is not regenerating in mature stands considering that many consider it a climax type on alkaline soils. The author concluded that although the overstory in this study area is similar to pre-settlement forest conditions, the understory lacks regeneration that was present in the pre-settlement condition. This was suggested to be a consequence of a rising deer population.

Reiners, W.A. 1974. Foliage production by *Thuja occidentalis* L. from biomass and litter fall estimates. *American Midland Naturalist* **92(2): 340-345.**

Estimating cedar foliage production is difficult due to the growth and abscission patterns of the foliage units (cladoptosis). The author reported difficulties in detecting differences between years of growth in the foliage due to a lack of bud scars. Annual production was estimated from litter fall measurements collected in 0.5-m^2 traps in a stand where foliar mass was previously estimated. This stand had a turnover value of 0.21, which is low compared with many other conifers (120 g/m^2 litter fall, 563 g/m^2 foliar biomass). The author presented a list of the assumptions that were needed for this study, including low year-to-year foliage mass differences, that collected foliage was consistent with long-term losses, and that corrections for fallen and fresh leaf litter can be made.

Ringius, G.S. 1979. Status of eastern white cedar, ***Thuja occidentalis*****, in western Nova Scotia.** *Canadian Field Naturalist* **93(3): 326-328.**

This is an observational study of specific locations of northern white-cedar in Nova Scotia. The author suggested that cedar is often only included offhandedly in publications, if at all. Though no data were collected or analyzed, Ringus observed ample reproduction and a lack of saplings and speculated that mortality of seedlings was high. This paper provided few analytical comparisons, however, it reveals early concern about cedar sustainability due to lack of recruitment.

Scott, M.L. and P.G. Murphy. 1986. Origin and composition of an old-growth cedar-hardwood stand: the role of dune activity. *The Michigan Botanist* **25(2): 57-65.**

Previous studies suggested that an old-growth forest on South Manitou Island in Lake Michigan had some cedar trees greater than 31 m tall and in excess of 500 years old. Contrary to earlier vegetation reports of the island, the authors found that only 5% of the cedar trees were 20 to 30 m in height, none were greater than 30 m or approached 500 years of age. The authors suggested that northern white-cedar on this site acted as an early successional species, colonizing dunes and later dominating the overstory. Limited cedar regeneration and abundant shade-tolerant hardwoods in the understory led the authors to conclude that a compositional shift would eventually occur.

Slaughter, B.S. and J.D. Skean, Jr. 2003. Comparison of cedar and tamarack stands in a relic conifer swamp at Pierce Cedar Creek Institute, Barry County, Michigan. *The Michigan Botanist* **42: 111-126.**

Northern white-cedar is a rare community type in southern Michigan, commonly replaced by tamarack. The authors studied a cedar-dominated stand that grades into a tamarack-dominated stand. Both stands had a wide diameter distribution and similar soil pH (6.69 to 7.37 in the cedar stand and 6.67 to 7.14 in the tamarack stand). However, the tamarack stand had more standing water (37% to 58% of stand area, depending on season) than the cedar stand (3% to 10% of stand area). The cedar stand had higher basal area and older trees than the tamarack stand; maximum ages were 85 years and 65 years, respectively. Data on herbaceous plant diversity were collected and suggested that the communities vary due to microtopography differences of the two stands.

Tardif, J. and Y. Bergeron. 1997. Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. *Canadian Journal of Forest Research* **27(1): 108-116.**

The authors suggested that hydric and xeric sites are best used for dendroclimatology analyses, as they may have a greater response to exceedingly dry and wet years than mesic sites. It was determined that northern white-cedar had the greatest radial growth increment during cool, moist growing seasons. Cedar from both xeric and hydric sites responded similarly to temperature and moisture stress during the growing season. The authors suggested that mesic populations tend to respond more to microsite and competition, whereas xeric and hydric populations respond more to environmental conditions (data were not provided from cedar on mesic sites to support this).

Tardif, J. and D. Stevenson. 2001. Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. *Dendrochronologia* **19(2): 179-187.**

The authors suggested that northern white-cedar is commonly noted as a species useable for dendroclimatology, however, little of its range has been sampled for radial growth–climate associations. This paper presented the hypothesis that cold winters limit radial growth (average January temperatures of -19.8°C). The data suggested that radial growth was negatively correlated with maximum August temperatures (a response to water stress) and positively correlated with maximum November and December temperature. The authors suggested that cedar may take advantage of an earlier growing season; spring maximum temperature was also positively correlated with radial growth. Because of low mean sensitivity scores and low correlations, the authors concluded that climate does not strongly limit radial growth at this range limit and that other disturbance factors may play a more important role.

Vaartaja, O. 1962. Ecotypic variation in photoperiodism of trees with special reference to *Pinus resinosa* and *Thuja occidentalis*. *Canadian Journal of Botany* **40: 849-856.**

Six photoperiod treatments were administered for northern white-cedar and red pine seedlings, including extremely long day (ELD, continuous light), very long day (VLD, 3 hour dark period), long day (LD, 6 hour dark period), short day (SD, 9 hour dark period), very short day (VSD, 12 hour dark period), and extremely short day (ESD, 15 hour dark period). The response of cedar to photoperiod treatment was small, suggesting no endogenously determined growth pattern. The critical day length for cedar was the VSD treatment, compared to the SD treatment for red pine. Most northern tree species have photoperiodic ecotypes that inhibit northern seedlings more than southern seedlings during shortened day lengths. The authors suggested that cedar is unique amongst northern tree species in possessing a weak photoperiodic response by responding more directly to temperature variations.

Yu, Z. 1997. Late quaternary paleoecology of *Thuja* and *Juniperus* (Cupressaceae) at Crawford Lake, Ontario, Canada: pollen, stomata, and macrofossils. *Review of Paleobotany and Palynology* **96(3-4): 241-254.**

Though *Thuja* and *Juniperus* have nearly indistinguishable fossil pollen grains, they can be differentiated through macrofossils and stomata found in lake sediment cores. Macrofossils are often scarce and time consuming to work with, while stomata are usually abundant due to their lignified nature in partially decayed conifer foliage. Yu suggests that stomata size and shape are most useful for separating *Thuja* from *Juniperus* in the fossil record; *Juniperus* stomata are larger with wider (3.4 to 4.3 µm) and longer (9.4 to 10.8 µm) polar lamellae. At the study site, the author found that *Thuja* was an important component of the mixed hardwood forest beginning 7,500 14C yr BP and *Juniperus* 13,000-10,000 14C yr BP. Peaks of these Cupressaceae genera were attributed to a warmer, drier climate than present. It was noted that troughs in the fossil record of these genera occurred during peaks of *Pinus* pollen.

Zollner, J.A. 1976. The cedar resource. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 5-7.

This paper reported the status of the cedar resource in Michigan in the early 1970s. The resource was considered in poor condition due to stand type conversions post-harvesting, poor sites and over-mature stands. Many stems were of poor quality and vigor; more than 50% of pole- and sawtimber-sized trees were estimated to be unmerchantable. This is interesting to compare with Botti's (1990) analysis of Michigan's cedar resource.

Genetics, Physiology, and Morphology

Bannan, M.W. 1941. Vascular rays and adventitious root formation in *Thuja occidentalis* L. *American Journal of Botany* **28: 457-463.**

The author observed that most vascular rays were one cell wide, but vary in height from one to many cells. Sporadic unusual rays that differed markedly in size and structure from normal rays were observed, with widths at times greater than 10 cells wide. Vascular rays extending from pith to cortex were generally parenchymatous throughout, though tracheids were commonly found in

Bob Seymour and Phil Hofmeyer tag-team the coring of a cedar tree.

the first-formed parts of the ray. The author described many types of unusual rays that do not follow this pattern, though it was stated that these are in low proportion to the common vascular rays. Any time a branch was covered in soil and an adventitious root formed, it corresponded to an unusual ray. However, unusual rays were found randomly distributed throughout the shoot system, regardless of adventitious root formation. In root systems, ray tracheids were rarely found, with rays nearly exclusively comprised of parenchyma cells. Abnormal rays were not a significant component of root rays.

Bannan, M.W. 1951. The reduction of fusiform cambial cells in *Chamaecyparis* **and** *Thuja***.** *Canadian Journal of Botany* **29: 57-67.**

Thuja occidentalis and three species of *Chamaecyparis* were used to investigate fusiform initials in the cambium. The Cupressaceae family lends itself to this type of study due to the simple structure of its secondary tissues. Many fusiform initials were transversely subdivided, resulting in either shortened segments or ray initials. In all examined species, nearly all of the new rays originated in this manner. Commonly, fusiform initials mature from the cambium and become imperfect phloem or xylem elements.

Bannan, M.W. 1953. Further observations on the reduction of fusiform cambial cells in *Thuja occidentalis* **L.** *Canadian Journal of Botany* **31: 63-74.**

Northern white-cedar trees 6 to 12 inches dbh were sampled and cut in radial, tangential, and transverse sections through the cambium and adjoining tissue to determine cell size and shape. During the active growing season, fusiform initials in cambium transversely subdivide with varying proportions converting to ray initials and others quickly maturing and dying. During this conversion, there is generally a decline in cell size and occasionally a loss so high that there is a stoppage of radial growth, especially at the cell ends. However, the rate of growth retardation varies greatly within different parts of the tree. In the latter stages of cell shortening, asymmetric division results in daughter cells of dissimilar lengths.

