

THE ECOLOGY OF CANADA YEW (*TAXUS CANADENSIS* MARSH.), A
DECLINING SPECIES

By

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A DISSERTATION

Submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

(Forest Science)

MICHIGAN TECHNOLOGICAL UNIVERSITY

2008

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This dissertation, "The Ecology of Canada Yew (*Taxus canadensis* Marsh.), A
Declining Species," is hereby approved in partial fulfillment of the
requirements for the degree of DOCTOR OF PHILOSOPHY in the field of
Forest Science.

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ABSTRACT

Canada yew (*Taxus canadensis* Marsh.) is an evergreen shrub native to forests of northeastern North America. Anecdotal accounts suggest that before Euro-American settlement Canada yew was a common plant across its range in many forest types. However, confusion persists about the historic role of Canada yew in eastern forests and other aspects of its autecology. Here, I synthesized available information on the ecology and management of Canada yew, with particular focus on its historic range and abundance and the impacts of browsing mammals. Several unique life history traits, including high shade tolerance and a dense clonal growth form, allowed it to become locally abundant or dominant in 5-20% of mainland forest stands in the northern parts of its range, and to reach extreme understory dominance on ungulate-free islands in the Great Lakes and coastal Canada. The species' range has declined significantly from its historic maximum as a result of a combination of several factors, including fire, intensive forest management, and clearing of land for agriculture and other development. Browsing by wild cervids, however, appears to be the most common and ubiquitous cause of its decline across its range. Canada yew appears incompatible with white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) except at low levels of animal abundance or in regions where sufficient snowfall protects stems. Increasing white-tailed deer populations and reduced snowfall as a result of climate change in eastern North America threaten to extirpate this species from additional parts of its range in the next century. Commercial harvest for this species for paclitaxel and other anti-cancer pharmaceuticals is another emerging threat.

To explore mechanisms by which white-tailed deer can impact populations of Canada yew, I investigated patterns of deer browsing on Canada yew at multiple spatial scales in the Upper Peninsula of Michigan. Browsing on Canada yew at the scale of individual forest stands followed a classic Type II functional response whereby average intensity of browsing on stems decreased as abundance of yew increased. Simultaneously, browsing intensity was also affected by the position of stems in relation to the edges of Canada yew patches. Stems not associated with dense patches were browsed most heavily while browsing intensity decreased toward the interior of patches. I speculate that deer avoid traveling through the interior portions of dense patches because it is energetically expensive to do so. I believe this is the first example of refugia from browsing created by the physical obstruction of individuals of the same species.

The decline of Canada yew from eastern forests has likely resulted in changes to several components of forested ecosystems, including structure and composition of understory vegetation and concomitant effects on understory vertebrates. I demonstrate that Canada yew does inhibit density of seedlings of deciduous woody plants but that it does not necessarily affect recruitment into sapling stages. I also show that an index of understory structure, foliage height density, is quadratically related to Canada yew density, such that maximum structure is attained at median values of Canada yew abundance in most forest stands. In older, closed canopy forests, however, Canada yew can provide structure that would not otherwise be provided by other species of woody or herbaceous plants.

I also assessed the potential effects of the loss of Canada yew from eastern forests on understory vertebrates by analyzing patterns of individual species abundance and community-level indices of diversity. As has been reported for many of the focal species in my study, most individual species of small mammals and breeding songbirds appear to be more closely associated with physiognomy (structure) rather than floristics, i.e., most species were not closely associated with Canada yew abundance *per se*. I suggest that the loss of Canada yew from individual forest stands can have indirect effects on selected species, and the direction and magnitude of those effects depend on the nature of other understory cover available.

ACKNOWLEDGEMENTS

I wish to thank the following agencies and organizations that provided financial support towards my dissertation research: Michigan Department of Natural Resources Natural Heritage Grant Program, The Nature Conservancy – Michigan, Michigan Technological University, the DeVlieg Foundation, the Wisconsin Academy of Arts, Sciences, and Letters Lois Almon Grant Program, Sandpiper Technologies, Chequamegon-Nicolet National Forest, and the National Park Service.

I thank my committee members, Tom Drummer, Linda Nagel, Jim Meeker, and Casey Huckins, for agreeing to serve on my committee and continuing to be supportive through my many years in the wilderness. I am forever grateful to David Flaspohler, my major advisor, for offering me an assistantship, giving me the freedom to pursue my ideas, and then continuing to support me in my efforts to finish even after I was long out of sight.

Many thanks to individuals who provided field assistance, including Marcel Potvin, Anne Chouinard, Adam Kavalunas, Richard Posey, Dan Oberg, and Laura Krueger. I also wish to thank staff at Pictured Rocks National Lakeshore, Hiawatha National Forest, and Shelter Bay Forests for providing access to study sites and occasional field support. In particular, I owe Jerry Belant (formerly of Pictured Rocks National Lakeshore) a large debt of gratitude for providing a sounding board for my ideas throughout the various stages of my dissertation and encouraging me to complete my dissertation even after I had started working full-time for the National Park Service.

I also wish to thank the many friends and colleagues I met during my short time at Michigan Tech. I especially am thankful for the friendships I formed with Joe Kaplan, Keren Tischler, Marcel Potvin, Anne Chouinard, Noah and Jen Karberg, Greg Wright, Greg Corace, and Yi and Jianzhen Zhang. It's amazing how many wonderful moments were packed into those few years. Thank you to my parents, Harvey and Jeannine Windels, and my in-laws, Jerry and Edna Baker, for their continued support over the years, and for learning when not to ask how my dissertation was coming. My co-workers at Voyageurs National Park have also been very supportive (and some of them will be glad when they don't have to see me in my office after hours anymore). Erik Beever also gets a nod for his constant encouragement as he started every phone conversation with, "How's the diss coming, man?"

By pure chance, Peter Jordan was assigned to me as my undergraduate faculty advisor at the University of Minnesota when I first transferred into the Department of Fisheries and Wildlife. It turned out to be a wonderful stroke of luck for me. He gave me my first experiences with field ecology and introduced me to the wonders of plant-herbivore interactions on Isle Royale. I have been fascinated by this subject ever since. Thank you for your encouragement, guidance, collaboration, and friendship through all the years.

I left Michigan Technological University in 2003 to accept a job as a full-time biologist in Voyageurs National Park, MN. At the time, I naively thought I could easily finish writing my dissertation in a year or so, despite having to adjust to a new job and my new role as father. I had heard the saying that getting a PhD was more

about perseverance than intelligence (or something like that), but I didn't truly appreciate it at the time. Five years after the move, the saga that originally began in 2000 is finally ending. However, this exercise in endurance was a team effort, and my wife, Jennifer, deserves half the credit for it making it happen. She has always encouraged me, even when my lack of productivity left me feeling like I was wasting our collective time. And even if I had wanted to quit along the way, she wouldn't have let me. She has sacrificed many hours and nights and weekends so that I could work on my "stuff." She has also unselfishly put some of her dreams on hold while I finished pursuing mine. Your turn is coming soon, I promise. Finally, my two daughters, Anna and Ellen, also deserve credit, as they provided daily inspiration with their cherubic faces and sacrificed precious family time so that their dad could accomplish his dream. This dissertation is dedicated to my three girls: Jenn, Anna, and Ellen. Thank you!

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Chapter 1:

The Ecology and Conservation of Canada Yew

(*Taxus canadensis* Marsh.):

A Review and Synthesis

This chapter is written according to the style of:

Forest Ecology and Management

Abstract:

Canada yew (*Taxus canadensis* Marsh.) is an evergreen shrub native to the understories of the boreal and deciduous forests of northeastern North America. Canada yew has a relatively unique growth form, with low sprawling branches capable of forming dense clusters of stems. Historic records and accounts regarding Canada yew suggest that before Euro-American settlement it was a common plant across its range in many different forest types but that it was locally abundant or dominant in 5-20% of forest stands in the northern part of its range. Canada yew's range has declined significantly from its historic maximum as a result of browsing by native ungulates, fire, intensive forest management, and clearing of land for agriculture and other development. It is considered uncommon throughout most of its present North American range, except for often isolated populations in areas that remain free from heavy browsing pressure by moose and deer (e.g., islands, areas with heavy snow cover, or areas naturally low in ungulate abundance). Its decline has likely resulted in changes to several components of forested ecosystems, including structure and composition of understory vegetation and concomitant effects on understory vertebrates. Increasing white-tailed deer populations and reduced snowfall as a result of climate change in eastern North America threaten to extirpate this species from additional parts of its range in the next century. Commercial harvest for this species for paclitaxel and other anti-cancer pharmaceuticals is another emerging threat.

1. INTRODUCTION

Canada yew (*Taxus canadensis* Marsh.) is of conservation interest for several reasons. First, it is frequently cited as an example of the negative effects of white-tailed deer (*Odocoileus virginianus*) on forested ecosystems (e.g., Leopold et al. 1947, Allison 1990a,b, Stromayer and Warren 1997, Waller and Alverson 1997, Soulé et al. 2003). Canada yew is often described as being “formerly abundant” or “common” in various forest types in eastern North America before deer or moose (*Alces alces*) functionally removed it from much of its historic range (e.g., Braun 1950, Curtis 1959). However, specific information on the historic abundance of Canada yew are usually lacking or anecdotal. Still, the general perception that Canada yew has disappeared from much of its historic range and declined where it still persists has raised concern about the potential cascading effects of its decline on other ecosystem components (e.g., Braun 1950, Waller and Alverson 1997). Finally, an incipient industry in eastern Canada based on harvesting leaves for extraction of paclitaxel (Taxol[®]) and other pharmaceuticals has added an economic component to the ecological rationale for its conservation. Unfortunately, little information exists on the natural history of Canada yew and the implications for commercial harvest of this declining species.

In this paper, we synthesize current available information on the ecology and management of Canada yew, including: historic range and abundance, life history characteristics, and ecological interactions, especially regarding vegetation dynamics in forest understories and impacts by browsing mammals. We also make recommendations

related to conservation and management of Canada yew and give suggestions for future research. This review includes information from published sources, the grey literature, and unpublished data. We do not review literature of Canada yew's pharmacological properties and related economics because these subjects have already received attention elsewhere (e.g., Goodman and Walsh 2001, Kingston 2005).

2. GENERAL DESCRIPTION

Canada yew (also known as American yew, dwarf yew, ground hemlock, ground spruce, *buis de sapin*, *sapin trainard*, and *l'if du Canada*) is an evergreen shrub native to mixed and deciduous forests of North America (Martell 1974, Darbyshire 2003). Canada yew has a low (< 3m), often straggling growth form that produces upright branches that can reach 2-4 m (Voss 1972, Pinto and Herr 2005). Needles of Canada yew are linear, flat, and measure 1-2.5 cm long and 1-3 mm wide and attach spirally along the stem (Pinto and Herr 2005). Live stems retain their foliage for up to eight years (Allison 1990a) while dead needles can remain for up to 2-5 years after twig/stem death (Krefting 1974, S. Windels, personal observation). Canada yew is monoecious and male and female cones are initiated in the leaf axils during the summer and overwinter as buds (Wilson et al. 1996). Ovules are wind-pollinated in the spring, with fertile female cones developing a single hard seed surrounded by a fleshy red aril (Wilson et al. 1996).

3. TAXONOMY AND GENETIC STRUCTURE

The genus *Taxus*, which is believed to date from the Jurassic Period (Florin 1958), is generally considered to be comprised of nine, mostly allopatric species, though some early taxonomists considered only a single species with many geographic subspecies

(Price 1990). Spjut (2007), by contrast, recently proposed recognition of 24 species and 55 varieties based on morphological characteristics. Members of the genus are defined largely by: 1) the production of a terminal seed on a lateral shoot that is only partly surrounded by a loose, cuplike reddish aril, and 2) by the development of stomata in rows (Spjut 2007). There is general agreement that four geographic species (chromosome number: $2n=24$) occur in North America in allopatry: Florida yew (*T. globosa* var. *floridana* [Nutt. ex. Chapm.]), Mesoamerican yew (*T. globosa* Schlecht. var. *globosa*), Pacific yew (*T. brevifolia* Nutt.), and Canada yew (Spjut 2007). Spjut (2007) also recognizes three subspecies of Canada yew, all of which may also occur in western Europe, northern Africa, and western Asia.

Senneville et al. (2001) believe Canada yew likely speciated from an extant species of *Taxus* citing as evidence its low level of genetic diversity and the presence of several monomorphic loci versus polymorphic loci found in other *Taxus* species. Further, Canada yew is the only monoecious member of the genus, and dioecy is typically considered an ancestral trait (Allison 1991). Senneville et al. (2001) suggested that Canada yew is more likely derived from Pacific yew due to the proximity of the two species within North America. However, Spjut (2007), based on paleobotanical data and observations of stomata from extant Canada yew, hypothesizes that Canada yew speciated from English yew (*T. baccata* L.) and may have emigrated to North America from Europe during the Eocene.

At the species level, Canada yew demonstrates low overall genetic diversity across its North American range (Senneville et al. 2001, Corradini et al. 2002). Senneville et al. (2001) found that genetic diversity was much lower in Canada yew than for any other

species of *Taxus* analyzed and, in fact, was lower than most other gymnosperms. However, they also reported that differentiation among geographically separated populations was greater than expected, leading them to suggest a mild metapopulation structure for Canada yew. Several barriers exist to long-distance seed dispersal in Canada yew, including irregular seed crops, low germination rates, and long periods of seed development, that may limit gene flow between isolated yew populations that likely started from a single seedling (Senneville et al. 2001).

Canada yew most often grows in patches and is considered a clonal plant, which is defined as individual, often interconnected, ramets (stems) comprising a genet (individual). Both Senneville et al. (2001) and Corradini et al. (2002) confirmed that Canada yew ramets within a single patch are genetically more similar to each other than to individuals from other nearby patches (but see Section 5.1.1).

4. DISTRIBUTION AND STATUS

4.1 Post-Glacial History

The post-glacial history of Canada yew in eastern North America is not as well understood as for most woody species. The oldest occurrences of macrofossils and/or pollen of Canada yew in North American sediment cores are as follows [range of years before present (BP)]: central Minnesota [ca 13,600 – 12,500] (Birks 1976); northeast Iowa [ca. 12,500-9,300] (Baker et al. 1996); northern Maine [ca. 10,500 - 8,800] (Anderson et al. 1986); New Hampshire [ca. 8400 – 7100] (Spears et al. 1994); and southwestern Quebec [ca. 8400] (Carcaillet et al. 2001). Carcaillet et al. (2001) suggest that Canada yew was the dominant understory shrub in white pine (*Pinus strobus*) forests in southwestern Quebec by ca. 6,500 years BP. Therefore, it appears that Canada yew

reestablished soon after glacial retreat and was likely present in conifer-dominated forests along the retreating edge of the glaciers.

The major tree species composing the current northern hardwood and mixed hardwood forests of northeastern North America - sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*), and white pine – migrated into the region between 9,000-4,000 years BP (Davis 1983, Pielou 1991). Canada yew's post-glacial migration appears much quicker than would have been predicted based on some aspects of its life history, including relatively slow growth, animal-dispersed seeds, and dependence on moist, organic soils (Martell 1974). American chestnut (*Castanea dentata*) also has an animal-dispersed seed, and its post-glacial northern migration in relation to other deciduous trees was markedly slower (Davis 1983). However, several authors have suggested that some Canada yew populations may have escaped glaciation in rocky cliffs or steep ravines and subsequently acted as local sources through which populations could have quickly reestablished (Gonsoulin 1975, Larson et al. 2000).