Bannan, M.W. 1954. Ring width, tracheid size, and ray volume in stem wood of *Thuja occidentalis* **L.** *Canadian Journal of Botany* **32: 466-479.**

Tracheid length in conifers is of interest to the paper industry for paper quality, workability, and associated properties. Previous work in this field has been concerned with cell length comparisons based on age, however the author suggested that a negative relationship exists between cell length and linear distance from the pith. Circumstances that favor accelerated growth commonly encouraged earlier transverse cell division and produced shorter tracheids. Radial growth rates of 0.7 to 0.8 mm/year had the longest tracheid lengths, generally exceeding 3.0 mm (stem size-dependent). As ring width increased, frequency of rays increased and greater ray height was observed across all stem sizes, leading to the conclusion that ray volume was positively correlated to radial growth.

Bannan, M.W. 1955. The vascular cambium and radial growth in *Thuja occidentalis* **L.** *Canadian Journal of Botany* **33: 113-138.**

The author described the vascular cambium as a "self-perpertuating uniserate initiating layer and the derived tissue of mother cells." In dormant conditions, the cambium is generally two to three cells wide and expands rapidly once reactivated in proper environmental conditions. In vigorous open-grown trees, there is a surge of growth and dividing in cambial initials. From mid-June to August, cell production declines from a reduction in the number of dividing initials. Phloem development begins after xylem development. By the end of May, phloem may be only 4 cells wide, whereas a file of xylem might contain 30 to 60 cells. Phloem expansion occurs from late May through early September. Annual xylem increment is more variable than phloem increment.

Bannan, M.W. 1956. Some aspects of the elongation of fusiform cambial cells in ***Thuja occidentalis*** **L.** *Canadian Journal of Botany* **34: 1956.**

The author suggested that phloem tissue is desired for examining changes through time in basic cell patterns; however, it is commonly difficult to distinguish annual increment boundaries in the phloem of northern white-cedar. Therefore, xylem tissue was used for cell morphology observations. The author observed a high degree of variability from cell to cell in fusiform initial elongation, attributed to differences in the local environment around each cell. Elongation followed a general trend, with early rapid extension generally tapering off to decreasing lengthening rates as the process proceeded. The elongation process varied in different regions of the tree, as well as with tree age. Smaller trees had strong bipolar lengthening differences, i.e. growth rates at opposite ends of the cell differ. This pattern was also evident in specific regions of mature individuals (e.g. distal parts of branches, outer regions of mature stems). The author hypothesized that bipolar elongation may be attributed to gravity, though it may be only a minor factor in bipolar growth.

Bannan, M.W. 1957. An occurrence of perforated tracheids in ***Thuja occidentalis*** **L.** *New Phytologist* **57: 132-134.**

Perforated tracheids were found in the xylem tissue of a large branch in northern white-cedar, a condition once discovered in *Sequioa sempervirens*. In a sample with narrow annual growth increment, a discontinuous tracheid wall existed through 6 annual rings, effectively connecting adjacent tracheids. The author suggested this was associated with internal changes in fusiform initials and a local deficiency in the wall-synthesizing mechanism. The author argued that this discovery cannot be regarded as having phytological significance, more that it is a discovery of physical abnormalities.

Bannan, M.W. 1957. Girth increase in white cedar stems of irregular form. *Canadian Journal of Botany* **35: 425-434.**

Irregularly shaped cedar stems were examined for growth anomalies in the cambium. In 14 of 16 trees studied, the rate of pseudotransverse cell divisions was higher in the concave portions of the stem than adjacent sides. A 156% gain of cell divisions was accompanied by a 19% decrease in the mean length of cambial cells. Despite this increased rate of divisions, the loss of cambial initials by maturation or reduction to ray initials was so high that a net loss of cells commonly occurred. Convex stem portions had a much higher cell survivorship leading to a larger net gain. A similar pattern was noted in cedar stems subjected to radial pressures (against fence railings, close-growing branches, lightning strike wounds); flattened sections had high cell division rates, lower mean cell length, and high mortality as compared to adjacent convex sections. The author concluded that compression has the effect of increasing the frequency of anticlinal division from vascular cambium initials.

Bannan, M.W. 1960. Cambial behavior with reference to cell length and ring width in ***Thuja occidentalis*** **L.** *Canadian Journal of Botany* **38: 177-183.**

The author compared cambial cell length of 145 cedar trees 15 to 50 cm in diameter. Trees were grouped according to diameter and ring width for analysis. Overall cell length was negatively correlated with ring width; longer cells were commonly associated with narrower ring widths and shorter cells were found in areas of wider rings. Results also suggested that the frequency of multiplicative divisions in the cambium is not dependant on tree growth rate. There was wide variation in the number of fusiform initials that survive indefinitely across all diameters and growth rates, however, it appears that the frequency of fusiform initial divisions is best correlated with radial increment. The author suggested that as frequency of division increases, within-tree competition in the cambium favors longer cells.

Bender, L., I.S. Harry, E.C. Yeung, and T.A. Thorpe. 1987. Root histology, and nutrient uptake and translocation in tissue culture plantlets and seedlings of ***Thuja occidentalis*** **L.** *Trees* **1(4): 232-237.**

The vascular xylem connection at the root–shoot junction in northern white-cedar was found to be well developed and uninterrupted. Tracers used to determine uptake and translocation rates were 32P and 86Rb because they appear to be positively correlated with fresh shoot weight. Tissue cultured plantlets absorbed nearly 50% more 86Rb than seedlings. No significant differences were detected in the uptake and translocation to the shoots in either plant type, however, translocation was significantly higher for 86Rb than 32P.

Briand, C.H., U. Posluszny, and D.W. Larson. 1991. Patterns of architectural variation in ***Thuja occidentalis*** **L. (eastern white cedar) from upland and lowland sites.** *Botanical Gazette* **152(4): 494-499.**

This paper challenged the notion that wetland and upland cedar express ecotypic differences, as suggested by Habeck (1958) and Musselman et al. (1975). The authors reported that architectural variations within sites were small, as were variations among sites. Tree size was statistically different among sites, however, the variation disappeared after correcting for age. The authors argued that the trees studied were part of a larger, homogeneous population. Because no differences were detected among sites, ecotypic variation was not supported by this study.

Briand, C.H., U. Posluszny, and D.W. Larson. 1992. Differential axis architecture in *Thuja occidentalis* (eastern white cedar). *Canadian Journal of Botany* **70(2): 340-348.**

The authors reported that little work has been done to quantify axis architecture in northern white-cedar and conifers in general. It was determined that *T. occidentalis* has very similar architecture to *T. plicata* and most closely follows Attims' architectural model, though elements of Mossart's model were also observed. The authors discussed the difficulty of determining differences between caulome (axes) and phyllome (foliage) on higher order branches; they appear to be caulome, but are functionally equivalent to compound leaves.

Briand, C.H., U. Posluszny, and D.W. Larson. 1993. Influence of age and growth rate on radial anatomy of annual rings of *Thuja occidentalis* L. (eastern white cedar). *International Journal of Plant Sciences* **154(3): 406-411.**

On the limestone cliffs of the Niagara Escarpment, radial growth less than 0.1 mm/yr has been documented in suppressed white-cedar. In the same habitat, growth rates of 5.0 mm/yr have been observed in open-grown cedar. This difference allowed the authors to determine if xylem anatomy was better predicted by tree age or growth rate. A total of 34 sample trees parsed into four categories based on age and growth (old and slow-growing, old and fast-growing, young and slow-growing, young and fast-growing) were examined for tracheid characteristics. The slow-growing trees had an average of 9.2 tracheids per file per growth ring, while fast-growing trees averaged 60. There was no statistical difference among the tree ages sampled. Earlywood tracheid cell diameter had a positive correlation with ring width; latewood tracheids were not correlated with ring width. A majority of the variance in tracheid cells was attributed to growth rate, suggesting little age-related senescence of vascular cambium. The authors suggested that smaller cells are less prone to cavitation, protecting the trees in times of water stress.

Collier, D.E. and M.G. Boyer. 1989. The water relations of *Thuja occidentalis* L. from two sites of contrasting moisture availability. *Botanical Gazette* **150(4): 445-448.**

The authors reported that northern white-cedar has a bimodal site distribution, occurring on xeric cliff sites and lowland saturated sites. Cell water potential has been shown to correspond with habitat moisture conditions in many species, allowing cedar to be tested for ecotypic variation. Branches of mature individuals and seedlings grown from seed of two natural cedar populations with contrasting moisture regimes were sampled. Branch samples were fully hydrated and placed in a pressure bomb for pressure-volume (P-V) analysis. Seedlings from each population were grown in either a saturated or moisture-limited condition for five months; they were then cut and underwent P-V analysis. Water potential was found to be more negative in the xeric moisture regime. In the seedlings, these differences were independent of parent stock. The authors argued that the upland population was under higher water stress than the lowland population. They concluded that cedar can cope with a wide range of moisture conditions through osmotic adjustment, and that these populations do not have inherent ecotypic variation.

Colombo, S.J. and E.M. Raitenin. 1991. Frost hardening in white cedar container seedlings exposed to intermittent short days and cold temperatures. *Forestry Chronicle* **67(5): 542-544.**

Northern white-cedar has been planted in Ontario to reforest abandoned farmlands and wet sites. Frost-hardiness increased most significantly when seedlings were given concurrent short day and cold temperature treatments. A green-brown phenotypic color difference was observed in trees that were most frost-hardy. The authors suggested that tree improvement programs could select for these individuals to enhance the genotypic frost-hardiness of the stock.