4.2 Historic Distribution

At the time of European settlement, Canada yew was found in forested regions of northeastern North America, from southeastern Manitoba to Newfoundland and south as far as northeastern Iowa, eastern Kentucky and western Virginia (Figure 1; Little 1971, Martell 1974). Canada yew has been documented in 19 states (Connecticut, Illinois, Indiana, Iowa, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island,

Tennessee, Vermont, Virginia, West Virginia, and Wisconsin) and seven Canadian provinces (Labrador, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Islands, and Quebec; Little 1971, NaturServ 2007). In Tennessee, Virginia, and southern West Virginia it is confined to higher elevations in the Appalachians.

Although descriptions of its northern limit are imprecise, its southern limit is generally well-defined. Canada yew's pre Euro-American settlement distribution generally was limited to cool, mesic forest areas, with mean annual precipitation ranging from 550-1650 mm and mean annual temperature between -5.1-13.0°C (Table 1; Thompson et al. 1999). The core of Canada yew's range also generally overlaps with an area of relatively high mean winter snowdepth (range = 3.9-69.5 cm), extending from the Great Lakes to the Canadian Maritime provinces.

The more recent historic range of yew is well-established from herbarium records and observations of early ecologists. Unfortunately, there is little written record of Canada yew's historic distribution at finer spatial scales, namely 1) its frequency of occurrence at the landscape scale (i.e., among forest stands), and 2) its frequency, percent cover, and relative dominance within forest stands. The lack of a precise historic picture of pre Euro-American settlement Canada yew in North America has caused confusion about the relative importance of Canada yew in forests across its range that has, in our opinion, ultimately influenced its priority for conservation and management. In an attempt to fill this information gap, we compiled data from anecdotal accounts and published sources to better describe Canada yew's historic context in the North American landscape. The date of the observations in these accounts ranges from 1822 to 2007. However, because of

Canada yew's sensitivity to overbrowsing by herbivorous mammals, fire, and forest disturbance, this plant likely experienced declines from its historic maximum in parts of its range where it has experienced Euro-American settlement the longest. In other words, the paucity of anecdotal observations or quantitative data on the functional extirpation of Canada yew in much of the northeastern United States suggests that yew may already have been severely reduced by the time ecologists first began making observations about plant community dynamics in the early 20th century. Therefore, inferences made about its historic distribution and abundance should be considered conservative.

4.2.1 Mainlands

Nichols (1935) and Martell (1974) described Canada yew as “common” throughout the northern and mixed hardwood forests of northeastern North America. More specifically, Martell (1974) states Canada yew “is (or was, before eradication by deer) a common shrub” in the white pine-northern hardwood forests of the Northeast and mixed mesophytic forests of the Alleghany Mountains, and is “scattered” in the oak-chestnut forests east of the Alleghanies. Curtis (1959) reported Canada yew as a “characteristic shrub” of Wisconsin’s mesic northern hardwood forests and Braun (1950) listed Canada yew as “frequent” in white cedar (*Thuja occidentalis*) bogs within beech-maple forests of the southern Great Lakes states.

Some quantitative data on frequency of occurrence within landscapes is available. Two different studies that spanned large portions of Canada yew’s North American range reported that it occurred in 31% of boreal forest stands (La Roi 1967) and 20% of hemlock stands (Rogers 1980; Appendix A). At finer landscape scales, Curtis (1959)

found it in 27% of northern/mixed hardwood forest plots across northern Wisconsin and Ohman and Ream (1971) documented yew in 56% of virgin lowland conifer stands in northern Minnesota. At the finest scales of studies that documented stand level frequency of occurrence, Canada yew was present in 20% of boreal forest stands in north-central Minnesota (Buell and Niering 1957), 14% of hemlock stands in New Hampshire (Lauren Howard, personal communication), 12% of northern/mixed hardwood stands in the Green Mountains of Vermont (Siccama 1974), and up to 70% of northern/mixed hardwood stands in the Berkshire Plateau, Massachusetts (Egler 1940). Based on this limited information, it thus appears unlikely that Canada yew was uniformly distributed across local landscapes before Euro-American settlement but more likely was an important component in less than half of forest stands within a landscape. Senneville et al. (2001) speculate that Canada yew's patchy and erratic distribution at the landscape level is a result of its limited seed dispersal ability.

Where Canada yew is present in mainland habitats, however, there are numerous cases of it dominating the understory. Canada yew is known as ne'bagandag in Ojibwemowin, which may be translated as "laying everywhere on the ground" (Jim Meeker, personal communication). Leopold et al. (1947) stated that parts of Wisconsin, Michigan, Pennsylvania, and New York had "accumulated heavy growths of ground hemlock." Canada yew has been described as "dominant", "abundant", or "dense" in boreal and northern mixed hardwood stands of Connecticut (Nichols 1913), Michigan (Braun 1950, Stearns 1951, Richards 1952), Minnesota (Buell and Bormann 1955), New York (Braun 1950), Ontario (Holmes and Pitt 2007), Pennsylvania (Braun 1950), Quebec (Lamoureux and Lacoursiere 1976, De Grandpe and Bergeron 1997), and Wisconsin (Braun 1950).

Canada yew was described as “dense” on north facing slopes but generally absent elsewhere in forest stands in Indiana (Friesner and Potzger 1934) and the Twin and Hunter Mountain regions of New York (McIntosh 1972). In two lowland conifer (i.e., white cedar) stands in Upper Michigan, the General Land Survey noted Canada yew on 33-75% of survey lines, suggesting it was the dominant understory component (Van Deelen et al. 1996). Other studies have also suggested that Canada yew was one of the most important components of lowland conifer understories in Indiana (Collins et al. 1979) and Minnesota (Ohmann and Ream 1971).

Some quantitative information regarding the historic importance of Canada yew is also available. Maximum cover values reported for Canada yew in boreal forest stands range from 12-64% in Minnesota (Buell and Bormann 1955, Buell and Niering 1957) and 57% in Quebec (De Grandpre et al. 1993). Rogers (1980) reported a mean cover value of 13% for all 71 hemlock stands sampled in northeastern North America while Canada yew comprised 2% of the understory in a single hemlock stand in New Hampshire (Lauren Howard, personal communication). Maximum values for Canada yew cover in northern and mixed hardwood stands range from 33-100% in Massachusetts (Egler 1940), 1-54% in Michigan (S. Windels, unpubl. data), 30% in Wisconsin (Foster 1993), 1-21% in Ontario (Holmes and Pitt 2007), and 25% in Quebec (St. Louis et al. 2004).

4.2.2 Islands

In the special case of islands (particularly in the Great Lakes and the Atlantic Provinces) it appears that Canada yew attained its highest frequency of occurrence and coverage. Many of these examples come from ungulate-free islands in the Great Lakes. Holt (1905 in Krefting 1974) stated that Canada yew was “everywhere abundant in the

upland forest” of Isle Royale (Lake Superior) and McMurray (1933, cited in Krefting 1974) estimated that it covered 1/3 of the island (or approximately 18,000 ha) based on presence of dead stems. Canada yew occurred in 67% of sample plots during the original land surveys of Isle Royale (Snyder and Janke 1976). Judziewicz and Koch (1993) speculate that before European settlement, yew was “dominant” on 21 of the 22 islands in the Apostle Islands (Lake Superior) archipelago; as of 1992 surveys, Canada yew was still described as “dominant” or “dense” for 11 of the 22 islands, with cover values ranging from 24-83%. Beals et al. (1960) further describes the likely historic state of Canada yew on the Apostle Islands: "On favorable sites yew grows in almost impenetrable thickets and occasionally reaches a height of over 8 feet. The general aspect of yew in these stands is that of a dense tangle of stems." Canada yew on other Great Lakes islands has been described as forming “a dense impenetrable ground cover” (Manitou Islands, Lake Superior; Richards 1952), “abundant” (Garden and South Fox Islands, Lake Michigan; King 1975), and a “tangle of ground hemlock” (Espinore Island, Lake Huron; Leopold et al. 1947).

Canada yew also appears to have historically dominated the understories of islands in the Atlantic Provinces. During an expedition across Newfoundland Island in 1822 Cormack (1928) described Canada yew as “the chief underwood, as in forests of Canada and Nova Scotia.” Telfair (2004) states that the forest floor in mature spruce-hemlock stands in Nova Scotia was historically “carpeted with Canada yew.” Viera (2003) reported coverage values of 20% for Mingan Island (Quebec) and speculated that nearby Anticosti Island historically contained similar amounts of Canada yew. Glen (1999)

reported Canada yew occurred in 12% of northern and mixed hardwood forest plots across Prince Edward Island, with coverage values ranging from 1-100%.

4.3 Current Status and Distribution

At this time, Canada yew is present in all of the states or provinces listed as part of its native range (NaturServ 2007). Canada yew's global status was last reviewed in 1983 and was ranked as G5 (globally secure; NaturServ 2007). It is ranked as N5 (nationally secure) in the United States and Canada. As of 2007, it was considered "vulnerable", "imperiled", or "critically imperiled" in 12 states and 1 province in eastern North America (NaturServ 2007). It is also a Regional Forester Sensitive Species in five National Forests in the eastern U.S.: Monongahela National Forest (WV), Allegany National Forest (PA), Huron-Manistee National Forest (MI), Superior National Forest (MN), and the Chippewa National Forest (MN; US Forest Service 2007).

Though Canada yew has not yet been completely extirpated from any state or province listed as part of its native range, its current distribution has been reduced dramatically since the beginning of the 20th century, particularly in the United States. Nevertheless, areas remain where Canada yew is still a dominant component of northern forest understories. In general, these are areas where winter white-tailed deer or moose abundances are generally low or where access to Canada yew is restricted as on islands or by steep slopes, rocky terrain, or sufficient snowfall to cover individual stems or clusters of stems (Stachowicz and Allison 1995, Waller and Alverson 1997). At least 25 islands in the U.S portion of the Great Lakes contain significant populations of Canada yew (Ewert et al. 2004).

5. LIFE HISTORY

5.1 Growth and Reproduction

5.1.1 *Growth form and growth rates*

Canada yew typically grows as a low, straggling shrub but often produces upright branches growing up to 2 m tall. Individuals up to 4 m tall and 90 mm in diameter at breast height have been reported (Voss 1972, Pinto and Herr 2005). Means and ranges of stem attributes and growth rates from several populations are shown in Table 2. Growth rates vary with site conditions but appear to be greatest in relatively small canopy gaps (50-450 m²; S. Holmes, personal communication, Martell 1974). Mean annual mortality rate for individually marked ramets over a nine-year period in Wisconsin ranged from 1.7% in fenced enclosures to 4.1% in adjacent sites exposed to deer browsing (S. Windels and D. Foster, unpubl. data). Stem length, height, diameter (at first root), and age are significantly correlated (Foster 1993, S. Windels, unpubl. data) and can be used to derive length or diameter-biomass relationships (King 1975).

Because of its clonal nature, Canada yew can form dense patches of stems. Densities of live stems from northern mixed hardwood forest stands in the Upper Peninsula of Michigan ranged from 0.1 – 20.0 stems/m² (Danz 1998, S. Windels, unpublished data); Finér et al. (1997) reported stem densities ranging from 0.1-9.6 stems/m² in boreal forest stands in northwestern Quebec. Canada yew stem density is closely correlated with percent foliar cover of Canada yew across its range: Percent cover = 4.6042 + 2.895*(stems/m²) ($R^2 = 0.844$; Figure 2).

Estimates of rates of vegetative reproduction are lacking. In northern Wisconsin, mean production of new ramets/m²/year was 0.056 in fenced enclosures and 0.004 in adjacent sites exposed to deer browsing (S. Windels and D. Foster, unpubl. data).

Contiguous patches of stems up to several hectares in size have been reported (Beals and Cottam 1960, Judziewicz and Koch 1993, S. Windels pers. obs.). Corradini et al. (2002) reported patch sizes at their study site in Quebec ranged from 3-20m in diameter, with most patches roughly circular and physically separated from each other. Similar patterns have been observed across several sites in the Upper Peninsula of Michigan, with measured patches exceeding 100 m in diameter (S. Windels, unpublished data). Quantitative estimates of annual growth rates of Canada yew patches (m²/yr) appear limited. Allison (2006) estimated growth rates (in cross-sectional area) for individual ramets to extrapolate areal growth of a single population on the Apostle Islands, Wisconsin. Growth rates ranged from 39 cm²/yr for small plants (<1000 cm²) to 197 cm²/yr for large plants (>2500 cm²).

Underground connections of rooted branches or shoot systems eventually rot out, making identification of individual genets difficult (Allison 1991). Corradini et al. (2002) hypothesized that the shape of clones is dictated by radially symmetrical “founder” ramets that are produced from seed. These founders then vegetatively produce bilaterally symmetrical ramets that radiate out from the center in a centrifugal manner (see Figure 3 in Corradini et al. 2002). Individual clones can persist within the same space when older, perhaps less vital, ramets layer and produce radially symmetrical ramets, thereby starting the entire process over. Presumably via a similar mechanism,

Hansen et al. (1973) noted that individual patches of Canada yew can migrate over time within a site.

Smaller clones tend to be comprised of a single genet (Senneville et al. 2001, Corradini et al. 2002) but it is unclear how often larger clones comprise intertwining clusters of multiple genets. Only one of four disjunct colonies (patches) genetically mapped by Corradini et al. (2002) was comprised of multiple networks. Though genetic tests identified the individual networks within this patch as distinct, they were in fact not genetically different enough for the authors to conclude they were from more than one genet. Corradini et al. (2002) instead concluded that this was further evidence that colonies tend to perpetuate themselves within their original space through the production of radially symmetrical ramets. While genets may live for hundreds of years, individual ramets are relatively short-lived (Table 2).

5.1.2 Underground dynamics

The decumbent, or prostrate, portions of branches of Canada yew are frequently covered by litter and/or debris along much of their length. Covered portions of branches are generally rooted, with the roots typically grouped near the bases of lateral branches (Bannan 1942). Canada yew tends to produce short, thick roots relative to other woody taxa, and root biomass is predominantly concentrated in the organic layer, leading Finér et al. (1997) to speculate that Canada yew is adapted to understories with deep organic layers, e.g., climax conditions. Corradini et al. (2002) report that older genets tend to be buried deeper in the organic layer (10-20cm deep) than younger genets. Roots of Canada yew also appear to be relatively slow growing; Finér et al. (1997) reported that roots of

Canada yew represented 25% of the standing root (1-10 mm diameter) biomass in a 232 year-old boreal forest stand in Quebec but made up less than 5% of total root biomass production. Berliner and Torrey (1989) reported that Canada yew was “heavily colonized” by vesicular-arbuscular endomycorrhizal fungi during the entire growing season but found no evidence of ectomycorrhizae. A more detailed description of root physiology of Canada yew is contained in Bannan (1942).