Dixon, M.A., J. Grace, and M.T. Tyree. 1984. Concurrent measurements of stem density, leaf and stem water potential, stomatal conductance and cavitation on a sapling of *Thuja occidentalis* L. *Plant, Cell and Environment* **7: 615-618.**

Acoustic emissions (AE) from vascular plants are generally considered the result of breakages within tracheid and vessel water columns. Using higher frequencies allows for studying AE without need for a soundproof room. The sapling used for this study was 2 meters tall and 40 mm in diameter at the base. During dehydration, initial leaf and stem water potential declined slowly, with a rapid decline as stomatal conductance increased. A peak in AE coincided with a leveling of the water potential decline. There was a distinct negative correlation between stem density (g/cm^3) and cumulative AE. The authors concluded that AE were caused by cavitation of water in tracheids, and that given the high variability of minor shoot water potentials during rehydration, cavitation is a reaction to water stress that aids in the relocation of water reserves.

Edwards, D.R. and M.A. Dixon. 1995. Mechanisms of drought response in *Thuja occidentalis* L. I. Water stress conditioning and osmotic adjustment. *Tree Physiology* **15(2): 121-127.**

Water stress conditioning resulted in lower osmotic pressure and transpiration rates in water-stressed 6-year-old northern white-cedar, relative to untreated controls. The authors suggested that the reduction in transpiration rates is more critical than the decreased osmotic pressure in response to water stress. Stomata closure occurred quickly in response to moisture stress in even mildly conditioned trees, contrary to results of Matthes-Sears and Larson (1990). It appeared that stomata regulation and osmotic adjustment are easily influenced by conditioning to water stress in this species. The authors speculated that these adjustments may be greater in mature individuals.

Edwards, D.R. and M.A. Dixon. 1995. Mechanisms of drought response in *Thuja occidentalis* L. II. Post-conditioning water stress and stress relief. *Tree Physiology* **15(2): 129-133.**

No significant differences were detected in transpiration rates and osmotic adjustment between well-watered and stress-conditioned individuals in subsequent moisture stress relief. Drought-stressed trees had a lower transpiration rate and water potential integral than the controls in subsequent drought events. Osmotic adjustment occurred after a single induced drought instance and was restored once soil water potential was recharged. The authors suggested that ecotypic genetic variables do not influence cedar's tolerance to a wide range of water availability.

Kutscha, N.P., F. Hyland, and A.R. Langille. 1977. Salt damage to northern white cedar and white spruce. *Wood Fiber* **9(3): 191-201.**

The authors stated that few studies have compared anatomical effects of salt accumulation in trees. Northern white-cedar tends to accumulate salt in the root system, whereas white spruce tends to accumulate salt in the shoot system. Soil applications of salts caused less damage

Cedar trees are cut into bole sections to help recontruct the stand development.

in both species than foliar salt applications. Anatomical damage of the salt treatments included fragmented cuticles, disrupted stomata function, disintegrated protoplasts, granular cytoplasm, disintegrated cholorplasts, disintegrated nuclei, and disorganized phloem tissue. Cedar appeared to be more tolerant to salt applications than white spruce, both morphologically and anatomically. Response differences led the authors to conclude that northern white-cedar may be more salt resistant than white spruce and consequently might be a better roadside planted species.

Lamy, S., A. Bouchard, and J.P. Simon. 1999. Genetic structure, variability, and mating system in eastern white cedar (*Thuja occidentalis*) populations of recent origin in an agricultural landscape in southern Quebec. *Canadian Journal of Forest Research* **29(9): 1383-1392.**

In southern Quebec, northern white-cedar is often a component of mixed-species stands, rarely forming pure communities. The authors determined that cedar has a low level of outcrossing, relatively high levels of self-fertilization, and high rates of vegetative reproduction. This led them to conclude that there is a low level of genetic differentiation in this species, though they speculate that this will increase over time. They also reported that sexual reproduction is more likely to occur in low-density populations and 60 to 80% of the cedar trees on abandoned agriculture lands in this study were of vegetative origin.

Larson, D.W., J. Doubt, U. Matthes-Sears. 1994. Radially sectored hydraulic pathways in the xylem of *Thuja occidentalis* as revealed by the use of dyes. *International Journal of Plant Sciences* **155(5): 569-582.**

The authors hypothesized that white-cedar xylem is radially sectored, unlike most competing species (i.e. individual roots determine productivity and survival of connected branches). To test this hypothesis, 1-, 2-, and 7-year-old seedlings (n=102 total) had targeted rots washed, cut, and placed in flexible plastic dye tubes. A subsample of 7-year-old seedlings were also wedge-cut to remove 30 to 70% of their main stem cross-sectional area. The authors observed distinct and complex sectoring in the 7-year-old specimens, with straight dye courses from roots to particular shoots. The degree of sectoring was less evident in 2-year seedlings, and barely evident in the 1-year seedlings. Wounded stems had little or no dye movement around wounds. Though hydraulic conductivity values dropped to nearly zero in some wound treatments, widely spaced opposing cuts did not completely block flow. Because fibers are not abundant in this species, the authors suggested that they are not barriers to hydraulic flow, and that tracheids without pits or blocked pits may be present.

Lewis, A.M, V.D. Harnden, and M.T. Tyree. 1994. Collapse of water-stress emboli in the tracheids of *Thuja occidentalis* **L.** *Plant Physiology* **106: 1639-1646.**

Water stress can induce xylem dysfunction when tracheid fluids are replaced by air bubbles (emboli). The objective of this study was to determine the quantity and composition of emboli entering a conduit when cavitation occurs. White-cedar was used for this study due to its simple anatomy (e.g. few parenchyma cells, free of resin ducts, short and straight tracheids). Sample stem segments were cut, hydrated overnight, dehydrated under a microscope until cavitation (embolus formation), then rehydrated until last embolus collapsed. Observed emboli were argued to be either a) 100% air (or non-aqueous gas), b) 100% water vapor, or c) some combination of water vapor and other gas. Their results indicated that rehydration time was a positively correlated function of dehydration time (for up to 15 minutes of dehydration time). The authors suggested that emboli collapse in rehydration is consistent with Fick's Law and reach an equilibrium concentration of gases in water consistent with Henry's Law. They also noted that field conditions may vary from laboratory results due to pressure differences between cut and intact stems.

Melcher, L.E. 1933. Freezing injury to arborvitae and junipers in Kansas. *American Journal of Botany* **20(9): 593-595.**

Large temperature fluctuations during February and March 1932 (23-81° F) caused damage to many varieties of *Thuja* and *Juniperus* species in a nursery. The arborvitae varieties with yellow foliage suffered the least frost damage. This phenotype was attributed to frost hardiness of some varieties. Only five varieties of Junipers showed freezing injury.

Nour, K.A., E.C. Yeung, and T.A. Thorpe. 1993. Shoot bud histogenesis from mature embryos and shoots of eastern white cedar (*Thuja occidentalis* L.) cultured in vitro. *International Journal of Plant Sciences* **154(3): 378-385.**

Shoot primordia developed in the peripheral region of the shoot apex, after which phenolic substances terminated further growth. The apex was divided and gave rise to two shoot buds. Unlike many other conifers, cedar shoot buds are not adventitious; they originate from the main axis of the embryonic axis, not the cotyledon axils.

Perry D.J. and P. Knowles. 1989. Inheritance and linkage relationships of allozymes of eastern white cedar (*Thuja occidentalis*) in northwestern Ontario. *Genome* **32(2): 245-250.**

Though many conifers have 12 to 13 pairs of chromosomes, *Thuja* have only 11 pairs. Twelve enzyme systems were studied and results suggested that, with few exceptions, genetic control of enzyme systems in *T. occidentalis* is consistent with many other conifers. Due to similar enzyme characteristics, *Abies* and *Thuja* may have closer common ancestry than previously considered.

Perry, D.J. and P. Knowles. 1990. Evidence of high self-fertilization in natural populations of eastern white cedar (*Thuja occidentalis*). *Canadian Journal of Botany* **68(3): 663-668.**

Open-pollinated northern white-cedar seeds were tested for allozyme polymorphisms to estimate outcrossing rates. The authors determined that outcrossing rates were very low, selfing rates (with embryo survival) were high, and that these relationships may be stand-shape dependent. The authors suggested that thin, linear stands may have lower outcrossing potential. Their outcrossing estimates suggested that there is heterogeneity among both individual trees and populations.

Perry, D.J., P. Knowles, and F.C. Yeh. 1990. Allozyme variation of *Thuja occidentalis* L. in northwestern Ontario. *Biochemical Systematics and Ecology* **18(2): 111-115.**

Samples from six discrete populations of northern white-cedar were examined for gene flow among populations. The authors used electrophoresis and assayed 18 loci encoding 12 enzymes. They observed little heterogeneity among the populations and only one of nine polymorphic loci demonstrated allelic heterogeneity. Testing indicated approximately 1.6% of the total genetic variation was among populations. The number of migrants exchanged among populations per generation was high. The authors suggested that this indicates extensive gene flow among populations.

Pronk, A.A., P. De Willigen, E. Heuvelink, and H. Challa. 2002. Development of fine and coarse roots of *Thuja occidentalis* 'Brambant' in non-irrigated and drip irrigated field plots. *Plant and Soil* **243: 161-171.**

The objective of this study was to quantify cedar root growth patterns as related to several irrigation strategies. The authors suggested that too much water leads to nutrient leaching, while too little could reduce crop growth. Total root mass and fine root mass were not affected by irrigation. No soil moisture differences were found among treatments, but this was attributed to a wet, cloudy summer. The authors concluded that irrigation may not always be an important factor for optimal cedar crop production. Their study results were incorporated into a decision support and modeling tool for field-grown conifers.

Pronk, A.A., M. Heinen, and H. Challa. 2005. Dry mass production and water use of non- and drip-irrigated *Thuja occidentalis* 'Brambant': Field experiments and modeling. *Plant and Soil* **268: 329-347.**

The authors used irrigation to determine cedar dry mass production under several water management regimes. Long periods of water stress caused a decrease in stem dry mass, though leaf area index and leaf dry mass were not affected. The authors noted that northern white-cedar has a higher water use efficiency for dry mass production than many crops (7.6×10^{-3} kg dry mass/kg H_2O transpired); irrigation may not be necessary to increase dry mass production. The authors created a model to simulate dry mass production, but it commonly underestimated leaf area and leaf dry mass while overestimating stem dry mass. Several alternatives to the model were presented, but not tested.

Sucoff, E.I., P.Y.S. Chen, and R.L. Hossfeld. 1965. Permeability of unseasoned xylem of northern white cedar. *Forest Products Journal* **15: 321-324.**

Darcy's Law was tested for its applicability in describing the flow of water through northern white-cedar xylem. As water was forced through the sample at a constant rate of flow (parallel to the grain), the pressure drop across the sample was recorded. Water purity, preparation and storage of samples, and the amount of sample reversal were suggested as variables that affected the permeability of the xylem. Sample reversal (reversing the sample face at which the pressure is applied) raised the permeability of the cedar sapwood. Air drying reduced permeability to 1/10 uniformly over the pressure range, suggesting that air drying reduced the number of microchannels, but not their size. Data suggested that cedar sapwood was homogeneous along the axis parallel to the channels of flow, but not along the axis perpendicular to flow. The authors concluded that measures of permeability have meaning only in the context of the particular experiment. Variations in water purity, channel of flow, and sample preparation strongly influence results.

Tyree, M.T. and M.A. Dixon. 1983. Cavitation events in *Thuja occidentais* L.: Ultrasonic acoustic emissions from the sapwood can be measured. *Plant Physiology* **72: 1094-1099.**

The authors stressed that cavitations are often detrimental to the water economy of plants because cavitated tracheids restrict fluid movement. In many species, ultrasonic acoustic emissions (AE) can be detected in the sapwood; the frequency range tends to be species and season specific, and is useful in understanding dehydration and rehydration events. AE in the frequency range of 0.1-1 mHz were detected in northern white-cedar sapwood, transmitted as vibrations (e.g. oscillations of hydrogen bonds in water, elasticity of tracheid walls, torus aspiration). The balance pressure threshold for AE in cedar was determined to be -0.9 to -1 MPa.

Tyree, M.T., M.E.D. Graham, K.E. Cooper, and L.J. Bazos. 1983. The hydraulic architecture of *Thuja occidentalis*. *Canadian Journal of Botany* **61(8): 2105-2111.**

Leaf specific conductivities (LSC) were measured over a range of stem diameters to determine the influence of branch size on water flow rate. The authors suggested that large diameter stems (>100 mm) have up to 30 times the LSC of small diameter stems (1 mm). Shoot water potentials become increasingly negative during transpiration because 15% of the total water evaporated from green shoots comes from stored water. It has been previously argued that having larger water potential in the main stem and lower in the lateral branches could offset cavitations and reduction in hydraulic conductivity found in upper leaves. The authors presented a static model for hydraulic architecture, but suggested the need to publish a dynamic model as well.

Whalley, B.E. 1950. Increase in girth of the cambium in *Thuja occidentalis* **L.** *Canadian Journal of Research Section C* **28: 331-340.**

Northern white-cedar wood samples were used to test Priestley's (1930) theory of cambial cell adjustment. Cedar was used due to its availability, lack of resin ducts, and short fusiform initials. Both root and shoot samples were studied. The author discovered that fusiform initials frequently disappear from the cambium and that a higher number of pseudotransverse cell divisions occurred than previously considered to maintain and increase cambium. Because of the rapid generation of new fusiform initials and the high rate of disappearance of older initials, the cell pattern in the cambium does not remain fixed. This led the author to conclude that Priestley's hypothesis was not supported in this study.

White, W.C. and J.C. Weiser. 1964. The relation of tissue desiccation, extreme cold, and rapid temperature fluctuations to winter injury of American arborvitae. *American Society for Horticultural Science* **85: 554-563.**

Winter injury is a common problem to the periphery of shoot tips in many clones of arborvitae in the nursery. The clone 'Woodwardi,' which is particularly susceptible, was used to test treatment effects on winter injury. Five treatments tested were: plants dipped in polyvinyl chloride solution, heated root media (to 36°F), bark removal from a small portion of a branchlet, addition of heat lamps to induce desiccation, and an untreated control. Eight trials were employed to determine causes of winter injury. Results suggested that low temperature could cause injury on non-acclimated plants. More importantly, the authors discovered that a rapid temperature decrease from an initial temperature of approximately 32°F resulted in severe damage. Larger temperature swings that were more gradual resulted in no to slight damage.

Regeneration

Caulkins, H.L., Jr. 1967. The ecology and reproduction of northern white-cedar. M.S. Thesis. University of Michigan.

Without many viable competitors, cedar often dominates swamps.

This thesis investigated many aspects of cedar regeneration and general ecology. The author challenged Habeck's (1958) conclusions that distinct ecotypes exist, suggesting that the investigation was not continued long enough to detect true differences. Caulkins argued that cedar is more abundant on lowland sites, but achieves better form and higher growth rates on upland sites. The author suggested that tree-level leaf area is low in swamp sites, yielding small radial growth increments. Investigation of seedling response to light intensity suggested that high light levels inhibit germination, but do not prevent it completely. Partial shade yielded the best germination results. High temperatures and late spring frosts were fatal to seedlings. Seedling survival was often dependant upon the rooting media. Sphagnum and rotten logs are excellent germination sites; however, they tend to dry out quickly. Logs in more advanced stages of decay retain moisture for longer periods of time while offering less resistance to root penetration. The author argued that mature cedar stands often originated under conditions of high moisture. Advance regeneration in studied stands suggested that a species composition shift to competing hardwoods and balsam fir was likely. Stands with no advance reproduction commonly shifted to brush when harvested intensively. Caulkins concluded that cedar regeneration is difficult and perplexing. With high deer browse pressure, wildlife ecologists and foresters are recommended to work together to protect young stands from destruction.

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(3): 389-393.**

A positive correlation was found between the percentage of hummocks in a wetland site and the likelihood of maintaining cedar in future cohorts. The authors determined that stands with less than 70% of the ground area in hummocks are likely to regenerate to hardwoods and brush, whereas successful cedar regeneration occurs on sites with greater than 70% of the area in hummocks. Findings suggested a linear decrease in shrub regeneration and an exponential increase in cedar regeneration as the percentage of hummocks increases on wetland sites.

Cornett, M.W., P.B. Reich, and K.J. Puetmann. 1997. Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. *Ecoscience* **4(3): 353-364.**

Two mixed conifer-hardwood forests were compared to determine relationships between microsite availability and overstory characteristics as they affect regeneration. The authors reported that microtopography differences between coniferous and deciduous stands were relatively minor. They observed that cedar seedling establishment was highly correlated with dead and decaying coarse woody material, which occurred on a small proportion of the forest floor. Because balsam fir seedlings were not well correlated with a specific microtopographic feature and were well distributed throughout the fir-poplar stand type, the authors concluded that balsam fir may be more of a generalist species.

Cornett, M.W., P.B. Reich, K.J. Puettmann, and L.F. Frelich. 2000. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* **(Cupressaceae) regeneration.** *American Journal of Botany* **87(12): 1807-1814.**

Seven seedbed types were subjected to three water treatments (high, medium, low). Decaying wood was found to be an excellent safe site for northern white-cedar regeneration due to adequate temperatures, fungal associations, and moisture. During droughty periods, decaying logs retain enough moisture to keep seedlings from desiccating, however, during extreme drought, no differences were expected between logs and mineral soil. Larger roots were found on log seedbeds as compared to litter seedbeds. Root mass, root:shoot ratio, and root length were lower for seedlings growing on cedar litter than other seedbed types. Water abundance was the most important factor in determining safe seed beds for cedar.

Cornett, M.W., K.J. Puettmann, L.E. Frelich, P.B. Reich. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* **forests in northeastern Minnesota.** *Restoration Ecology* **9(4): 386-396.**

Some late-successional conifer species may require specialized safe sites for germination and establishment (e.g. decaying wood) in combination with specific overstory conditions that affect seed supply, light quality and quantity, and moisture availability. The authors compared natural and manipulated seedbeds in late-successional cedar and early-successional birch stands. Conifer logs were colonized twice as frequently as hardwood logs, four times more often than forest floor mounds, and twenty times more often than forest floor pits. Though cedar seedlings had increased height growth rates on manipulated seedbeds in birch stands, they suffered high mortality rates due to moisture stress. The authors attributed high mortality rates of cedar under cedar canopies to dense overstory conditions, causing light to be a limiting factor.