5.1.3 Reproduction

The reproductive ecology of Canada yew has received more attention than most other aspects of its life history. Canada yew is the only yew that grows primarily in a shrub form and is also primarily monoecious (Wilson et al. 1996), i.e., it produces both male and female cones. Wilson et al. (1996) hypothesized that monoecy evolved in Canada yew to counteract either chronic pollen limitation or chronic seed predation as a result of its prostrate growth form. As expected for self-fertile plants, male cones tend to be produced on newer, higher growth than female cones (Allison 1993). Phenotypic sexual expression (i.e., relative proportion of male to female reproductive effort) in ramets can vary by stem size, site, year, and history of deer browsing (Allison 1990*a,b*, Allison 1991, Allison 1992). Stems that produced more growth tended to produce more cones, i.e., there does not appear to be a negative trade-off between growth and reproduction in this species (Wilson et al. 1996).

Pollination success for populations of Canada yew, a wind pollinated species, can be highly variable; median pollination success varied from 50-100% in Massachusetts and from 23-93% in Wisconsin (Allison 1990*a*, Wilson et al. 1996). Factors affecting

pollination success include density of male and female cones and distance to nearest neighbor (i.e., stem density; Allison 1990c); deer browsing can have both direct and indirect effects on these factors (Allison 1990a,b).

Fertilized ovules produce a single hard seed surrounded by a fleshly red aril. Seeds begin ripening in mid-summer and most are mature by the early fall (Wilson et al. 1996). Densities of mature seeds ranged from 0.03-7.5 seeds/stem in Wisconsin and Minnesota (Allison 1990c). Seed production appears limited by both relatively high abortion rates (8-50% in Massachusetts) and chronic seed predation (Allison 1990c, Wilson et al. 1996). Wilson et al. (1996) reported that 74% of seeds were predated by rodents or birds, most within a few days of the aril turning red. Similar seed predation rates have been reported for English and Pacific yews (Difazio et al. 1996, Hulme 1996). Canada yew's fleshy red aril likely evolved to attract seed dispersers with color vision that void the seed intact (e.g., frugivorous birds), though mammalian seed predators consume all or part of the seed in addition to the aril in at some parts of Canada yew's range (Wilson et al. 1996).

Like other yews, seeds of Canada yew have relatively low germination rates (Young and Young 1992, Hulme 1996). Seeds require 60-120 days of cold stratification and temperatures of ~15°C for germination (Rudolf 1974). Microsite requirements for germination are unknown. Canada yew seedlings have been reported growing from nursery logs in northern mixed hardwood forests in Michigan (L. Frelich, personal communication), but in general, seedling production under natural conditions appears rare (Foster 1993, Senneville et al. 2001). Endozoochory, i.e., seed passage through an animal's digestive tract, has also been thought to enhance seed germination in other yews

(Bartkowiak 1978 in Svenning and Magård 1999, Sakakibara 1989, Garcia et al. 2000).

We (SKW and DJF) attempted to test the effects of bird [European starling (*Sturna vulgaris*) and domestic chicken (*Gallus gallus*)] gut passage and mechanical and chemical scarification on Canada yew seeds in laboratory conditions. None of the >500 seeds germinated at the completion of the 18 month trial (including two cold stratification periods) although the medium we used may not have kept seeds sufficiently moist.

Canada yew most often reproduces vegetatively, i.e., by layering whereby arching branches are pressed to the ground when a stem is covered by litter, coarse woody debris, or soil, produce adventitious roots, and then begin growing as trophically and physiologically autonomous ramets (Wilson et al. 1996, Corradini et al. 2002; see also Section 5.1.1). Stem height and stem length are correlated, though longer stems tend to have lower stem height:stem length ratios, i.e, they grow more prostrate (Figure 3). Long, prostrate stems are more likely to be pressed against the ground (by leaf litter, coarse woody debris, or their own weight) and produce adventitious roots than are short, erect stems (King 1970).

5.2 Habitat

Canada yew can be found in mesic to wet-mesic forests <1500m above sea level in the three major forest divisions of northeastern North America as defined by Comer et al. (2003): boreal, Laurentian-Acadian, and Central Interior-Appalachian. It is a common species throughout much the northern hardwood-pine-hemlock and spruce-fir (boreal) forests of the region (Braun 1950, Curtis 1959, Martell 1974). It can also be locally dense in mixed mesophytic forests of the Alleghany and Appalachian mountains (Braun

1950, Martell 1974), in pure hemlock forests (e.g., Nichols 1913, Dansereau 1959, Rogers 1980, Howard and Lee 2002), and in lowland conifer (i.e., northern white cedar) forests in the Great Lakes region (e.g., Ohmann and Ream 1971, Collins et al. 1979, Foster 1993, Van Deelen et al. 1996). It rarely occurs in dry or fire-dependent forests, e.g. jack pine (*Pinus banksiana*). See Appendix A for frequency and abundance of Canada yew reported for various geographic regions, ecoregions, and tree species associations.

Canada yew is generally limited to mid to late-successional forests (e.g., Nichols 1913, Glenn 1999 but see Stachowicz and Allison 1995) and is rarely found in old fields or other non-forested habitats (Egler 1940). It occurs on most soil types found within its range but it generally grows best on calcareous, moist loam or silt-loam soils with a pH of 5.0-7.5 (Wilde 1933, Kittredge 1938, Martell 1974, Pinto and Herr 2005). It has also been observed growing densely in poorly drained sites, e.g., wet areas dominated by red maple (Glen 1999, S. Windels, personal observation). It is not consistently associated with any particular tree species but can form close associations with some tree species within certain locales, e.g., with yellow birch and white cedar in the Apostle Islands, Wisconsin (Beals and Cottam 1960)

Forest composition and structure can affect presence and abundance of Canada yew within sites. The amount of canopy cover directly affects the amount of light (or photosynthetic photon flux, PPFD) available to Canada yew. Canada yew is a highly shade tolerant species and therefore does not require substantial amounts of PPFD to grow or survive. However, it will not grow under dense conifer saplings (Cooper 1913, Risenhoover and Maass 1987), which can absorb up to 95% of available light above 1m

(Aubin et al. 2000). Conversely, as a highly shade tolerant species, Canada yew is not expected to be equally adapted to open environments; growth rates on south-facing slopes in Massachusetts were one quarter those on level or north-facing slopes (Stachowicz and Allison 1995). Martell (1974) noted that Canada yew can grow in open sites provided its roots are kept moist and cool. Optimal growth and survival of Canada yew should be expected under 50% of full sunlight, the value for which most small temperate trees experience their maximum photosynthetic rate (Pothier and Margolis 1991). In northern mixed hardwood stands in Michigan, Canada yew is often most dense in small canopy gaps or along the north side of roads or other forest edges where more light is available than under full canopy (S. Windels, personal observation). Data from a four year experiment in Michigan where Canada yew cuttings were transplanted into deer-proof enclosures suggests optimal growth rates occur in small canopy gaps, such as those created by individual tree falls (S. Holmes, C. Webster, and D. Flaspohler, unpubl. data). Growth rates (cm/yr) were greatest in small canopy gaps (50-150m² in diameter; $\bar{x}$ = 3.0), intermediate in medium (151-250m²; $\bar{x}$ = 2.5) and large (251-450m²; $\bar{x}$ = 2.8) gaps, and least in closed canopy sites ($\bar{x}$ = 1.7). Canada yew decreased in abundance after 400m² canopy gaps were created above yew patches in closed-canopy forests in Quebec (De Grandepre and Bergeron 1997).

Although forest structure and soil characteristics are important, presence and abundance of Canada yew may be most closely tied to moisture conditions at and below the soil surface due to Canada yew's relatively shallow root system. In general, Canada yew appears to grow best in sites that provide cool moist understory microclimates. For example, Canada yew is generally more prevalent and abundant in late versus early-

successional forests (Whitney and Foster 1988, Glen 1999), north-facing versus south-facing aspects (Stachowicz and Allison 1995, Glenn 1999), and concave versus convex slopes (Stachowicz and Allison 1995). This is especially evident in the southern portion of its range where remnant populations are often found at the base of limestone cliffs (e.g., Stachowicz and Allison 1995, Larson et al. 2000) or on north-facing slopes (e.g., Friesner and Potzger 1934, Stachowicz and Allison 1995, Glen 1999). In Michigan, isolated populations of Canada yew are often located along streams, especially near waterfalls, presumably where humidity is greater (Voss 1972, S. Windels, personal observation). Hagan et al. (2006) made similar observations in western Maine.

Areas influenced by a maritime climate (e.g., the Canadian Maritime Provinces and Great Lakes islands and nearshore areas), may have higher soil moisture and more humid understory conditions on average than similar areas outside of the maritime influence (Davis et al. 2000). Conditions in these areas may therefore allow Canada yew to exist in forest types or soil conditions that would not be favorable in other climates (Hansen et al. 1973). For example, Canada yew thrives on south-facing slopes on Passage Island near Isle Royale, Michigan, or in Krumholtz-type forests on some islands in the Apostle Islands despite the relatively poor development of overstories (<50% canopy cover), suggesting that yew requires cool moist conditions rather than a shaded overstory *per se*.

Why does Canada yew appear to grow so much better on islands than on mainland habitats? We suggest that four factors unique to island habitats create optimal conditions for Canada yew. First, it is well-known that islands tend to support less stable populations of ungulates, and often lack herbivores found on mainlands (e.g., Caughley 1970). As a result, islands are more likely to become ungulate-free or avoid colonization

and remain so for greater periods. Net annual growth rates for Canada yew are greatest in the absence of browsers (S. Holmes, unpubl. data). Second, the cool and moist conditions associated with the maritime climates of islands allow Canada yew to grow faster in and in higher conditions than in most mainland habitats. This maritime effect would also essentially expand the realized niche of Canada yew into areas where it may otherwise be limited by available microclimates. Third, fire frequencies are generally lower on islands than on mainland habitats. Water buffers fire spread from the mainland and maritime conditions also likely reduce fuel moisture. Lastly, islands likely experience more frequent windthrow and therefore more frequent formation of small canopy gaps where Canada yew grows best. Trees growing on islands tend to be more exposed, experience greater windspeeds, and grow in shallower soils than their mainland counterparts, particularly those growing inland from coastal areas (Kramer et al. 2001, Ellie and Ruel 2005).

5.4 Diseases and Pests

Little information is available on diseases and pests affecting Canada yew. Canada yew leaves are apparently well defended against insect herbivory. High mortality to insect eggs exposed to Canada yew leaf extract has been reported (Perusse et al. 1977).

English yew (*Taxus baccata*) also appears well defended through various antifeedant compounds (Daniewski et al. 1998). Several species of exotic weevils have been observed feeding on the bark of Canada yew in the Great Lakes Region, including black vine weevils (*Otiorhynchus salcatus*), strawberry root weevils (*O. ovatus*), and an unnamed weevil (*Polydrusus impressifrons*) (S. Katovich personal communication).

6. ECOLOGICAL INTERACTIONS

6.1 Forest Dynamics

When considered together, Canada yew's high shade tolerance and patchy (clonal) growth form can influence understory forest dynamics in at least five ways: 1) understory plant biomass/density, 2) stratification of understory vegetation, 3) plant species richness, 4) nutrient cycling and below-ground processes, and 5) fire frequency. Understory vegetation cover is typically inversely related to overstory vegetation cover (Constable and Lieffers 1996, Aubin et al. 2000). However, Canada yew's high shade tolerance allows dense patches to populate forest understories in undisturbed forests where near continuous canopy cover precludes growth of other woody and herbaceous plants. In some closed-canopy northern hardwood forests in Michigan, Canada yew can comprise more than 90% of total woody stem density and up to 27% of total ground cover in otherwise sparse understories (S. Windels, unpubl. data). Similar conditions were observed by Finér et al. (1997) for old-growth boreal forest stands in Quebec. Additionally, under optimal conditions Canada yew grows in dense patches with stand level (i.e., 20-60ha) stem densities of Canada yew (0.0-20.0 stems/m²) approaching those of all other woody stems combined (0.9 – 32.9 stems/m²; Finér et al. 1997, S. Windels, unpubl. data).

Canada yew can affect stratification of understory vegetation by limiting establishment and growth of other species within or underneath patches of stems. Several authors have observed that abundance of Canada yew is often negatively correlated with

abundance of other understory species. For example, Nichols (1913) observed that Canada yew frequently grew in dense patches “to the exclusion of all undergrowth” and Egler (1940) stated that “unless yew is absent, an herb layer is not present.” Other authors have specifically noted the inhibitory effect of dense yew on herbaceous growth (e.g., Buell and Bormann 1955, Judziewicz and Koch 1993, De Grandpre and Bergeron 1997). Patches of Canada yew may limit available growing space for other understory plants. Aubin et al. (2000) determined light extinction coefficients, k , for components of understory vegetation in southern boreal forests in Quebec, including Canada yew. Canada yew ($k=0.54$) intercepted more light reaching the forest floor than deciduous seedlings (0.49), conifer seedlings (0.45), and herbaceous vegetation (0.37) but less than deciduous shrubs (0.69). Alternatively, it is possible that Canada yew excludes other species through allelopathy. Relatively high concentrations of allelopathic chemicals have been documented in other *Taxus* species (Del Moral and Cates 1971, Iszkul’o and Borantyński 2004), but have not been examined in Canada yew.

Canada yew most noticeably affects understory structure by inhibiting the establishment of seedlings of woody plants such as eastern hemlock, balsam fir, sugar maple, and American beech (Braun 1950, Risenhoover and Maass 1987, Tyrell and Crow 1994, Chapter 3). Danz (1998) compared seedling and sapling densities of sugar maple and American beech within patches of Canada yew to open areas between patches. Densities of small and large hardwood seedlings were 100 times and two times lower, respectively, inside Canada yew patches versus adjacent open areas, though it is unclear if dense Canada yew inhibits seedling establishment or seedling survival. Danz (1998_ also documented faster growth rates of sugar maple and beech seedlings growing within

patches and suggested these species respond to the presence of dense Canada yew through growth plasticity. Dense Canada yew did not affect recruitment to sapling or tree stages, similar to observations made by Risenhoover and Maass (1987) and S. Windels (unpubl. data). In essence, Canada yew can increase both vertical and horizontal heterogeneity by limiting growth of other woody plants within patches. In some cases, though, Canada yew has been reported to form a distinct layer up to 50-100cm tall underneath a layer of hardwood saplings (Nichols 1913, S. Windels, unpubl. data).

Plant species richness also appears to be affected by the patchy growth form of Canada yew. Judziewicz and Koch (1993) and Balgooyen and Waller (1995) reported that herb species richness was negatively related to abundance of Canada yew in northern Wisconsin. Interestingly, Braun (1950) suggested that some herbaceous plants are able to escape competition from dense deciduous seedlings by growing in small gaps in Canada yew patches, i.e., establishment and persistence of some species may be facilitated by the presence of Canada yew.

Below-ground processes and nutrient cycling are also likely affected by Canada yew. Canada yew's dense growth form can act as a trap for woody leaf litter that would otherwise be scattered more evenly across the forest floor (S. Windels, personal observation), resulting in potentially greater organic matter inputs. Conversely, Canada yew's apparent ability to outcompete other plants may simultaneously reduce organic matter inputs that originated from these other species. Canada yew also appears to have shallower root systems than other woody plants (Finér et al. 1997) and therefore root

biomass beneath dense patches of Canada yew may be apportioned differently than in areas without yew.

Average fire-return intervals for the forest types throughout the range of Canada yew are relatively long. However, Hely et al. (2000) speculated that in closed-canopy deciduous and coniferous forests in southern Canada, Canada yew likely increases fire risk over stands without Canada yew because: 1) Canada yew foliage contains flammable oils, 2) it typically grows in higher stem densities than other woody plants, and 3) it generally displaces non-flammable herbaceous plants. Considering how poorly adapted Canada yew is to fire (e.g., shallow roots, slow growth, limited dispersal ability) however, it seems unlikely that Canada yew would have co-evolved with frequent fire.