Curtis, J.D. and G.P. Steinbauer. 1947. Effects of variations in moisture and depth of planting on germination of seeds of northern white cedar. *Journal of Forestry* **45(8): 592-593.**

Cedar germination was observed in seven moisture treatments over four planting depths. Cedar germination occurred on a wide range of moisture conditions, though maximum germination occurred at 40 to 80% of water holding capacity. Germination was negatively correlated to sowing depth; from 63% at the surface to 24% at 0.5 inch depth. Germination was negatively correlated with the relative humidity in which seeds were stored for eight months. No germination was observed in seeds that were stored above 25% relative humidity.

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, U.S. Department of Agriculture, Forest Service, North Central Experiment Station. 9 p.

Cedar-dominated deeryards are critical wintering habitat for white-tailed deer, and the perpetuation of these is of utmost importance in the Lake States. The authors considered site preparation (burning, full tree skidding, slash retained in-woods) and browse treatments (fencing to remove competition of rodent, hare and/or deer) for stand regeneration. Regeneration was highest on leaf litter seedbeds, followed by sphagnum moss and burn-type bryophytes. Among the site preparation treatments, the burn treatment had the highest seedling regeneration. Ten years post-harvesting, no cedar seedlings were observed in unfenced plots. The authors found that heavy shade is detrimental to cedar regeneration, which requires significant overstory disturbance. Because cedar is slow growing and preferentially browsed, it is heavily impacted by deer for long periods of time and frequently out-competed by balsam fir in mixed-species stands.

Harlow, W.M. 1928. Reproduction of Adirondack white cedar by natural cuttings. *Journal of Forestry* **26: 244.**

In the western Adirondacks of New York, cedar stands are commonly associated with sphagnum muck soils. These cedar stands are multi-aged, but it is difficult to discern regeneration dynamics because regeneration is rarely present. The author found examples of seedlings without juvenile leaves that likely arose from "natural cuttings." The observed seedlings had callous tissue over the base of the stem, suggesting a mechanism of vegetative reproduction not previously reported for this species.

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: 1953-1961.**

The authors suggested that poor regeneration and recruitment of northern white-cedar under recent (in 1997) management regimes have created a need to understand historical stand development and dynamics associated with cedar stands. Stem analysis suggested that the study stands originated around the turn of 1900s after stand-level disturbances, including exploitative harvesting. Poor recruitment after recent disturbances was attributed primarily to a large increase in the deer population in the study sites, exacerbated by cedar's poor growth efficiency. The authors recommended that silvicultural treatments focus on stand regeneration and recruitment in order to sustain the cedar resource.

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

Many cedar stands in the Lake States regenerated during the early 1900s following clearcutting. At that time, deer populations were low and advance cedar regeneration was abundant. The authors attributed recent cedar regeneration failures in strip clearcuts to deer browse and logging slash interference, confirming that abundant seedlings do not necessarily translate to adequate sapling recruitment. The authors suggested that prolonging the establishment period up to several decades before removing the overstory may facilitate recruitment of cedar saplings.

Holcombe, J.W. 1976. The bryophyte flora of *Thuja* seedbed logs in a northern white-cedar swamp. *The Michigan Botanist* **15: 173-181.**

Decaying logs frequently act as nurse logs for tree species with small seeds that have difficulty becoming established in thick organic layers. The author suggested that bryophyte species on moderately decayed stumps can act as a seed trap and keep seeds moist until germination. Seventy-three percent of cedar seedlings found in this study were on logs; bryophytes were present on all of these. Because no seedlings were found on logs without mosses, the authors concluded that the role of mat-forming bryophytes in cedar regeneration may be more significant that previously considered.

Lanasa, M. and Zuidema, M. 1991. Site preparation for northern white cedar. CEDAR Action Group Note No. 2. 6 p.

This paper discusses four methods of site preparation. Prescribed burning is recommended if advance regeneration is not prevalent or if nutrients are needed in the soils; this is discouraged if advance regeneration is prolific. A detailed "how to" list is provided for burning in cedar stands. Mechanical scarification and mounding are suggested as alternatives for altering microsites for natural regeneration. Lastly, herbicides (imazaphr and glyphosate) are suggested with the caveat that many cedar stands have very shallow water tables that may be impacted by herbicides.

Larouche, C., J-C. Ruel, J-M. Lussier, and L.S. Kenefic. 2006. Regeneration of *Thuja occidentalis* L. in mixedwood stands on mesic sites after partial cuts in Quebec. In: Proceedings of the Eastern Canada – USA Forest Science Conference. 19-21 Oct. 2006, Quebec, QC: 90-94.

Browsing, seedbed type, and three regeneration method treatments in three uneven-aged mixed-species stands in Quebec were studied for cedar regeneration responses. Harvesting >50% of the overstory basal area resulted in poor seedling establishment and survival due to desiccation. Height growth of established saplings increased proportional to light intensity. Natural seed rain was found to be inadequate for seedling stocking, but the authors suggested it can be supplemented by artificial seeding. Deer, hare, and moose browsing were found to be detrimental to cedar regeneration under certain population conditions.

Nelson, T.C. 1951. A reproduction study of northern white cedar including results of investigations under federal aid in wildlife restoration project Michigan 49-R. Department of Conservation Game Division. Lansing, Michigan. 100 p.

This study emphasized regeneration and general ecology attributes of northern white-cedar. Cedar germinants develop a tap root during the first years of growth, which is soon replaced by a fibrous root system in poor drainage conditions. Germination was not affected by partial light or shading, but was inhibited by full sunlight. Soil pH did not influence germination between 4.0 and 8.0, however, pH below 4.0 inhibited germination. Soil pH below 6.0 negatively affected the number of seedlings per milacre. This species was reported to be the only northern conifer to have no mycorrhizal association. Aside from deer and hare browse, desiccation was observed to be the most common cause of seedling mortality regardless of rooting medium. Of the vegetative reproduction observed, over 80% was through layering. Data indicated that light, pH, and germinating media are rarely critical factors in establishing vegetative reproduction; adequate moisture is most important. Cedar height and diameter growth were reported to be slow, with trees reaching 300 years common on the Upper Peninsula of Michigan. In reference to silvicultural practices and regeneration, the author noted that heavier cuttings tended to favor balsam fir and alder reproduction. Silvicultural practices favoring the buildup of advance vegetative regeneration were recommended.

Laura Kenefic looks through a thin bole cross-section to determine the sapwood area.

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: 119-130.**

Seventy-seven lowland stands throughout northern Wisconsin and the Upper Peninsula of Michigan were investigated for factors limiting northern white-cedar regeneration. The authors suggested that factors resulting in poor cedar regeneration include desiccation of seedlings, late frosts, varying seed production and herbivory. Though seedling establishment was common in many stands, little recruitment into the sapling class was observed. This was attributed primarily to the inability of seedlings to achieve heights above deer browse lines due to slow growth and palatability. The authors suggested that white-tailed deer at high levels will continue to inhibit cedar regeneration and recruitment.

Scott, M.L. and P.G. Murphy. 1987. Regeneration patterns of northern white-cedar, an old-growth forest dominant. *American Midland Naturalist* **117: 10-16.**

This study analyzed seedling establishment and survival, age–size relationships and stem establishment patterns in a 10.9-ha old-growth, mixed-species stand that originated on sand dunes in Michigan. The authors concluded that the successional niche and shade tolerance of cedar are difficult to categorize. They suggested that cedar on dunes exhibits characteristics of an early successional species, but has high shade-tolerance and requires disturbance to replace itself. The authors found a lack of cedar sapling recruitment and predicted a transition to a hardwood-dominated community in their study area.

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: 672-681.**

This paper provided a methodology for testing microsite dependence of conifer regeneration. The authors determined that white spruce and northern white-cedar seedlings are more likely than balsam fir to survive on nurse logs as compared to bare mineral soil. They suggested that increasing the number of decaying logs on the ground could increase the proportion of cedar in the stand. Cedar regeneration was higher in experimental plots under an aspen overstory than under a cedar overstory, though cedar seedlings are rarely present under aspen stands under natural conditions.

The authors concluded that cedar seems to be shade-tolerant but understory intolerant due to its competitive disadvantages against larger-seeded balsam fir.

Verme, L.J. and W.F. Johnston. 1986. Regeneration of northern white-cedar deeryards in northern Michigan: their ecology and management. *Journal of Wildlife Management* **50: 307-313.**

Stands harboring high deer populations frequently suffer a lack of recruitment into the sapling sizes due to extensive seedling herbivory. Several post-clearcutting site preparation treatments of slash removal (broadcast burning, full-tree skidding, and no slash removal) were tested to compare regeneration and recruitment in stands with a clearly defined browse line. Post-overstory removal burning may improve long-term regeneration prospects as compared to other treatments; however more time was needed to adequately quantify this. In stands with abundant advance regeneration, burning may reduce sapling recruitment. The authors stressed that deeryards must be managed to perpetuate adequate winter habitat for white-tailed deer.

Silviculture

Botti, W. 1990. Condition of the northern white cedar resource. Proceedings of the Northern White Cedar in Michigan Workshop. D.O. Lantagne, Ed. Michigan State University Agricultural Experimental Station Research Report 512: 50-53.

The author provided an overview of changes in the cedar resource in Michigan from the mid 1960s through the 1980s. A drop of only 14,000 acres (1%) of the cedar type was noted from 1965 to 1985, however trends in size classes were of concern. Acres in cedar sawtimber remained relatively constant, an increase in pole stands of over 100,000 acres was observed and a decrease of nearly 100,000 acres of seedling and sapling stands occurred over this time span. Frequent windthrow, inadequate regeneration, high deer populations, poor stem quality and poor sites were among the problems mentioned. The author encouraged collaboration of foresters and wildlife managers to focus regeneration efforts in areas with low deer populations.