6.2 Wildlife

6.2.1 Browsing mammals

Taxus spp. contain relatively high concentrations of the alkaloid taxane and are generally toxic to grazers such as domestic cattle, sheep, and horses (Miller 1980, Mysterud and Østbye 2004). Wild cervids, however, readily browse on yews that occur in their ranges. Besides white-tailed deer and moose, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and Sika deer (*Cervus nippon*) demonstrate a high preference for yews and subsequent ability to negatively affect population traits such as recruitment and mortality (Parks et al. 1988, Mysterud and Østbye 1995, Mitchell 1988, Mysterud and Østbye 2004). Snowshoe hare (*Lepus americanus*) and rabbits (*Sylvilagus* spp.) do browse on Canada yew but generally in

insignificant amounts (Sweetman 1944, King 1970, Martell 1974, S. Windels, unpubl. data).

There are several factors unique to Canada yew that may explain why it is preferred by white-tailed deer and moose. In contrast to many other conifer species, Canada yew appears to be poorly defended against wild cervids. It does not contain significant quantities of antifeedant chemicals (e.g., terpenoids in balsam fir and spruce) or aromatic compounds that reduce palatability. It is not mechanically defended with spines or thorns, and as a sprawling shrub rarely outgrows the reach of browsers as with many other woody species. It is also possible that Canada yew is high in digestible energy due to relatively high concentrations of essential oils (Hely et al. 2000).

Digestible energy is the product of gross energy content and digestibility and is an important factor affecting winter forage selection in moose and deer (Robbins et al. 1987). Nutritional information for Canada yew browse is surprisingly sparse given its wide recognition as an important deer forage. The closely related English yew (*Taxus baccata*) is reported to be highly digestible (70-75%) to roe deer and relatively high in protein (Mysterud and Østbye 1995).

White-tailed deer prefer Canada yew over most other winter browse species, including high preference items such as eastern white-cedar, mountain maple, and eastern hemlock (Hosley and Ziebarth 1935, Howard 1937, Leopold 1938, Hamerstrom and Blake 1939, Beals et al. 1960, Verme 1965, King 1970). Where supply surpasses demand, white-tailed deer can thrive on a diet comprised almost exclusively of Canada yew (Beals et al. 1960, King 1970). It is not surprising, then, that deer can quickly reduce the local abundance of Canada yew, often to the point of extirpation. Published examples where

white-tailed deer (and other cervids) are implicated in severe reductions in abundance or local extirpations across northeastern North America are summarized in Appendix B.

The best documented cases of deer-caused decline of Canada yew are generally from the Great Lakes region or from islands (e.g., Leopold 1938, Leopold et al. 1947, Beals et al. 1960, Judziewicz and Koch 1993, Viera 2003). We speculate that the greater abundance of such examples is not because deer-mediated decline was necessarily more prevalent in the Great Lakes region or islands, but instead that Canada yew may have already been extirpated from the parts of its range with a longer history of human settlement by the time early botanists and others made note of its disappearance. In general, local extirpations followed soon after deer populations erupted in the first half of the 20th Century (McCabe and McCabe 1997). For islands, reductions or extirpations often occurred after deer became naturally established or were purposely introduced (Leopold et al. 1947, King 1970, Beals et al. 1960).

The effects of deer browsing on sexual reproduction of Canada yew are well-documented (Allison 1990*a,b*, Allison 1992; also see Section 5.2). Other population-level effects of browsing by deer have received attention in the published literature. Several unpublished studies that used deer-proof exclosures in Michigan and Wisconsin provide some information of the effects of deer browsing on stem height, horizontal cover, and mortality of individual stems in both healthy and depressed Canada yew populations. Deer browsing negatively affects stem mortality, stem production, stem height, and stem growth rates, even over relatively short time frames (Table 3).

Tolerance levels of Canada yew stems to various amounts of ungulate browsing have not been adequately tested. King (1970) performed artificial clipping experiments to

determine the response of Canada yew to various levels of deer browsing. Severely browsed (75% of twigs clipped annually) stems had higher mortality rates than unbrowsed stems. However, overall annual mortality rates over the two-year study were relatively low (Table 3). Based on his data, King (1970) deduced that Canada yew can sustain ~10% annual removal of biomass. He further speculated that it can withstand up to 25% removal in a single winter if allowed to recover for two years (because new buds formed the spring after the browsing occurred typically produce little growth until their growing season), and >50% removal if allowed more than 4 years to recover. His observations parallel those of Stachowicz and Allison (1995), Leopold et al. (1947), and B. Dalton (personal communication) who observed that Canada yew can persist in areas with highly variable browsing pressure that offer occasional reprieves from intense browsing.

There are several other factors, however, that can influence whether stems are browsed or not. Intensity of browsing on Canada yew stems was negatively related to its abundance in northern and mixed-hardwood stands in Michigan (Chapter 3). Further, in Upper Michigan, stands that contained <10-20% cover of Canada yew appeared to be experiencing unsustainable rates of browsing, i.e., removal was exceeding growth. Independent of its abundance, browsing intensity was also affected by stem location in relation to other stems of Canada yew. Stems that grew outside of discrete patches were browsed more intensively than those within patches. Further, stems on the outer 1m of patches (ranging up to ~1ha in area) were browsed more intensively than those in the interior portions of patches, presumably because it was more energetically efficient for deer to browse around the outside of patches rather than walk through the dense tangle of

stems in the patch interior. Combined, these interactions can create refugia of unbrowsed stems that are able to continue sexual and vegetative reproduction (Allison 1990a, Chapter 3).

An equally important factor determining intensity of browsing on Canada yew stems is amount and timing of snow cover (or snow depth). The long, prostrate stems with spreading branch structures is an ideal architecture for catching snowfall. King (1970) observed that 15cm of wet snow was enough to press large stems to the ground and completely cover them, thus protecting stems from browsing in early winter. Smaller stems tend to be more erect (Figure 3) and thus are not as easily buried; in Lake Michigan islands and Michigan's Upper Peninsula most stems sticking above the snow tend to show evidence of browsing (King 1970, S. Windels, personal observation). Likewise, the duration of permanent snow cover also affects intensity of browsing; fewer days of snow coverage increases the amount of time stems are exposed to browsing (King 1970). An analysis of snowfall data did not detect negative trends in average winter snowdepth or number of days with at least 50cm of snowdepth from 1949-2001 throughout Canada yew's historic range, suggesting that changes in snowfall over the last half century alone are not responsible for the decline in Canada yew (D. Kluver, unpubl. data, Kluver 2007).

King (1970) suggested two possible mechanisms whereby Canada yew-white-tailed deer systems can be altered from a state of equilibrium. A mild winter with late or little snowfall can result in a short-term increase in browsing pressure, which will reduce stem height and foliar biomass, reducing snow holding capacity, exposing stems to increased browsing pressure the next winter. A sudden increase in deer density can cause a similar

reaction. Mean annual snowfall and duration of snow cover in northeastern North America are generally predicted to decrease in the 21st Century as a result of climate change (Kunkel et al. 2000, Federer 2001). Under such conditions, the impacts of browsing will be exacerbated, particularly along the southern edge of its range.

White-tailed deer can create alternate stable states among plant communities in forested ecosystems (Stroymayer and Warren 1997, Augustine et al. 1998). As previously discussed (e.g., Sections 4.2 and 5.1), Canada yew tends to be either a dominant component of the forest understory, or a rare species that persists as heavily browsed individuals or small clusters of stems. Therefore, Canada yew also appears to exist in two alternate steady states, i.e., Canada yew populations will tend to shift towards one of those states depending on deer density and initial plant abundance. For dense populations of Canada yew, such as those that exist on many Great Lakes islands with few or no deer, yew can persist as an understory dominant until deer densities exceed ~7-12 deer/km², at which point biomass removed by browsing exceeds biomass produced by the entire population (Figure 4; King 1970, Judziewicz and Koch 1993). Alternatively, at a relatively low but constant deer density, such as those that predominated before Euro-American settlement in northeastern North America (2-6 deer/km²; McCabe and McCabe 1997, Waller and Alverson 1997), deer browse removal can exceed growth in forest stands with <15% cover of Canada yew, moving it towards rarity or extirpation, while stands with >30% cover remain in a robust state (Chapter 2).

Even in regions with heavy snow, moose are reported to browse on Canada yew year-round (Peterson 1955) and consider it a highly preferred browse plant when present (Pimlott 1963, Krefting 1974). Canada yew's disappearance from Isle Royale, Michigan

after the arrival of moose in 1909 is well-documented (Murie 1934, Krefting 1974, Snyder and Janke 1976; Appendix B). Canada yew was the dominant ground cover across much of the 52,000 ha island but was functionally extirpated by the early 1930's as moose densities approached 4-10/km² (Murie 1934). On the main island, it currently only grows well in large moose-proof exclosures (Krefting 1974, Risenhoover and Maass 1987). Moose also quickly eliminated Canada yew from Newfoundland Island after they colonized the island between 1878-1904 (Pimlott 1963). In both cases, continued browsing by moose after the initial reduction in abundance of Canada yew has maintained the plant's population in a persistent state of scattered, stunted individuals (Krefting 1974, Risenhoover and Maass 1987, Connor et al. 2000). It is not clear if moose browse patterns are as affected by Canada yew's patchy growth form. Moose have much longer legs than deer and dense Canada yew patches may be a less significant obstacle.

Woodland caribou (*Rangifer tarandus*) primarily consume lichens in winter but they will also browse on woody plants, including Canada yew. However, contrary to white-tailed deer and moose, woodland caribou exhibit low preference for Canada yew versus other woody plants such as mountain maple (*Acer spicatum*) and mountain ash (*Sorbus americana*; Bergerud et al. 2007). In fact, evidence from the Slate Islands (Lake Superior) suggests that Canada yew is a starvation food (W. Dalton, personal communication). Considering its low preference, Canada yew populations are much more likely to persist in areas with caribou only than areas with viable populations of either white-tailed deer or moose. Nevertheless, overabundant caribou are capable of functionally extirpating Canada yew. On the Slate Islands, Canada yew experienced only

light browsing by caribou throughout the 1970s but its abundance declined by as much as 98% in a 3-4 year span during the 1980s when mean caribou densities exceeded 10.0 caribou/km² (W. Dalton, personal communication, Bergerud et al. 2007; Appendix B).

6.2.2 *Small mammals, birds, and amphibians*

Individual species of understory vertebrates may respond directly to the abundance of Canada yew in forest understories. The abundance and distribution of Canada yew can also have indirect effects on species by altering structure and composition of forest understories, e.g., by reducing the amount of bare ground or altering horizontal patchiness (Section 6.1; also see Chapter 3). Despite its unique growth form and large geographic range, the relationship of Canada yew with individual taxa of small mammals, birds, and amphibians, remains largely unstudied.

Limited information is available regarding interactions between non-browsing mammals and Canada yew. Dense tangles of Canada yew stems might create physical barriers or visual obstruction to potential predators of small mammals. Further, some rodent species (e.g., red-backed voles and deer mice) forage vertically in shrubs and trees and Canada yew stems may provide foraging substrate in otherwise sparse understories. Diversity and abundance of small mammals, including red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), short-tailed shrews (*Blarina brevicauda*), and masked shrews (*Sorex cinereus*), was greater in northern hardwood forest understories containing dense Canada yew than in adjacent sites that were similar structurally except for the absence of yew (Belant and Windels 2003). Similar patterns were observed in southern Quebec for the same suite of species (C. Maissonneuve,

personal communication). However, few direct relationships were found between Canada yew density and abundance of individual species in a broader study across a gradient of Canada yew abundance representative of current forests in the Upper Peninsula of Michigan (see Chapter 3). The results do suggest that Canada yew may indirectly affect some species via effects on general understory vegetation structure. Brower and Cade (1966) reported similar capture rates of woodland jumping mice (*Napeozapus insignis*) in Canada yew and other species of woody plants, including hobblebush (*Viburnum alnifolium*) and maples (*Acer* spp.). Several species of mammals have been observed eating Canada yew arils, including black bears (*Ursus americana*), eastern chipmunks (*Tamias striatus*), and deer mice (*Peromyscus maniculatus*; Wilson et al. 1996, S. Windels, personal observation).

Eastern chipmunks and deer mice are also nest predators (e.g., Reitsma et al. 1989). Although patches of Canada yew may be beneficial to these species by providing cover, yew may also provide more opportunities for depredating understory and ground-nesting birds. Predation rates on artificial nests increased as Canada yew cover increased for 22 forest stands in northern Michigan ($R^2 = 0.56$, $P < 0.01$; S. Windels unpubl. data). Small mammals were the principal predators identified even though small mammal abundance was not closely related to Canada yew abundance in that study. Though Canada yew may be a preferred nesting habitat for some bird species, at higher abundances, Canada yew may homogenize understory structure and therefore potential nest sites to the point where small mammals can more efficiently depredate songbird nests (Martin 1988).

In some systems birds may respond more closely to the presence or abundance of certain plant species rather than to the general structure they provide (Wiens and

Rotenberry 1981). Black-throated blue warblers (*Dendroica caerulescens*) appear to have a high preference for nesting on Canada yew stems or within patches of Canada yew patches (Bent 1963, Holmes 1994, S. Windels personal observation). Holmes and Pitt (2007) reported higher abundance and greater productivity for black-throated blue warblers in a forest stand in Ontario with >20% cover of Canada yew compared to stands with little or no Canada yew cover, and attributed this to the abundance of Canada yew as a nesting substrate. However, a study of stand-level associations between understory songbirds and Canada yew found no such direct relationships (Chapter 3). Some indirect effects were detected, though, whereby dense Canada yew affected other measures of understory physiognomy (e.g., hardwood stem density and foliage height diversity (FHD)) that were significantly correlated with abundances of some individual bird species and community-level indices of species richness and diversity.

As previously discussed (Section 5.1.3), the bright, fleshy aril of Canada yew is likely adapted to attract frugivorous birds as has been reported in other species of *Taxus*. Ruffed grouse (*Bonasa umbellus*), cedar waxwings (*Bombycilla cedrorum*), American robins (*Turdus migratorius*), ring-necked pheasants (*Phasianus colchicus*), and European starlings (*Sturnus vulgaris*) have been reported to feed on ripe arils (Martell 1974). Birds are not widely known to feed on Canada yew seeds (Wilson et al. 1996) though black-capped chickadees (*Poecile atricapilla*) have been observed caching Canada yew seeds in early fall in Michigan (D. Flaspohler, personal observation).

There have been no published studies of associations between Canada yew and amphibians or reptiles. Abundant Canada yew may affect distribution and abundance of leaf litter, an important habitat component for terrestrial salamanders and frogs (Jaeger

1980). Canada yew can negatively affect growth and establishment of deciduous seedlings and herbaceous plants within yew patches and therefore affects the amount of litter produced at the ground level. However, clusters of Canada yew stems do appear to retain greater amounts of deciduous leaf fall than other plants (S. Windels, personal observation), creating pockets of dense litter that may provide unique conditions for foraging, overwintering, or other life history requirements for terrestrial amphibians such as redbacked salamanders (*Plethodon cinereus*). Conversely, wood frogs (*Rana sylvatica*) prefer areas with bare soils or where the leaf litter has been flattened by snow (Heatwole, 1961, Licht, 1991) and therefore may be less abundant in areas with dense Canada yew.

7. CONSERVATION AND MANAGEMENT OF CANADA YEW

7.1 Forest Management

Canada yew does not persist after deforestation (Egler 1940, Glenn 1999). It also appears highly sensitive to clearcutting or other intensive timber harvest (Nichols 1913, Egler 1940, Leopold et al. 1947, Metzger and Schultz 1984, Stachowicz and Allison 1995, Glen 1999). Overstory removal likely reduces soil moisture and understory humidity below the tolerance of Canada yew (Section 5.2). However, it appears that maritime conditions can moderate these effects. Canada yew remained dominant in primary forests after clearcutting on several of the Apostle Islands, Wisconsin, in the 20th century (Judziewicz and Koch 1993). Reestablishment or recolonization of Canada yew on land cleared for agriculture or heavily logged can occur naturally, though only after a minimum of 30-100 years depending on site conditions including presence of remnant

individuals, distance to source populations, and herbivore density (Stachowicz and Allison 1995, Howard and Lee 2002).

Canada yew does appear to tolerate less intensive timber harvest. In a northern hardwood stand in Ontario, selection harvest reduced Canada yew cover by 40% one year after harvest but yew recovered to near pre-treatment levels after three years (Holmes and Pitt 2007). Similarly, Canada yew was often most abundant and lush in actively managed stands in Upper Michigan (S. Windels, unpubl. data). Canada yew experiences optimal growth rates in canopy gaps $<300 \text{ m}^2$, such as those created in a single-tree selection harvest system (Section 5.2). Creation of larger gaps can decrease Canada yew abundance (De Grandepre and Bergeron 1997). Rutting from equipment often kills Canada yew stems directly (S. Windels, personal observation) but it may also cause unsuitable conditions for establishment or survival of new stems by compacting the soil and decreasing drainage (Buckley et al. 2003). Patches of Canada yew can often be found cleanly bisected by haul roads and skid trails >30 years after the last harvest (S. Windels, personal observation). Negative effects of timber harvest can be mediated by: 1) creating canopy gaps $<300\text{m}^2$, 2) creating buffers around existing patches of Canada yew, particularly with respect to use of heavy equipment that can compact the soil, and 3) leaving slash in place to increase moisture conditions and provide protection from browsing mammals.

7.2 Fire Management

Fire frequency in many forests types of northeastern North America are generally low, e.g., 700-800 year intervals for stand-replacing fires in the mesic deciduous forests

of the Great Lakes and New England (Lorimer 1977) and >500 years for the humid boreal forests of eastern Canada (Foster 1983). It is therefore not surprising that Canada yew, a species mostly confined to mesic forest types, is poorly adapted to fire. Above-ground stems readily burn while the shallow root system is vulnerable to heat and loss of organic matter (Finér et al. 1997, Hely et al. 2000). Anecdotal examples of Canada yew being eliminated or greatly reduced after fires are available for Isle Royale (Hansen et al. 1973, Janke et al. 1978), several of the Apostle Islands (Judziewicz and Koch 1993), and the Peshtigo fire area of northeastern Wisconsin (Foster 1993). However, fire intensity is rarely uniform across landscapes, creating a natural patchwork of burned and unburned areas. Mean cover of Canada yew was not significantly different between burned and unburned portions of Outer Island, Lake Superior, Wisconsin (J. Meeker, unpubl. data). However, between-plot variation was greater in the burned areas suggesting that some areas may have escaped the effects of the fire. Topographic features can also protect populations of Canada yew from fire. For example, populations or individuals of Canada yew can often be found in depressions, ravines, north-facing slopes, and cliff faces in areas after a fire (Cooper 1913, J. Meeker, personal communication).

Canada yew does appear capable of readily recolonizing burned areas. De Grandpre et al. (1993) suggest that Canada yew does not begin to recover in boreal forest stands until approximately 50-75 years post-fire, with stands >200 years old having the highest abundance of yew. Foster (1993), however, notes that Canada yew was not found throughout much of the Pestigo fire area in Wisconsin >120 years post-fire and suggested that fire-mediated changes in soil properties may be a factor limiting its reestablishment.

Considering its apparent sensitivity to fire and the length of time required for natural reestablishment, managers should consider avoiding prescribed burns in areas with remnant Canada yew populations. Likewise, suppression of wildfires, both natural and accidental, should be considered for areas where preservation of Canada yew is a high priority.

7.3 Commercial Harvest

All *Taxus* species contain relatively high concentrations of taxanes. One taxane derivative, paclitaxel, was first isolated from the bark of Pacific yew in the 1960s as a potential anti-cancer agent. Methods to extract paclitaxel from other species of *Taxus* soon followed. Paclitaxel (also known as Taxol[®]) and other analogs, e.g., docetaxel (Taxotere[®]), have since been proven to be very effective treatments for several types of cancer, including breast, ovarian, and non-small cell lung cancer, and other diseases (Cragg and Newman 2005). Paclitaxel and related compounds are difficult to synthesize. Therefore, demand for taxane-derived pharmaceuticals, whose sales exceeded \$2.3 billion USD in 2001, was most economically met by harvesting biomass from wild yews, including Pacific yew and Himalayan yew (*Taxus baccata* subsp. *wallichiana*). Commercial harvest, however, was largely unregulated and unsustainable, resulting in significant reductions to native populations in the U.S. and India (Duke 1993, Rikhari et al. 1998, Smith and Cameron 2002).

Harvesters turned their attention to wild populations of Canada yew in the early 1990s. Canada yew contains higher concentrations of paclitaxel than Pacific yew and other species (Duke 1993) and abundant Canada yew in eastern Canada was viewed as a

means to provide a non-timber source of income and jobs for local communities. Annual harvest in eastern Canada may have exceeded 5-6 million kg/yr by 2001, a rate considered unsustainable (Cameron and Smith 2002). In response, federal and provincial natural resource agencies in Canada developed “Minimum Standards for Harvesting Ground Hemlock” in 1999 to guide ecologically sustainable harvest of wild populations on public and private lands (Smith and Cameron 2002). Briefly, these guidelines suggest harvest should: 1) be done by hand with pruners; 2) be limited to stems >1m in height (to eliminate heavily browsed stems that may not sustain additional tissue loss; 3) remove only the last three years of growth on terminal twigs; and 4) only occur on individual sites that have been unharvested for $\geq$ four years to allow stems to recover.

Global demand for taxane-derived pharmaceuticals likely means harvest will continue in eastern Canada, particularly on private lands where harvest cannot be regulated. Given the other factors discussed that have reduced Canada yew’s range and abundance, it appears that commercial harvest will further cause declines in wild populations in Canada. Despite some initial interest (e.g., Duke 1993), it does not appear any wide-scale commercial harvest of wild Canada yew has occurred in the United States for pharmaceuticals, though this situation could change. There are efforts underway in the U.S. and Canada to develop cultivars of Canada yew for nursery propagation to reduce reliance on wild populations, with special focus on increasing rates of biomass production and paclitaxel concentration over wild-growing populations (Smith and Cameron 2002).

7.4 Overabundant herbivores

Overabundant or newly introduced white-tailed deer and moose can reduce Canada yew growth, reproduction, and local persistence. Therefore, overabundant herbivores are typically the primary management problem for natural resource managers concerned about preserving or restoring Canada yew. In many parts of eastern North America, current white-tailed deer densities may be more than 2-4 times greater than at the time of European settlement (Alverson et al. 1988, McCabe and McCabe 1997). In general, Canada yew does not appear able to persist under these densities. Unfortunately, reducing white-tailed deer densities appears infeasible in most of the range of Canada yew. Even if enough hunter effort could be applied on the landscape to effectively reduce populations, the hunting public and the agencies that manage the resource frequently demand higher deer population levels for recreational and economic reasons.

Local population control is a more viable alternative. Public hunting can be used to reduce densities within protected areas throughout North America (Coffey and Johnson 1997). Similarly, lethal control, e.g., trapping or sharpshooting, can also be an effective means to reduce deer abundance (DeNicola et al. 1997). In both cases, though, effort needs to be reapplied periodically, often annually, in order to keep deer abundance at acceptable levels. Recently, the U.S. National Park Service implemented a program to reduce white-tailed deer from two islands in the Apostle Island archipelago, Wisconsin, where deer had not been known prior to Euro-American settlement, principally because overbrowsing was threatening persistence of Canada yew on these islands. Previous evidence from the Apostle Islands and other Great Lakes islands suggests that populations of Canada yew can recover after a significant reduction or elimination of

herbivores (Leopold et al. 1947, Beals et al. 1960, Judziewicz and Koch 1993, W. Dalton, personal communication).

Landscape composition can be an additional factor influencing the severity of local deer browsing on various plants. For example, Augustine and Jordan (1998) report that the amount of agricultural fields within the landscape context influenced deer densities and ultimately the degree to which trilliums (*Trillium* spp.) were browsed within forest fragments. Reducing the amount of cultivated fields adjacent to protected forest fragments may therefore result in decreased browsing pressure on trilliums and other sensitive forest herbs. Likewise, resource managers should consider landscape level factors that may influence probability of browsing on Canada yew, such as distance to winter thermal cover or degree of forest fragmentation from development or forest management practices.

Perhaps the most effective way to protect natural Canada yew populations from browsing herbivores is to build exclosures (Risenhoover and Maass 1987, J. Meeker, unpubl. data). Building and maintaining exclosures can be expensive and labor-intensive, and thus complete enclosure of sites containing yew is not always possible. Alternatively, individual patches or portions of patches can be protected. Exclosures can be built from woven wire fencing, interconnected livestock fencing panels, or polyethylene mesh (S. Wilson, personal communication). Exclosures can permit passage of hares and rabbits as these species rarely browse on yew.

7.5 Restoration

Canada yew can be planted to restore it to sites where it has been extirpated or to enhance existing populations. The easiest and most established way to do so is through rooted cuttings propagated in greenhouses (Martell 1974). Cuttings taken from new growth (1-3 years old) and started in appropriate media in greenhouses typically do well when transplanted into natural settings. Cuttings can be dipped in rooting hormone though neither use of rooting hormone nor initial size of cuttings had a significant effect on rooting percentage (Smith and Cameron 2002). In general, larger cuttings produce greater growth (Smith and Cameron 2002). Cuttings should be planted in relatively dense patches to mimic natural conditions (e.g., 10-40 stems/m²). In most cases, cuttings will need to be protected from deer or moose browsing with fencing or other exclosures; annual stem mortality for rooted cuttings planted outside of deer exclosures was >95% in Upper Michigan (S. Holmes, personal communication). Assuming average growth rates, unbrowsed stems could reach 1m in height in 15-30 years. Canada yew can also be grown from seed sown directly in the ground, though results are often mixed (Martell 1974).

8. CONCLUSIONS

Canada yew appears to have been an important component in many temperate forests in northeastern North America. As such, its loss from forest ecosystems has likely resulted in significant but until recently unexamined changes in ecological processes. Although its actual historic distribution and importance in forest understories may never be known, we suggest its loss from the landscape is analogous to the past decline in

American chestnut or the current decline in eastern hemlock from many of these same forests. Solutions to preserving remaining populations of Canada yew are neither simple nor perhaps even economically feasible. However, interest in conserving this species appears to be increasing in both the U.S. and Canada.

Canada yew was likely able to persist in its current range (current forest types) over the last 3,000-5,000 years for two main reasons. First, compared to the last 100 years, deer and moose densities across much of northeastern North America were relatively low during this period (Alverson et al. 1988, McCabe and McCabe 1997). Second, Canada yew populations likely experienced local extirpations from episodic irruptions of these two species but enough source populations remained to eventually repopulate areas. Second, the last 5,000 years was a relatively cool and moist period and snowfall was likely sufficient to protect yew from browsing. We believe that changes in herbivore densities and climate patterns combine to pose the greatest risk to Canada yew persistence as an important species in North American forests. The specter of unsustainable commercial harvest of wild Canada yew for pharmaceutical products also remains.

There is abundant anecdotal information related to Canada yew in the published literature and there are a few published studies specifically related to limited aspects of Canada yew's unique ecology (e.g., Allison 1990^{a,b,c}, Finér et al. 1997, Corradini et al. 2002, Belant and Windels 2003). However, several areas remain understudied given this species' historic importance in eastern North America:

- Additional studies should be done to determine the historic importance of Canada yew at local scales via analysis of historic journals or General Land Office (GLO)

notes (e.g., Janke et al. 1978, Van Deelen et al. 1996). Unfortunately, individual GLO surveyors had different styles and priorities for recorded information; not all surveyors recorded the presence or absence of Canada yew (S. Windels, personal observation).

- Some aspects of Canada yew's life history remain understudied. In particular, more research is needed on attributes of stems in older yew populations, on rates of vegetative reproduction and expansion of individual patches, and on below-ground processes. Some aspects of seed ecology warrant additional study, including the prevalence of seedling production and dispersal distances in natural settings, microsite requirements for germination, and the role of small mammals and birds as seed predators or dispersers. More research is also needed on the impacts of herbivores on Canada yew and the ability of overbrowsed populations to respond to removal of browsing pressure.
- Some limited studies have been done to elucidate interrelationships between Canada yew and other components of the northern forests. The role of Canada yew in nutrient cycling and soil dynamics have received some attention but should be repeated in deciduous forest types. Spatially-dependent habitat relationships between understory vertebrates and Canada yew should also receive additional attention.
- Lastly, we believe enough information currently exists for various Canada yew life history characteristics to model the combined effects of forest dynamics, herbivore effects, and Canada yew patch dynamics on the persistence of Canada

yew at local scales. Such modeling efforts may yield valuable insights for conservation and management of this species.

9. ACKNOWLEDGEMENTS

We thank L. Nagel and J. Meeker for providing comments that improved an earlier draft of this manuscript. J. Meeker, D. Foster, S. Holmes, and C. Webster provided unpublished data. Partial support for this work was provided by the U.S. National Park Service and Michigan Technological University's Graduate School.

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Table 1. Climatic variables for Canada yew within its North American range as described by Little (1971). Temperature, precipitation, and growing degree days are from Thompson et al. (1999). Snowdepth data are from D. Kluver (unpubl. data) and are based on analysis of North American snow depth data from 1947-2001. See Kluver (2007) for more details on how the data were calculated.

Climate Variable	Minimum	Median	Maximum
Mean Annual Temperature (°C)	-5.1	2.6	13.0
Mean January Temperature (°C)	-24.2	-13.4	0.8
Mean July Temperature (°C)	9.8	17.4	24.6
Mean Annual Precipitation (mm)	550	960	1650
Mean January Precipitation (mm)	17	68	163
Mean July Precipitation (mm)	60	98	212
Growing Degree Days ^a	0.3	1.3	3.2
Average Dec. Snowdepth (cm)	0.0	21.8	49.0
Average Jan. Snowdepth (cm)	0.0	39.3	71.2
Average Feb. Snowdepth (cm)	0.0	50.6	90.2
Average Mar. Snowdepth (cm)	0.0	44.8	97.1
Average Dec.-Feb. Snowdepth (cm)	3.9	37.0	69.5
Average Nov.-Mar. Snowdepth (cm)	3.6	34.5	65.1
Average # Days ≥ 50cm Snowdepth	0	38	114

^a 5°C base X 1000; represents the total amount of energy available to the plant through the course of the year.