Foltz, B.W. and W.F. Johnston. 1968. Gross basal area growth of northern white-cedar is independent of stand density over a wide range. Research Note NC-61. U.S. Department of Agriculture, Forest Service, North Central Experiment Station. 4 p.

Four replicates of 0.5-acre plots in an 85-year-old cedar stand were each thinned twice to 90, 110, 130, and 150 square feet of basal area per acre (20 plots total, including four unthinned controls). Analysis conducted within 10 years after the second thinning revealed that gross growth was independent of stand density, which ranged from 90 to 225 square feet per acre. For all species combined, ingrowth was independent of stand density. However, cedar ingrowth increased and balsam fir ingrowth decreased with increasing density. The authors concluded that stands could be thinned repeatedly to 90 square feet per acre without sacrificing gross growth, in order to focus growth on fewer residuals.

Gevorkiantz, S.R. and W.A. Duerr. 1939. Volume and yield of northern white cedar in the Lake States: a progress report. U.S. Department of Agriculture, Forest Service, Lake States Forest Experiment Station. 55 p.

Volume and yield tables for northern white-cedar are presented based on 227 widely distributed sample trees throughout the Lake States. The authors cautioned that the presented tables do not adequately address yield responses to soil conditions, mixed-species stands, or uneven-aged cedar stands. Presented volume tables include stem taper, total cubic-foot, merchantable cubic-foot, and board-foot to varying top diameters. Presented yield tables include site index, total basal area, cubic- and board-foot volume yields, and growth percent by density of stocking.

Hannah, P.R. 2004. Stand structures and height growth patterns in northern white cedar stands on wet sites in Vermont. *Northern Journal of Applied Forestry* **21(4): 173-179.**

Sixteen stands, 45 to 125 years in age, were measured to determine height growth curves for northern white-cedar on wet sites. Site index ranged from 25 to 50+ feet at 50 years, with the slowest height growth occurring on the wettest sites. Data from this study suggested that cedar is relatively slow-growing, attaining maximum heights of 75 to 80 feet at 125 years. Volume increment data suggested that on good sites, 15 cubic feet in 75 years could be expected per tree, while trees on poor sites may have only three cubic feet. Volume increment curves by site class are provided. Structurally, natural disturbances are converting the stands from even-aged with a uniform canopy to two-aged or multi-cohort stands. The author predicted that cedar might be replaced by more competitive species on the better sites. Shelterwood and group selection harvests are recommended for sustainable management of cedar.

Hofmeyer, P.V., L.S. Kenefic, R.S. Seymour, and J.C. Brissette. 2006. Growth comparison of northern white-cedar to balsam fir and red spruce by site class. In: Proceedings of the Eastern Canada – USA Forest Science Conference. 19-21 Oct. 2006, Quebec, QC: 62-66.

Sixty sites throughout northern Maine were used to compare basal area growth of cedar to red spruce and balsam fir. Decay was present in all species; however, significant difference occurred by species (fir – 34%, spruce – 11%, cedar 80%) and by soil drainage class (drier site classes had higher decay incidence in fir and cedar). No detectable differences in cedar basal area growth by soil drainage or canopy position were observed. Cedar in Maine seem to be much older than previously considered; many sample trees had >150 readable rings at breast height, though total age was not possible to determine due to high incidence of central decay.

Johnston, W.F. 1972. Balsam fir dominant species under rethinned northern white-cedar. Research Note Number NC-133. U.S. Department of Agriculture, Forest Service, North Central Experiment Station. 4p.

The 20-year thinning study reported by Foltz and Johnston (1968) was used in this study to make observations on understory competition and cedar regeneration. The author suggested that cedar stands with fir in the overstory and high deer populations will likely shift to a higher percentage of balsam fir in future cohorts. To keep a higher proportion of cedar in the future, he recommended repeated thinnings to 90 to 150 ft^2 per acre that remove overstory fir.

Johnston, W.F. 1976. Growing better cedar forests. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 7-11.

Johnston reported that silvicultural practices used in the early 1970s to manage cedar were yielding unpredictable and unacceptable results. The author stressed the need to fully understand cedar ecology before manipulating stands and suggested that treatments should focus on the better sites where the trees are more likely to respond. As an example, Foltz and Johnston (1968) was used to illustrate potential stand density management options for managing timber yields and deer yards.

Johnston, W.F. 1977. Manager's handbook for northern white cedar in the North Central States. General Technical Report NC-35. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 18 p.

Managers in the region will need to consider both timber management and wildlife concerns concurrently in many lowland cedar stands. A dichotomous key is presented for management recommendations that include intermediate treatments, regeneration strategies, and site preparation based on current stand conditions. The author discouraged intensive management in stands with a site index less than 25 at 50 years of age. Management recommendations focus primarily on establishing new stands; strip clearcutting and strip shelterwood methods are suggested. Deeryard management recommendations are also given. Providing ample cover and browse opportunities in a sustainable fashion are given high priority. Selected site index and yield tables from Gevorkiantz and Duerr (1939) are included for management guidelines.

Miller, R.O., D. Elsing, M. Lanasa, and M. Zuidema. 1990. Northern white-cedar: stand assessment and management options. Proceedings of the Northern White Cedar in Michigan Workshop. D.O. Lantagne, Ed. Michigan State University Agricultural Experimental Station Research Report 512: 47-56.

The authors report that unpredictable and commonly unacceptable management for cedar led the state and federal forests of Michigan to enact a partial moratorium on cedar harvesting until regeneration techniques were refined. Stand type conversions were common in cedar stands with two probable causes noted: silvicultural (in terms of seedling establishment and recruitment) and wildlife (white-tailed deer browsing). The authors outlined a detailed stand assessment tool that addresses social concerns, financial analyses and species requirements with some management options. The focus of this outline is on stand regeneration and recruitment.

Roe, E.I. 1947. Thinning in cedar swamps. USDA Forest Service Lake States Forest Experiment Station Technical Note Number 279. 1 p.

Thinning trials were established in 1935 in a 45-year-old cedar stand. Thinning removed more than half of the original basal area, which had nearly grown to the control plot density within 12 years. Quality and tree vigor improved through thinning in comparison to the control plot. Merchantable stems (5 to 8 inches) increased on the thinned plot to 320 stems/acre as compared to the control (80 stems/acre), suggesting that a second thinning might be possible sooner in the previously thinned plot. The author suggested that thinnings should be focused on better drained swamps, as stands on poor sites with stagnant water showed little response to thinning.

Thornton, P.L. 1957. Problems of managing Upper Michigan's coniferous swamps. *Journal of Forestry* **55: 192-197.**

Cedar-dominated, mixed-species forests in Michigan tend to occur on poorly-drained, peat and muck soils with moving water and a non-acidic pH. These stands are frequently clearcut, diameter-limit cut, or otherwise selectively harvested. The author argued that no single treatment is considered most effective due to the complexities of lowland sites. The most common problems with management revolved around regeneration and recruitment into the sapling class, though older stands were experiencing disease and windthrow. Though regeneration on swamp sites was occurring, a significant type shift was expected due to the dearth of cedar regeneration.

Thornton, P.L. 1957. Effects of cutting methods on advance reproduction in two mature mixed coniferous swamps in Upper Michigan. *Journal of Forestry* **55: 448-451.**

The author provided evidence that there would likely be a shift in species composition from conifer-dominated stands to hardwood-dominated stands due to the lack of concern for regeneration in common logging practices. Five cutting methods were compared: light selection, shelterwood, diameter limit, clearcut strips, and clearcut blocks. Though advance regeneration of all species was uniformly decreased due to harvesting, the author speculated that balsam fir and hardwood regeneration may outcompete cedar regeneration and alter future stand composition.

Verme, L.J. 1965. Swamp conifer deeryards in northern Michigan: their ecology and management. *Journal of Forestry* **63: 523-529.**

Historically, cedar swamps were multi-storied stands that had plentiful browse opportunities for deer, but sparse winter cover. Partial cutting, group selection and diameter-limit cutting were discouraged for deeryard management due to low browse potential under these systems. Patchy stands can provide some cover and browse, however the author suggested creating forests of many even-aged stands in differing stages of development. This cutting strategy would likely increase carrying capacity, which may be detrimental to future regeneration. The author argued that intensive silvicultural treatments should be restricted to the better site classes.

Wildlife Habitat

Aldous, S.E. 1941. Deer management suggestions for northern white cedar types. *Journal of Wildlife Management* **5(1): 90-94.**

Northern white-cedar is noted to be the most important winter browse for white-tailed deer in the Lake States. Many cedar stands associated with high deer populations have browse lines at a height that makes browse no longer available. Data suggested that cedar seedlings will not maintain their output of browse if >25% of their foliage is removed annually. The author reported that 4.5 pounds of cedar browse per day is needed to sustain healthy deer. Thinning stands during winter is suggested to make browse available in deeryards, targeting those of poor form or canopy position for removal. Clearcuts ranging from one-eighth to one-quarter acre in size, spaced one-fourth to one-half acre apart are also recommended for some sites.