Table 2. Selected attributes and growth rates for Canada yew (*Taxus canadensis* Marsh.).

Character	Mean	Range	N	State/Province	Source
Stem Attributes					
Length (cm)	48	12-228	1172	MI	S. Windels, unpubl. data ¹
	na	5-326	262	WI	Foster (1993)
Height (cm)	35	10-157	1172	MI	S. Windels, unpubl. data ¹
	73	4-250	262	WI	Foster (1993)
Diameter (mm)	5.7	1.4-22.2	515	MI	S. Windels, unpubl. data ¹
	9.9	1.0-34.0	262	WI	Foster (1993)
Age (yr)	14	3-41	262	WI	Foster (1993)
	18	11-25	40	MI	Danz (1998)
	na	9-30	na	QUE	Senneville et al. (2001)
Growth Rates					
Twig length (cm/yr)	4.3	1.1-11.6	126	MI	S. Windels, unpubl. data ²
	3.4	0.6-10.5	429	MI	S. Windels, unpubl. data ³
	na	1-8	na	MA	Wilson et al. (1996)
Stem height (cm/yr)	~7.0	na	262	WI	Foster (1993)
	2.6	na	477	MI	S. Holmes, pers. comm. ⁴
Stem diameter (mm/yr)	~0.7	na	262	WI	Foster (1993)

¹Only stems >10cm in length were measured

²Terminal twigs

³Lateral twigs

⁴Transplanted cuttings protected in exclosures

Table 3. Selected effects of deer browsing on individual and population level parameters from Michigan and Wisconsin, USA. Source: 1 = S.Windels and D. Foster, unpubl. data; 2 = King (1970); 3= J. Meeker, unpubl. data; 4 = S. Holmes, C. Webster, and D. Flaspohler, unpubl. data

Character	Protected	Browsed	P-Value	# of Years	Source
Annual Mortality Rate (%) ^a	1.7	4.1	<0.001	9	1
	2.6 ^b	5.7	0.4	2	2
Annual Production Rate (ramets/m ² /yr)	0.056	0.004	<0.05	9	1
Horizontal Growth Rate (Δ % Cover/yr)	1.7	-4.0	<0.001	9	3
Stem height (cm/yr)	0.4	-0.9	<0.01	9	1
	2.5 ^c	-0.2	<0.001	4	4
Maximum Stem Height (cm) ^d	44.3	29.5	<0.05	9	1
	62.6	22.6	<0.001	9	3
Diameter Growth (mm/yr)	0.10	0.01	0.2	9	1
	0.20	0.21	0.8	1	2

^aCalculated as total no. stems died / total no. stems marked / no. years of study

^bAll stems were protected in exclosures; Protected = 0% clipped, Browsed = 25-75% clipped

^cTransplanted yew cuttings

^dMaximum stem height in each sample plot at the end of the experiment

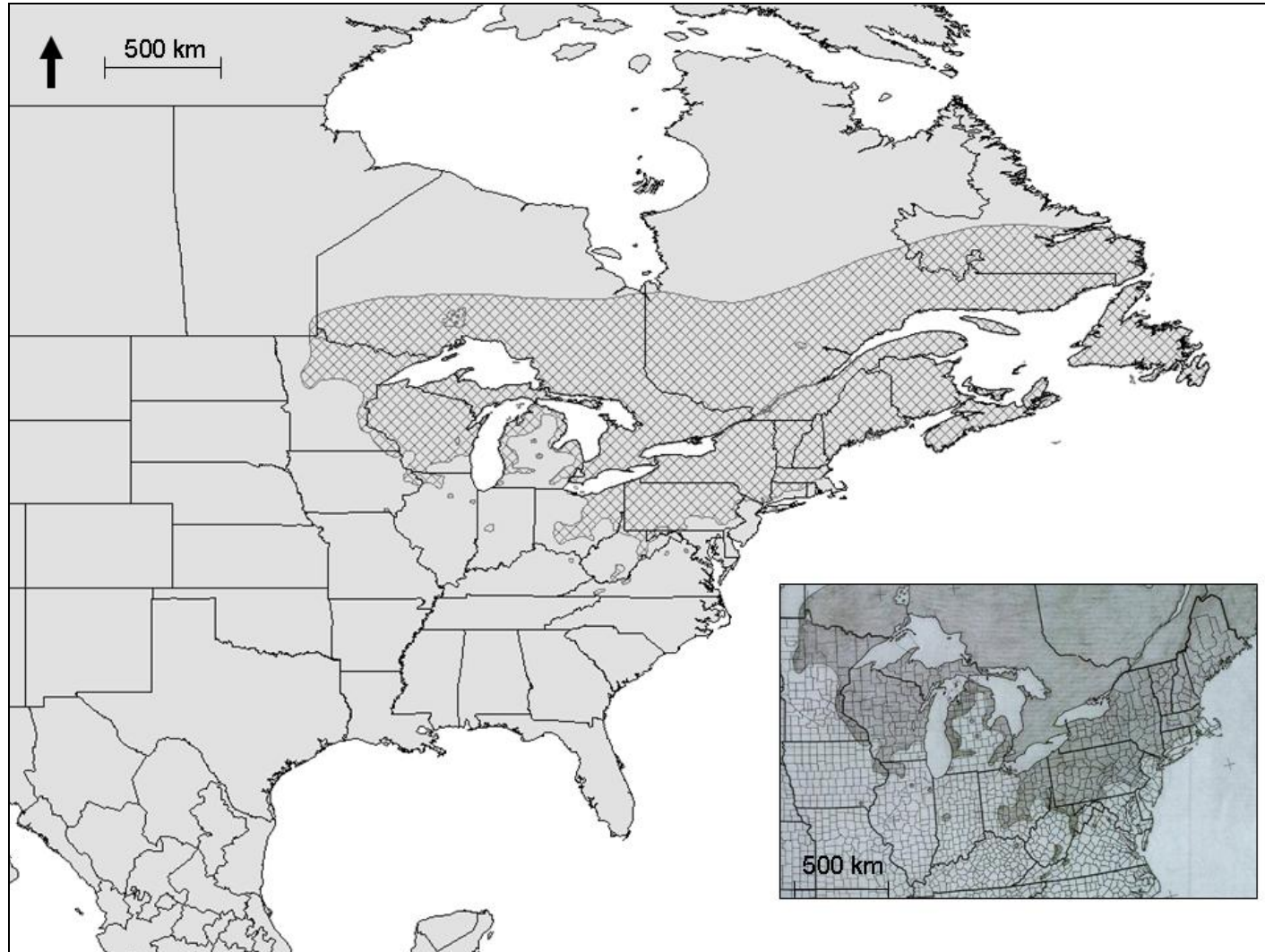
Figure Legends

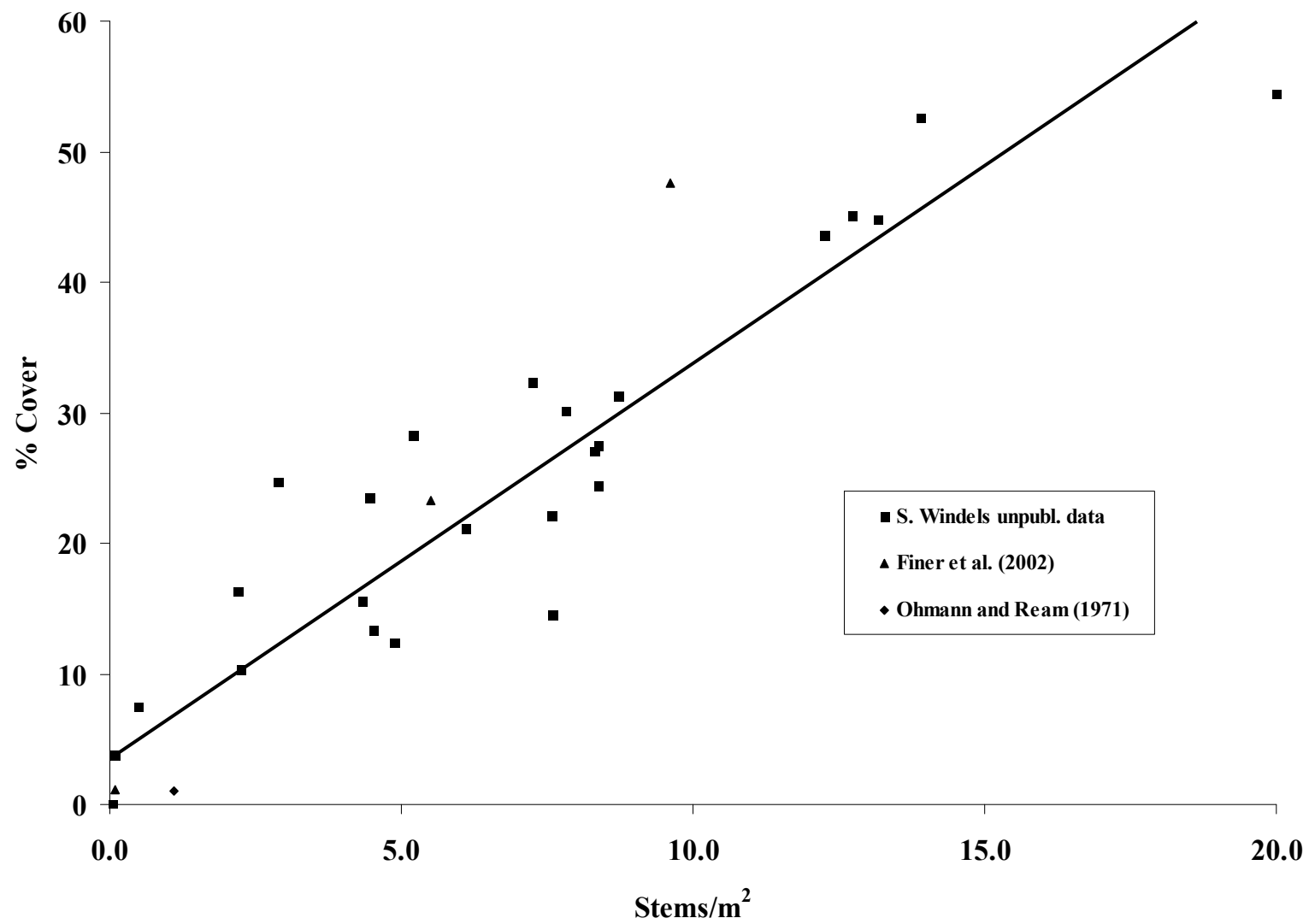
Figure 1. Distribution of Canada yew (*Taxus canadensis*) in North America. Inset details distribution across counties in the United States. Maps are derived from Little (1971).

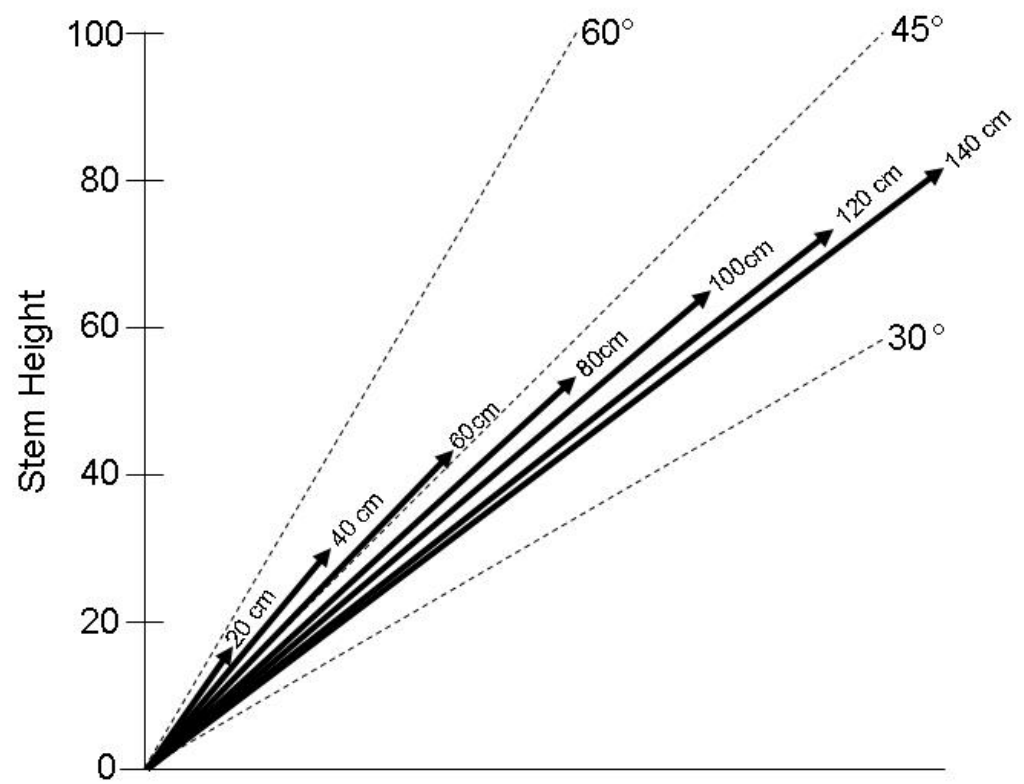
Figure 2. Relationship of stem density (stems/m²) to % cover for Canada yew in Michigan, Minnesota, and Quebec. $\% \text{ cover} = 4.6042 + 2.895 * (\text{Stems/m}^2)$ ($R^2 = 0.844$). Data from S. Windels, unpubl. data; Finer et al. 1999; and Ohmman and Ream 1971.