Avitabile, A. 1982. The eastern white cedar, ***Thuja occidentalis*** **L., an early pollen source for honeybees, Apis mellifera L.** *American Bee Journal* **122(4): 261-262.**

Since the introduction of the honeybee to North America nearly 400 years ago, new plants pollinated by honeybees have continually been discovered. The author reported that northern white-cedar was observed to be a pollen source for honeybees, which serve as a vector for sexual reproduction. The author suggested that cedar might be an important pollen source for honeybees in certain environmental conditions due to its importance as a horticulture species.

Bazinet, N.L. and M.K. Sears. 1979. Factors affecting the mortality of leafminers ***Argyresthia thuiella*** **and** ***Pulicalvaria thujaella*** **(*Lepidoptera*: *Yponomeutidae* and *Gelechiidae*) on eastern white cedar in Ontario. Canadian Entomology 111(11): 1299-1306.**

There are four species of leafminers that feed on northern white-cedar in Canada. A description of their life stages is presented; juvenile larvae are the defoliation concern rather than the adult moths. Leafminer population crashes are attributed to severe winters with cold temperatures. The authors noted that leafminers have historically not reached epidemic status.

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: 359-369.**

Perpetuation of a tree species is dependent upon recruitment of seedlings into larger size classes. Effects of deer browsing were investigated using exclosures in seven cedar stands in northern Minnesota. Though northern white-cedar has adequate seed production on the sites studied, herbivory is severe enough to prohibit recruitment into the sapling class (due to inhibited height growth). Poor seedling survival rates were associated with low light availability and high browse pressure. Within three years, >75% of the cedar seedlings outside of exclosures were browsed. Simulations suggest that under current browsing intensities, there will likely be shifts in stand species composition from northern white-cedar to hardwoods. The authors concluded that resource managers must focus attention on sapling recruitment if cedar is going to be sustained on these sites.

King, D.R. 1975. Estimation of yew and cedar availability and utilization. *Journal of Wildlife Management* **39(1): 101-107.**

There is a need for practical quantitative methods to estimate browse availability and utilization by herbivores. The author developed regression equations for northern white-cedar and yew (*Taxus canadensis*) using growth habit variables of the two species. High correlation coefficients were found in branch weight–diameter regressions for both cedar and yew. No significant differences in regression equations could be attributed to canopy position, tree size, position of branches on the tree, or site in northern white-cedar. Resource managers can estimate browse availability by measuring branch diameters in the field to a given browsing height. The author suggested that these methods are likely applicable for other conifers as well.

Miller, R.O. 1990. Ecology and management of northern white-cedar. Proceedings of the Regenerating Conifer Cover in Deer Yards Workshop. North Bay, Ontario. 13 p.

General species silvics were discussed, primarily in terms of the importance of cedar-dominated stands to birds, mammals, reptiles and amphibians. The author presented estimations of Michigan's deer carrying capacity and addressed the necessity of managing deer yards. Arguments were presented that there was increasing pressure on the cedar resource due to increasing stumpage, increasing deer herd size, and a paucity of silviculture. The author2w proposed an improved stand assessment and silvicultural methods outline for use by practicing foresters in order to implement sustainable management in these stands (see Miller et al. 1990).

Miller, R.O. 1990. Guidelines for establishing animal exclosures for research in cedar stands. CEDAR Action Group Note No. 1. 7 p.

The author stated that animal exclosures are often improperly used in quantitative studies. A series of guidelines for designing proper exclosures were presented, addressing number needed, size, building materials and costs. This paper described hare and deer exclosures for cedar stands, however, it has applicability in other ecological studies as well.

Sabine, D.L., W.B. Ballard, G. Forbes, J. Bowman, and H. Witlaw. 2001. Use of mixedwood stands by wintering white-tailed deer in southern New Brunswick. *Forestry Chronicle* **77(1): 97-103.**

Deer frequently congregate in deeryards when there is greater than 30 cm of snow, in order to benefit from reduced snow cover and wind, communal trails, more stable, warmer temperatures, and predator avoidance. The authors reported that deer preferred mixedwood stands with a high proportion of softwood cover, rather than pure coniferous stands, during winter months. They suggested that this might be due to the cover provided by the conifers and the browse provided by the hardwoods. They cautioned about managing entirely for even-aged, pure coniferous deer-yards.

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): 791-797.**

Fourteen pregnant white-tailed deer (two to five years old) were used to test differences in the quality of cedar and aspen browse. Intake of cedar browse was significantly higher than aspen browse over the course of the study. The digestibility of aspen appeared to decease throughout the study, while cedar digestibility increased as the study progressed. Deer feeding on aspen experienced a 21% reduction in weight while deer feeding on cedar had a 16% weight reduction by the end of the study. The authors reported that during harsh winters, weight loss is common even with the best of food options; however, death was imminent for deer on an aspen-only diet.

Ullrey, D.E., W.G. Youatt, H.E. Johnson, L.D. Fay, and B.E. Brent. 1967. Digestibility of cedar and jack pine browse for the white-tailed deer. *Journal of Wildlife Management* **31(3): 448-454.**

Thirty-six pregnant white-tailed deer (2.5 to 3.5 years old) were used to test differences in the quality of cedar and jack pine browse. Nutrient analysis showed that jack pine browse contained the same amounts of crude protein, fiber, ether extract, nitrogen-free extract, and calories as cedar browse. Intake of cedar browse was significantly higher than jack pine browse over the course of the study (approximately six times higher). Weight loss was significantly greater in all groups of deer fed jack pine than those fed cedar. Because of the nutrient analysis, it appeared that jack pine is a better browse than aspen, though both are inferior to cedar.

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(1): 162-171.**

Forty-eight pregnant white-tailed deer (1.5 to 7.5 years old) were used to test differences in the quality of cedar and balsam fir browse. There were no significant nutrient differences between cedar and balsam fir. Browse consumption of balsam fir was significantly lower than cedar (approximately eight times lower). Digestibility of dry matter, crude protein and nitrogen-free extract were lower in balsam fir browse than cedar. Deer fed balsam fir experienced severe weight losses during the study. During this trial, two deer fed balsam fir died; one was replaced. The authors concluded that balsam fir browse plays little role in sustaining deer during winters in Michigan.

Van Deelen, T.R. 1999. Deer-cedar interactions during a period of mild winters: Implications for conservation of conifer swamp deeryards in the Great Lakes Region. *Natural Areas Journal* **19: 263-274.**

Cedar swamps are noted as the preferred winter habitat for white-tailed deer in the Lake States because they provide both shelter and browse. They stated that conventional stand-level management is inadequate in perpetuating deeryard stands and examined assumptions implicit to management of two northern Michigan deeryards. Approximately half of the 95 deer that were radio collared and monitored for three years had overlapping winter and summer ranges, though most deer used deeryard sites more heavily during winter months. Deer were observed to remain in deeryards until the beginning of April, increasing the cedar browse damage during periods of snowmelt before herbaceous plants emerge. Cedar seedlings are reported to require 12 to 40 years to grow beyond browsing height of white-tailed deer. The author suggested reducing the number of deer in philopatric herds to reduce regeneration stress at the stand level while adapting a more natural silvicultural regime (gap dynamics rather than clearcutting).

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): 181-194.**

Current overstory and understory composition was compared to presettlement conditions using surveyors' witness tree records and notes in two cedar-dominated deeryards. The Stonington deeryard had a decrease in cedar dominance through time (41 to 21%) while in Whitefish cedar remained stable (37%). The diameter distribution did not differ among the deeryards, however, the mean age of cedar in Stonington was 87 years, while it was 100 in Whitefish. Future species composition shifts were expected by the author due to preferential browsing by white-tailed deer and poor recruitment of cedar and hemlock.

Verme, L.J. 1961. Production of white-cedar browse by logging. *Journal of Forestry* **59(8): 589-591.**

Four cutting intensities (6-, 8-, and 10- inch diameter limit, and clearcutting) were studied for quantities of white-tailed deer browse made available by harvesting in a northern Michigan cedar deeryard. Foliage from felled cedar was collected and fed to penned deer at a nearby wildlife experiment station. The greatest browse production was in the clearcutting treatment (5,340 pounds per acre) while the 10-inch diameter limit cutting yielded 2,530 pounds per acre. Using an average consumption of five pounds of foliage per deer per day and 90 days per yarding season, carrying capacity ranged from 10.7 deer per acre in the clearcutting treatment to 5.1 deer per acre in the 10-inch diameter limit treatment.

Wood Properties and Products

Bannan, M.W. 1941. Wood structure of *Thuja occidentalis*. *Botanical Gazette* **103: 295-309.**

The author described the properties of 230 wood samples taken from cedar trees growing on a wide range of site conditions. Root samples were included. Rooting habit varied in response to drainage; shallow, spreading roots occurred in wet conditions while vertical roots extending deeply into the ground were found in well-drained conditions. Several wood properties described varied considerably from tree to tree, often without definite trends. However, some important trends were noted, namely that tracheids increased in size from the pith outward in stems but not in roots; rays decreased in number outward from the pith in stems but were constant in roots; and ray height increased outward from the pith in stems but not in roots. The author cautioned that because of this high variability in wood properties, one must carefully choose identification features to distinguish *T. occidentalis* from other members of the *Thuja* genus.

Behr, E.A. 1974. Distinguishing heartwood in northern white cedar. *Wood Science* **6(4): 394-395.**

There are difficulties in distinguishing heartwood from sapwood in northern white-cedar, unlike western red-cedar (*Thuja plicata*). The author suggested that the sapwood-heartwood boundary can be observed with a solution of ammonium oxalate that reacts with tropolones in the cedar heartwood. Sapwood was observed to cut across several growth rings at times. Occasionally internal sapwood can be found within the heartwood, though this phenomenon was reportedly rare.