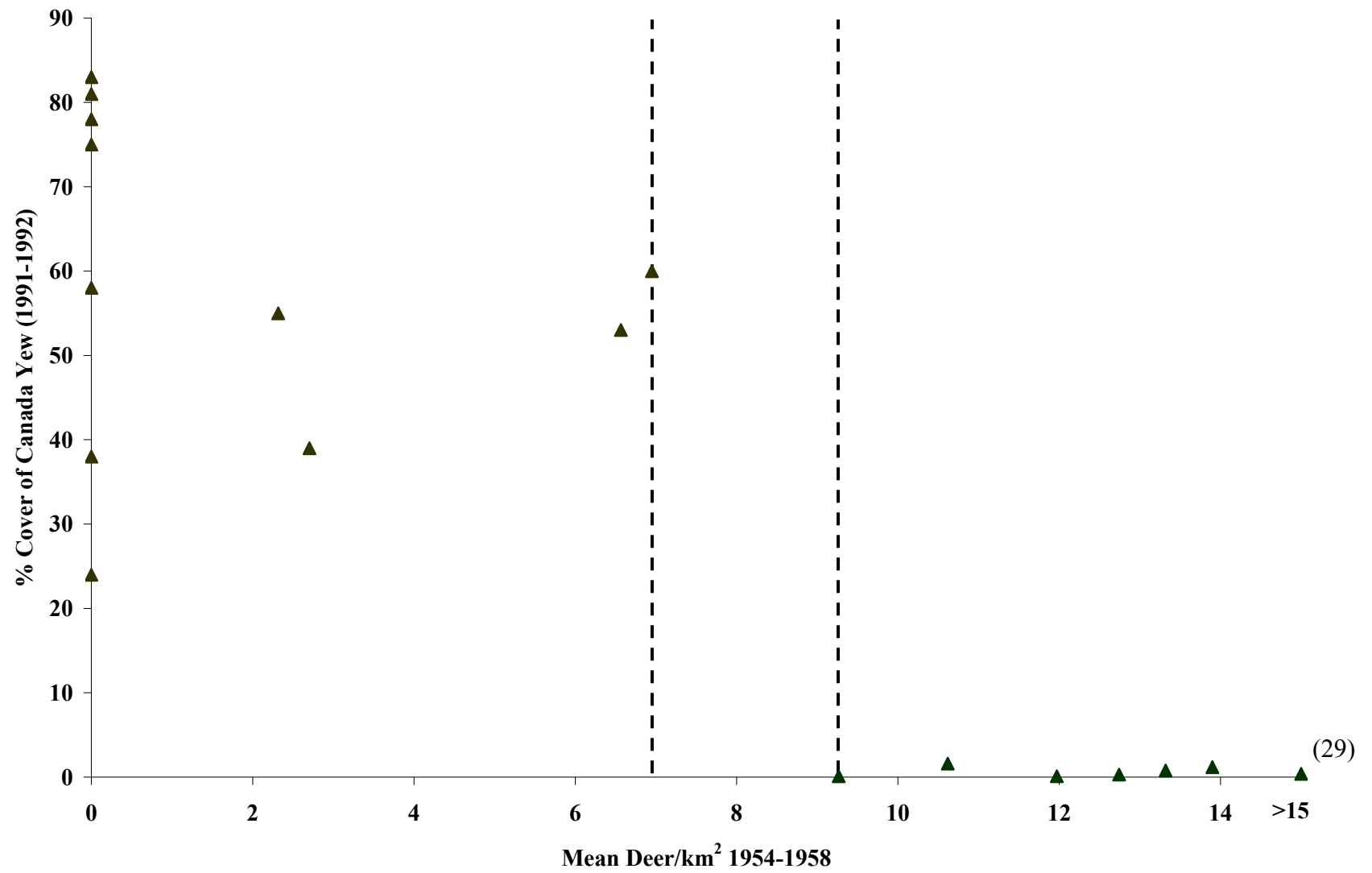
Figure 3. Expected stem height (cm above surface) for stems of various lengths based on the equation $\text{HEIGHT} = 1.4387 * \text{LENGTH}^{0.8274}$ ($R^2 = 0.996$, $N=1106$). Angle of stem growth is shown to illustrate that longer stems tend to be more prostrate.

Figure 4. Abundance of Canada yew on individual islands in the Apostle Islands (Wis.) as a function of white-tailed deer density during an irruption phase (1954-1958). Dashed lines suggest a threshold deer density above which Canada yew can be quickly extirpated. Deer density was estimated by multiplying hunter harvest (deer killed/km²) * 5 (Balgooyan and Waller 1995). Data adapted from Judziewisz and Koch (1993).









Appendix (Supplementary Materials)

Table A-1. References of Canada yew (*Taxus canadensis* Marsh.) frequency, abundance, and height in North America.

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Northeast NA	Conn., Mass., Mich, Minn., N.H., N.Y., Penn., Vt., Wis., Newf., Ont., Prince Edward Isl., Que.	LA	SM/B/H/YB/WP	General	<1935	na	na	"The Canada yew... [is] common throughout most of the region..." Tends to "form well-marked layer societies."	"Tall"	Nichols (1935)
Northeast NA	Mich, N.Y., Penn., Wis.	LA	SM/B/H/YB/WP	General	<1947	na	na	"Thus parts of WI, MI, PN, and NY accumulated heavy growths of ground hemlock."	na	Leopold (1947)
Northeast NA	Mich., N.B., Newf., Ont., Que.	B	WS/BF	General	1960-1965	31% (5/16 stands)	<1%	na	na	La Roi (1967)
Northeast NA	Mich., N.H., N.Y., Vt., Wis., Ont., Que.	LA	H	General	1972-1975	20% (14/71 stands)	13% (mean)	na	na	Rogers (1980)
Atlantic Canada	N.S.	B	RS/H	General	~late 1800s	na	na	"Before the arrival of white-tailed deer [late 1800's], the forest floor in mature spruce-hemlock stands was carpeted with Canada yew"	na	Telfair (2004)
Atlantic Canada	Newf.	B	BF/WS	General	1822	na	na	"...constitutes the chief underwood, as in forests of Canada and Nova Scotia"	na	Cormack (1928)
Atlantic Canada	Prince Edward. Isl.	LA	SM/B/H/YB/WP	General	1991	12% (145/1200 plots)	1-100%	na	na	Glen (1999)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Atlantic Canada	Que.	LA	SM/YB/HM	Saint Lawrence Valley	1940-1958	na	na	"patchy (locally dense)"	0.1-0.5m strata	Dansereau (1959)
Atlantic Canada	Que.	LA	H	Saint Lawrence Valley	1940-1958	na	na	"patchy (locally dense)"	0.5-1.0m strata	Dansereau (1959)
Atlantic Canada	Que.	LA	SM/B/H/YB/WP	Three Rivers (Trois Rivières)	1973	na	na	"dominant"	na	Lamoureux and Lacoursiere (1976)
Atlantic Canada	Que.	B	A/WB/BF/WS	Abitibi region	1990	na	na	"understory dominated by"	na	De Grandpre and Bergeron (1997)
Atlantic Canada	Que.	B	A/WB/BF/WS	Abitibi region	1990	na	1-57%	na	na	De Grandpre et al. (1993)
Atlantic Canada	Que.	LA	SM/B/H/YB/WP	Dushesnay	1999	na	25%	"...dominated" shrub layer with hobblebush and sugar maple	na	St.-Louis et al. (2004)
Atlantic Canada	Que.	B	BF/WS	Mingan Is.	2001	15% (12/80 plots)	21%	na	na	Viera (2003)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
New England	Conn.	CIA	H	Salisbury	1913	na	na	Canada yew is "abundant."	na	Nichols (1913)
New England	Mass.	CIA	SM/YB/WP	North Central Mass	<1935	na	na	"...is found in quantity."	na	Hosley and Ziebarth (1935)
New England	Mass.	CIA	SM/B/H/YB/WP	Berkshire Plateau	<1940	≤70% (stands)	33-100%	Canada yew is "very characteristic of the northern hardwood type of forest" and "common throughout the Area..."	45-75 cm	Egler (1940)
New England	N.H.	LA	SM/YB/B/H & WP/RM	Hanover	<1995	19% (37/200 plots)	na	"0.23-0.83 stems/m ² "	na	Stachowicz and Allison (1995)
New England	N.H.	LA	H	Strafford County	1998	50% (1/2 stands)	58%	"type composed primarily of Canada yew"	na	Howard and Lee (2002)
New England	N.Y.	LA	SM/B/H/YB/WP	Catskill Mountains	1960-1963	na	na	"Not Prevalent"	na	McIntosh (1972)
New England	N.Y.	LA	SM/B/H/YB/WP	Twin and Hunter Mountains	1960-1963	na	na	"Dense mats on north slopes"	na	McIntosh (1972)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
New England	Vt.	LA	SM/B/H/YB/WP	Green Mountains (< 550-730m asl)	1963-1965	12% (2/16 stands)	na	na	na	Siccama (1974)
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale	"Pre-settlement"	na	na	"...originally covered some 40,000 acres, about 1/3 of the main island"	na	McMurray in Krefting (1974)
Great Lakes	Mich.	LA	A/WB/BF/WS/SM	Isle Royale	"Pre-settlement"	56% (GLO lines)	na	na	na	Krefting (1974)
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale	1847-1848	67% (GLO lines)	na	"prevailing understory shrub"; "major ground cover"	na	Janke et al. (1978)
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale	<1905	na	na	"Everywhere abundant in the upland forest"	120-150 cm	Holt in Krefting (1974)
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale	1909-1910	na	na	"Most important species of all the understory vegetation"	na	Cooper (1928)
Great Lakes	Mich.	LA	A/WB/BF	Isle Royale	1945-1960	na	0.7-1.7%	"scraggly"	na	Hansen et al. (1973)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale - 1936 Burn	1967-1969	na	na	0.08 stems/m ² (0.5 stems/m ² > 30cm tall)	na	Hansen et al. (1973)
Great Lakes	Mich.	LA	A/WB/BF/WS	Isle Royale	1967-1969	na	na	0.22 - 1.11 m ² (0.14 - 0.86/m ² > 30cm tall)	na	Hansen et al. (1973)
Great Lakes	Mich.	LA	SM	Isle Royale	1967-1969	na	na	0.17/m ² (all > 30cm tall)	na	Hansen et al. (1973)
Great Lakes	Mich.	LA	WC	Isle Royale	1967-1969	na	na	0.17/m ² (all > 30cm tall)	na	Hansen et al. (1973)
Great Lakes	Mich.	LA	BF	Passage Island	1995	na	5-75%	forms "dense, impenetrable thicket"	na	Aerial Information Systems (2000)
Great Lakes	Mich.	LA	WC	Delta County deer yards	1846-1850	33-76% (GLO line naratives)	na	na	na	Van Deelen et al. (1996)
Great Lakes	Mich.	LA	SM/B/H/YB/WP	Upper Peninsula	"early studies"	na	na	"abundant"	na	Stearns (1951)
Great Lakes	Mich.	LA	SM/B/H/YB/WP	Huron Mountain Club	1912	na	na	"Plentiful throughout"	na	Dodge (1918)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Great Lakes	cf. Mich.	LA	SM/YB/WP	Espinore Island	<1939	na	na	"...tangle of ground hemlock through a long deerless period."	na	Leopold (1947)
Great Lakes	Mich.	LA	A/WB/BF	Passage Island	1945-1960	na	28.5-32.4%	"...thrives on Passage Island..."	na	Hansen et al. (1973)
Great Lakes	Mich.	LA	A/WB/BF	Manitou Island	1952	na	na	"...forms a dense impenetrable ground cover..."	na	Richards (1952)
Great Lakes	Mich.	LA	SM/B/H/YB/WP	Upper Peninsula	1952	na	na	"Ground hemlock is dominant in the shrub layer in many places, and in these areas the forest lacks the continuous layer of small saplings which is usually a conspicuous figure."	na	Richards (1952)
Great Lakes	Mich.	LA	SM/YB/WP	Garden Is.	1967-1968	48% (33/69 plots)	na	"abundant"; 210-272kg/ha available browse	na	King (1970)
Great Lakes	Mich.	LA	SM	South Fox Is	1967-1968	na	na	"abundant"; 1075kg/ha available browse	na	King (1970)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Great Lakes	Mich.	LA	SM/B/H/YB/WP	Marquette and Alger Counties	2001-2002	na	1-54%	na	0.5-1.5m	S. Windels, unpubl. data
Great Lakes	Minn.	LA	BW/BF/BA	Red Lake	1948-1952	100% (within stand plots)	64%	"...very dense..."	≤1m	Buell and Bormann (1955)
Great Lakes	Minn.	LA	A/WB/BF	Lake Itasca area	1950	20% (1/5 stands)	12%	na	na	Beuell and Niering (1957)
Great Lakes	Minn.	LA	WC	BWCA (Virgin Forests)	<1971	56% (5/9 stands)	na	Average stem density ≈1/m ²	na	Ohmann and Ream (1971)
Great Lakes	Wis.	LA	SM/B/H/YB/WP	Apostle Islands	"Pre-settlement"	na	na	"Canada yew was the dominant shrub on many, if not all islands..."	na	Judziwicz and Koch (1993)
Great Lakes	Wis.	LA	SM/YB/WP	General	<1950	na	na	"formerly plentiful" or "dominant"	na	Braun (1950)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Great Lakes	Wis.	LA	SM/YB/WP	Apostle Islands	1956-1957	na	na	"...grows in almost impenetrable thickets and occasionally reaches a height of over 8 feet. The general aspect of yew in these stands is that of a dense tangle of stems."	≤240cm	Beals et al. (1960)
Great Lakes	Wis.	LA/CIA	SM/YB/WP	General	<1959	27% (7/27 stands)	na	"characteristic shrub"	na	Curtis (1959)
Great Lakes	Wis.	LA	SM/YB/WP	Apostle Islands	1990-1992	na	1-83%	Yew "dominant" and/or "dense" on 11 of 22 islands	na	Judziwicz and Koch (1993)
Great Lakes	Wis.	LA	SM/YB/WP	General	1991	na	≤60%	na	na	Foster (1993)
Great Lakes	Wis.	LA	H	General	1991	na	≤40%	na	na	Foster (1993)
Great Lakes	Wis.	LA	WC	General	1991	na	≤30%	na	na	Foster (1993)
Great Lakes	Ont.	B	SM/B/H/YB/WP	Stockley Forest (Sault Saint Marie)	1997-1999	na	1.2 - 21.1%	"unusually high density"	na	Holmes and Pitt (2007)

Table A-1. (cont.)

Region	State/Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Year of Observation	Frequency	% Cover	Description of Abundance	Description of Height	Reference
Midwest	IN	CIA	H/WP	Pine Hills Region	<1934	1-100% (within stand plots)	na	"Dense" on steep, north slopes	na	Friesner and Potzger (1934)
Midwest	OH	CIA	WC	Champaign County	1970s	9% (within stand plots)	na	"third most important understory shrub"	na	Collins et al. (1979)

¹North American Ecological Division (Coomer et al. 2003): B = Boreal Forest; CIA = Central Interior-Appalachian Forest; LA = Laurentian-Acadian Forest

²Dominant tree species: A = aspen (*Populus* spp.), B = American beech (*Fagus grandiflora*), BF = balsam fir (*Abies balsamea*), H = eastern hemlock (*Tsuga canadensis*), RS = red spruce (*Picea rubens*), SM = sugar maple (*Acer saccharum*), WB = white birch (*Betula papyrifera*), WC = white cedar (*Thuja occidentalis*), WP = white pine (*Pinus strobus*), YB = yellow birch (*Betula lutea*)

³Denotes whether reference was to the state/province generally or for a specific site (e.g., mountain range, county, island, etc)

Table A-2. Examples where local extirpation or reduction in abundance of Canada yew was linked to overbrowsing by wild cervids in North America.

Species	Region	State / Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Island?	Year of Observation	Browsing Effect	Description of Effect	Reference
Deer	Northeast U.S.	Mich, N.Y., Penn., Wis.	LA	SM/B/H/YB/WP	General	No	<1947	Functional extirpation / reduced abundance	"Thus parts of Wisconsin, Michigan, Pennsylvania, and New York accumulated heavy growths of ground hemlock...These growths are largely extirpated by the irrupting deer."	Leopold et al. (1947)
Deer	Atlantic Canada	N.S.	B	RS/H	General	Yes	1940s	Functional extirpation	"Before the arrival of white-tailed deer [late 1800's], the forest floor in mature spruce-hemlock stands was carpeted with Canada yew...and by the 1940s it had been eliminated from the forest."	Telfair (2004)
Deer	Atlantic Canada	Que.	Boreal	BF/WS	Anticosti Is.	Yes	2001	Functional extirpation	"Species such as <i>Taxus canadensis</i> ...have been extirpated or severely reduced on Anticosti."	Viera (2003)
Deer	New England	N.Y.	LA	SM/B/H/YB/WP	Catskill Mountains	No	1960-1963	Functional extirpation	"Yew, which is common understory shrub in some areas of northern hardwoods forests, is not prevalent in the Catskills, although there are dense mats of it on the north side of Twin and Hunter Mountains. A favorite deer food, it may be much reduced as it is in similar forests in Wisconsin."	McIntosh (1972)
Deer	Appalachian Mtns	W.V.	CIA	na	Upper elevations of Monongahela Natl. Forest	No	<1992	Functional extirpation	"...Yew, a northern evergreen shrub which was once common at high elevations but has been virtually extirpated by deer browsing."	Mueller (1992)

Table A-2. (cont.)