Behr, E.A. 1976. Special physical and chemical properties of northern white cedar. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 11-15.

Northern white-cedar has several unique physical wood properties; it is easy to glue, has favorably small shrinkage, holds paint well, is light weight, weak in compression and bending and has relatively poor nail-holding abilities. It is similar in chemical composition to other softwoods, though its extractives (thujaplicans) make it unique. Because of the high amounts of extractives in heartwood, ferric ammonium oxalate can be used to determine the heartwood-sapwood interface.

Behr, E.A. 1976. Resistance of cedar to stain, insects, and decay. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 16-19.

Cedar is one of the most decay- and termite-resistant softwoods in North America, though treated pine can be more durable (decay resistant) where in contact with soil. Cedar has no major stain problems and relatively few insect pests. The author suggested that there is a critical need for more research on this topic.

Cech, M.Y. 1976. Kiln-drying eastern white cedar. *Canadian Forest Industries* **96(1): 27-31.**

Though northern white-cedar is not as desirable as western red-cedar for many wood products, it is commonly used as fence posts, shingles and siding because of its natural durability and cheaper cost. Because of its variable within-stem moisture content, kiln drying is often problematic. The author suggested using high temperature drying schedules to reduce kiln-drying times up to 40% as compared to conventional kiln drying times. Though kiln-drying technology has improved greatly since the mid-1970s, this paper is valuable in that it demonstrates high moisture content.

Dyer, R.F. 1967. Fresh and dry weight, nutrient elements, and pulping characteristics of northern white cedar. University of Maine Technical Bulletin T-27. 40 p.

Twenty-one trees >5.6 inches dbh and 36 seedlings/saplings between 1.0 and 35.0 feet tall from central Maine were used for this study. Equations were presented to predict whole tree, stem and branch, total stem, merchantable stem, branch, and large and small root fresh and dry weights using total tree height and diameter. Values for 12 nutrient elements (Al, B, Ca, Cu, Fe, K, Mg, Mn, Mo, N, P, and Zn) were provided for the tree components listed above. Ca, N, K, and Mg were found in higher proportions than the other elements in mature tree samples. Leaves had the highest proportion of all nutrients except Al and Cu in the seedling samples, with those nutrients being found at high levels in the roots. Though cedar is not commonly used as a pulp species, the author presented a series of figures for Canadian Standard Freeness, bulk curves, tear factors, burst factors, tensile strength, and stretch.

Sound cedar logs can be hard to find.

Haataja, B.A. and P.E. Laks. 1995. Properties of flakeboard made from northern white-cedar. *Forest Products Journal* **45(1): 68-70.**

The authors suggested that northern white-cedar is under-utilized for wood products. Reconstituted and composite forest products may be a valid use of this species due to its poor form and pest resistance. The strength, water absorption, expansion, stiffness, and pest resistance of northern white-cedar flakeboard are compared to those of aspen (*Populus tremuloides*). Due to its termite and fungal resistance, the authors suggested that cedar flakeboard could be used in exterior applications.

Hale, R.A. 1977. The relative durability of northern white-cedar when used for fence posts – A progress report. University of Maine, Forest Products Laboratory, Technical Note Number 66, Wood Products Note Number 2. 2 p.

This study was installed in 1945 to test the durability of five hardwood species and six softwood species historically used as fence posts in Maine. Ten posts from each species (6 feet long and 4 inches in diameter) were buried 18 inches into the soil. At the end of twenty years, all species except northern white-cedar failed a 50 pound side pull stress test. By 1971, three cedar posts failed the stress test. In 1976, all remaining seven posts passed the stress test, though upon removal the posts were decayed. After 30 years of use, the fence posts were considered weak, though usable for fence wire attachment.

Harkom, J.F., M.J. Colleary, and H.P. Sedziak. 1946. Results of the examination of seven ground-line treatments and one butt treatment on eastern white cedar poles after four years' service. Proceedings of the Forty-Fourth Annual Meeting of the American Wood Preservers' Association 44: 158-171.

Eight preserving treatments were applied to seven-foot cut cedar stubs from old and new poles and were examined after six years of service. A total of 231 stubs were examined; 88 treated old stubs, 19 old untreated control stubs, 88 treated new stubs, 36 new untreated control stubs. The eight treatments used include: sand creosote collar with borax, peat creosote collar, creosote copper-foil collar, osmo-creo paste and bandage, sodium fluoride and creosote earth, sodium fluoride creosote collar, cuprinol ground-line treatment, and cuprinol butt treatment. Results indicated that all treatments were effective against decay, with the exception of the cuprinol ground-line treatment. The treatments combining creosote and salt penetration showed the least decay after six years. The authors suggested that more attention was needed to creosote penetration in relation to treated stub diameter.

Hoover, W. 1990. The importance of cedar in Michigan's forest history. Proceedings of the Northern White Cedar in Michigan Workshop. D.O. Lantagne, Ed. Michigan State University Agricultural Experimental Station Research Report 512: 3-6.

This paper provided a historical review of the usage of northern white-cedar and other species throughout Michigan history. Much of the industry once revolved around railroad ties, telephone poles and mine timbers. Stories from logging camps about wages, working conditions and work days were used to relate the historical importance of cedar.

Huber, H.A. 1976. Kiln drying northern white cedar. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 25-28.

Northern white-cedar has excellent dimensional stability because its physical properties allow for fast drying without many negative effects. Though kiln drying is not required for most outdoor applications of cedar, it is beneficial for many interior uses. Several advantages of kiln-dried cedar are outlined as well as three commonly used kiln schedules from three different companies.

Huber, H.A. 1976. Machining of cedar. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 28-29.

Machining was defined as cutting of wood by sawing, planing or molding wood parts. Cedar is an exceptionally easy species to machine due to its straight grain, low density and small knots. Feed rolls may leave indentations on finished surfaces and may slip during processing due to cedar's low density. Optimal cutting angle is 5-10 degrees (low compared to many other species), while grinding and sharpening angle should be approximately 30 degrees (similar to many other species).

Kamdem, P.D., J.H. Hart, and E. Behr. 1998. Field performance of CCA type C non-pressure-treated northern white cedar (*Thuja occidentalis* L.) sapwood. *Forest Products Journal* **48(2): 49-51.**

Northern white-cedar is commonly used in outdoor applications due to its natural decay resistance, which increases from the pith outward to the sapwood boundary. Preservatives could be used to further enhance fungal resistance and durability. Seasoned, heated logs

Spiral grain is a common feature of the typically poorly formed cedar.

with non-pressure treated CCA had less than 10% of the log cross-section affected by fungi after 18 years. Knowledge of moisture content variability in this species prior to treatment was stressed by the authors to obtain the best results.

Leinfelder, R. 1976. Preservative treatment of cedar. Proceedings of the National Northern White Cedar Conference. Michigan State University Publication No. 3-76: 20-24.

Northern white-cedar has a high natural resistance to decay and insects that could be augmented with preservatives for many outdoor uses. Cedar's unique vascular system makes preservative treatments difficult due to the lack of resin canals in the ray structures. A list of preservatives and application techniques were presented with suitable uses of each. The author suggested that thermal and pressure treatments are the best for cedar ground line poles.

McDermott, M.D. 1981. An evaluation of selected physical and mechanical properties of northern white-cedar in Maine. Master of Science Thesis. University of Maine. Orono, Maine.

Northern white-cedar wood property values from forty trees sampled throughout Maine were compared to published values from Wisconsin to establish regional differences. Specific gravity, tension perpendicular to the grain and hardness did not differ regionally. Sheer parallel to the grain and end hardness were greater in Maine than in Wisconsin. Maximum crushing strength, compression parallel to the grain, fiber stress and cleavage values were lower in Maine than the published Wisconsin values. Wood property values were also compared among wet and dry sites in Maine. Dry sites had higher compression values; however, wet sites had slightly higher mean values in most other mechanical tests. Specific gravity and growth rates did not differ among drainage types. Rate of growth had low correlation with the strength properties measured. Strength properties had higher correlations with specific gravity.

Roy, D.N., S.K. Konar, and J.R. Purdy. 1984. Sublimation of occidentalol, a sesquiterpene alcohol, from eastern white cedar (*Thuja occidentalis*) in a drying kiln. *Canadian Journal of Forest Research* **14(3): 401-403.**

Occidentalol, a sesquiterpine alcohol, was found to condense on the cooling coils in a recirculating kiln during the drying process. This substance was thought to be released when drying freshly cut heartwood and raised concern about reduced fungal resistance, though none became apparent. Buildup of this material can be cleaned with an alcohol application. Depending upon the type of kilns used, this may be an important consideration for the forest products industry.

Literature Cited

McWilliams, W.H.; Butler, B.J., Caldwell, L.E., Griffith, D.M., Hoppus, M.L., Laustsen, K.M., Lister, A.J., Lister, T.W., Metzler, J.W., Morin, R.S., Sader, S.A., Stewart, L.B., Steinman, J.R., Westfall, J.A., Williams, D.A., Whitman, A., Woodall, C.W. 2005. The forest of Maine: 2003. USDA For. Serv. Resour. Bull. NE-164. 188 p.

This Research Report was designed and edited by Spencer R. Meyer, CFRU Research and Communications Coordinator. The CFRU publishes Research Reports and other types of articles primarily as web-based documents. To view this or other CFRU publications, please visit our website:

www.umaine.edu/cfru