Species	Region	State / Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Island?	Year of Observation	Browsing Effect	Description of Effect	Reference
Deer	Great Lakes	Mich.	LA	SM/B/H/YB/WP	Huron Mountains	No	<1938	Functional extirpation	"... the absence of yew, or ground hemlock, except on cliffs and inaccessible rocks..."	Leopold (1938)
Deer	Great Lakes	Mich.	LA	SM/B/H/YB/WP	Upper Peninsula	No	1952	Reduced abundance	"Ground hemlock is not as abundant as it formerly was, since in many areas it has been destroyed as a results of being severely browsed by deer."	Richards (1952)
Deer	Great Lakes	cf. Mich.	LA	SM/YB/WP	Espinore Is.	Yes	<1939	Functional extirpation	Espinore Island had a "tangle of ground hemlock through a long deerless period...In about 1941 deer from the irrupting mainland occupied the island...by 1945 it was mostly dead, and by 1946 it was all dead."	Leopold et al. (1947)
Deer	Great Lakes	Mich.	LA	H	Porcupine Mountains	No	<1950	Functional extirpation	"ground hemlock was one of the principal species of the hemlock forest [in the Porcupine Mountains]...., but has since been almost eliminated by deer."	Braun (1950)
Deer	Great Lakes	Mich.	LA	SM/B/H/YB/WP	Sylvania Wilderness	No	<1996	Functional extirpation	"Deer have almost eliminated yew...from the understory."	Davis et al. (1996)
Deer	Great Lakes	Mich., Minn., Wis.	LA	SM/B/H/YB/WP	General	No	<1950	Reduced abundance	"Taxus was formerly plentiful in many areas where it is now poorly represented. It is severely browsed by deer, which are over-plentiful in many of the northern forests."	Braun (1950)

Table A-2. (cont.)

Species	Region	State / Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Island?	Year of Observation	Browsing Effect	Description of Effect	Reference
Deer	Great Lakes	Mich., Wis.	LA	SM/B/H/YB/WP	General	No	<1996	Extirpation	"Canada yew, an understory shrub once common in the northern forests is now locally extinct in areas of high deer use."	Van Deelen et al. (1996)
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	Forest County	No	1932-1950	Functional extirpation	Large patches yew disappeared from Laona stand between 1932 and time of revisit (<1951); not observed in any stands despite specific searching for it. "The apparent explanation is that yew...has been almost completely eliminated in the areas where winter pressure is heavy."	Stearns (1951)
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	Basswood, Bear , Hermit, Madeline, Manitou, and South Twin Islands	Yes	1940s- 1950s	Functional extirpation	na	Judziewicz and Koch (1993)
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	Otter Is.	Yes	1940s- 1950s	Reduced abundance	"...Canada yew, while common, is seldom tall enough to impede hiking, perhaps because past deer populations were moderate..."	Judziewicz and Koch (1993)
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	Stockton Is.	Yes	1940-1960	Functional extirpation	"Canada yew was reported as common and extramely dense on...Presque Isle Point in 1940" but moderate deer outbreak "apparently reduced yew to its present negligible importance."	Judziewicz and Koch (1993)

Table A-2. (cont.)

Species	Region	State / Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Island?	Year of Observation	Browsing Effect	Description of Effect	Reference
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	Rocky Is.	Yes	1946-1954	Functional extirpation	"1955 photographs of the island show dense but completely dead thickets of yew. Deer were hunted and starved to extirpation by the late 1960's.	Judziewicz and Koch (1993)
Deer	Great Lakes	Wis.	LA	SM/B/H/YB/WP	General	No	<1959	Reduced abundance	"...Canada yew... is another characteristic shrub of the northern forests which is now more rare than formerly, due to the heavy browsing pressure of deer since the herds began to build up in the 1930's."	Curtis (1959)
Deer	Great Lakes	Wis.	LA	WC	Delta County deer yards	No	1990s	Functional extirpation	"Canada yew, a highly preferred browse species...has probably been extirpated."	Van Deelen et al. (1996)
Deer	Great Lakes	Wis.	LA	SM/B/BW	S. Wis.	No	<1995	Extirpation	"[Deer] numbers are so great that browse impacts are readily observed by the elimination of some plant species (e.g., orchids and Canada yew)."	Kotar and Matthiae (1995)
Moose	Atlantic Canada	Newf.	B	BF/WS	General	Yes	<1953	Functional extirpation / reduced abundance	"In 1953, [Canada yew} was still common in a number of areas in Newfoundland where the density of moose was low. However, in other parts of the island where moose populations were high it had become very rare."	Pimlott (1963)

Table A-2. (cont.)

Species	Region	State / Province	Forest Division ¹	Dominant Tree Species ²	General or Specific Site? ³	Island?	Year of Observation	Browsing Effect?	Description of Effect	Reference
Moose	Atlantic Canada	Newf.	B	BF/WS	General	Yes	<1968	Functional extirpation	"Yew...is the preferred coniferous browse of moose but it soon disappears in accessible sites soon after moose densities build up following logging."	Bergerud and Manuel (1968)
Moose	Atlantic Canada	Newf.	B	BF/WS	Gros Morne National Park	Yes	1977-1996	Functional extirpation / reduced abundance	"Overall, availability of Canada yew decreased from 6.8% of available forage in 1977 to 0.1% in 1996 and was eradicated on 2 sites"	Connor et al. (2000)
Moose	Great Lakes	Mich.	LA	WS/BF/A & SM/YB	Isle Royale	Yes	1930's	Functional extirpation	"Ground hemlock...has been practically exhausted. Today nothing remains of this spreading shrub except dead branches and a few leaves near the roots."	Murie (1934)
Woodland caribou	Great Lakes	Ont.	B	WB/BF	Slate Islands	Yes	1974-1985	Functional extirpation	"98% gone"; "functionally extirpated"	Bergerud et al. (2007)

¹North American Ecological Division (Coomer et al. 2003): B = Boreal Forest; CIA = Central Interior-Appalachian Forest; LA = Laurentian-Acadian Forest

²Dominant tree species: A = aspen (*Populus* spp.), B = American beech (*Fagus grandiflora*), BF = balsam fir (*Abies balsamea*), Basswood (*Tilia americana*), H = eastern hemlock (*Tsuga canadensis*), RS = red spruce (*Picea rubens*), SM = sugar maple (*Acer saccharum*), WB = white birch (*Betula papyrifera*), WC = white cedar (*Thuja occidentalis*), WP = white pine (*Pinus strobus*), YB = yellow birch (*Betula lutea*)

³Denotes whether reference was to the state/province generally or for a specific site (e.g., mountain range, county, island, etc)

Chapter 2:

Scale Dependent Browsing Patterns on Canada Yew (*Taxus canadensis*)

by White-Tailed Deer (*Odocoileus virginianus*)

This chapter is written according to the style of:

Biological Conservation

Abstract:

Canada yew (*Taxus canadensis*) is a clonal shrub that often forms discrete patches and is considered to have been an important component of forest understories in much of northeastern North America. Following Euro-American settlement, Canada yew has been locally extirpated or greatly reduced in abundance throughout many parts of its former range, particularly in the United States. Winter browsing by white-tailed deer (*Odocoileus virginianus*) has been implicated as responsible for much of its decline. However, little is known about the factors affecting deer browsing intensity on Canada yew, particularly in areas where Canada yew is still relatively abundant. We examined factors related to browsing intensity on Canada yew across various spatial scales in 29 northern and mixed hardwood forest stands in Michigan's Upper Peninsula. Intensity of browsing on stems was related principally to two factors acting simultaneously across multiple spatial scales. Intensity of browsing was negatively related to amount of Canada yew at the scale of the forest stand and negatively related to distance from the edge of Canada yew patches, effectively creating refugia from browsing. Amount of tree canopy cover, slope, aspect, and individual stem length explained only a small portion of variation in browsing intensity. The browsing patterns we observed also suggest that yew exists in two alternate stable states: 1) as loose aggregations of small stems or 2) large, dense patches of large stems. The implications of changes in deer density or winter snow cover to the probability of local persistence of Canada yew are discussed.

1. INTRODUCTION

It is well accepted that large mammalian herbivores make foraging decisions based on interactions with resources across several spatial scales (Senft et al. 1987, Bergman et al. 2005, Månsson et al. 2007). The collective result of foraging decisions made by herbivores at the individual or population level can ultimately influence plant populations, plant community structure, and ecosystem processes (e.g., Pastor et al. 1993, 1998; Waller and Alverson 1997; Månsson et al. 2007). Therefore, it is important to understand patterns in ungulate foraging at multiple spatial scales to allow management and conservation efforts to be scaled appropriately (Bailey et al. 1996, Senft et al. 1997).

Canada yew (*Taxus canadensis*), also known as ground hemlock or American yew, is a monoecious, evergreen shrub native to the mixed conifer-hardwood forests of the northeastern United States and southeastern Canada (Martell 1974). Canada yew reproduces predominantly by layering whereby arching lateral branches are pressed to the ground and take root, resulting in a spreading growth form that often produces roughly circular-shaped patches comprised of dense tangles of intertwining stems; this patchy growth form is especially evident in high-density areas with large individual stems (Allison 1990a). Prior to Euro-American settlement, it was likely a major ground cover component in late-successional mesic forests of this region (Braun 1950, Martell 1974, Foster 1993). Canada yew has been extirpated or its abundance significantly reduced from most of its range in the U.S. Several factors are often implicated in this decline, including the conversion of mid- to late-successional mesic forest habitats to agriculture and short-rotation forestry, intense

slash fires following the logging of primary forests, and the subsequent increases in white-tailed deer (*Odocoileus virginianus*) populations following these large-scale disturbances (Leopold et al. 1947, Allison 1990a, Foster 1993, Stachowicz and Allison 1995). High deer populations throughout the latter half of the 20th century are speculated to have further reduced Canada yew abundance and range (Alverson and Waller 1997). Nearly contiguous patches of >1 ha remain in core areas of Canada yew's range, including on Great Lakes islands lacking deer and along the southern shore of Lake Superior from which deer typically emigrate in winter due to heavy lake-effect snowfall (Verme 1973). Other large but often isolated populations of Canada yew still remain in other parts of its range in the U.S.

Taxus spp. are generally toxic to grazers such as domestic cattle, sheep, and horses (Mysterud and Østbye 2004). However, several members of the genus *Taxus* are listed as a highly preferred winter browse plant for browsing ungulates such as white-tailed deer (Leopold et al. 1947, Beals et al. 1960), moose (*Alces alces*; Pimlott 1963), elk (*Cervus elaphus*; Parks et al. 1988), and roe deer (*Capreolus capreolus*; Mysterud and Østbye 1995). As a result, many of these species of browsers have been documented to seriously impact populations of *Taxus*. English yew (*T. baccata*) is extremely sensitive to bark-stripping and browsing by high densities of introduced Sika deer (*Cervus nippon*) in Ireland (Mitchell 1988). Recruitment of English yew in Norway is negatively related to roe deer abundance (Mysterud and Østbye 2004). Mule deer (*O. hemionus*) and elk caused severe stem mortality and decreased reproductive output in a population of Pacific yew (*T. brevifolia*) (Parks et al. 1998). Moose colonized Isle Royale in Lake Superior in 1908 and quickly reduced Canada

yew on the main island from the dominant ground cover to isolated, heavily browsed stems (Snyder and Janke 1976); dense, nearly impassable populations of Canada yew remain on nearby Passage Island where moose have never established.

White-tailed deer densities are currently at least 2-4 times greater in the Great Lakes states than the time of European settlement and their impacts on the region's forests have been well studied (e.g., Beals et al. 1960, Frelich and Lorimer 1985, Alverson et al. 1988, Alverson and Waller 1997, Augustine and Frelich 1998). Wisconsin's Apostle Islands in Lake Superior illustrate the effect of deer presence and abundance on the persistence and vigor of Canada yew populations. Where deer populations had been long-established, such as on Madeline and Oak Islands, Canada yew became rare (Beals et al. 1960, Judziewicz and Koch 1993). On Rocky, Devils, Sand, North Twin, and Raspberry Islands, where deer never became established, Canada yew remains the dominant ground cover with some stems reaching nearly 3 m in height (Judziewicz and Koch 1993). Beals et al. (1960) reported that browsing on Canada yew tended to decrease with increasing Canada yew abundance when compared across islands in the archipelago.

Canada yew is considered one of the most highly preferred winter forage items for white-tailed deer (Leopold et al. 1947, Beals et al. 1960). Its high preference is thought to be a result of low chemical defense against native herbivores and relatively high digestibility (King 1970). Anecdotally, deer appear to concentrate browsing around the edges of large patches of Canada yew in the Great Lakes region (S. Windels, pers. obs.; J. Meeker, Northland College, pers. comm.). Canada yew is presumed to be consumed mainly in the late fall/early winter period or late spring

when stems are typically not covered by snow (J. Ozoga, Munising, MI, pers. comm.; King 1970). However, browsing during later portions of winter can occur when stems are accessible, either during periods of low snow cover or on those stems sticking above the snow pack (S. Windels, pers. obs.; King 1970). Deer have also been observed pawing through the snow to reach Canada yew stems (S. Windels, pers. obs.; King 1970).

As of 2007, Canada yew was or has been considered “vulnerable”, “imperiled”, or “critically imperiled” in 12 states and 1 Canadian province in Eastern North America (NaturServ 2007). It is also a Regional Forester Sensitive Species in five National Forests in the eastern U.S. (US Forest Service 2007). Although most populations of Canada yew in core parts of its range in Ontario, Quebec, and other eastern provinces have heretofore not been subjected to high ungulate browsing pressure, white-tailed deer populations are generally increasing across southern Canada as a result of mild winters and declining hunting (Patterson and Power 2002). Persistence of Canada yew in Canada and elsewhere may also be threatened by the largely unregulated harvest of Canada yew stems for extraction of paclitaxel and other anti-cancer compounds found in the genus *Taxus* (Senneville et al. 2001).

Despite many anecdotal accounts, little is known about browsing patterns by white-tailed deer on Canada yew in the Great Lakes region, an historically important portion of Canada yew’s range. Specifically, it is unknown what stem, patch, and stand-level factors affect browsing intensity on Canada yew. Here, we attempt to identify scale-dependent factors influencing browsing by deer on Canada yew. This

information is needed to assist in the conservation and management of Canada yew in areas of its range that overlap with white-tailed deer.

2. METHODS

2.1 Study Area

This study was conducted in Marquette and Alger Counties, Michigan, USA (Figure 1). Vegetation is predominantly upland forest dominated by the deciduous sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and American beech (*Fagus americana*) but also contains patches of codominant eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and white spruce (*Picea glauca*). Climate is greatly moderated by Lake Superior, with cool summers and mild winters with heavy snowfall. Average (1949-2001) winter snowfall (November-April) in the study area is 353 cm and average maximum snow depth, typically reached between mid-February to Mid-March, is 114 cm (National Weather Service Marquette, MI Weather Forecast Office 2006). Total winter snowfall and maximum snow depth were ~10% below average in 1998-1999 and 1999-2000 and >25% above average in 2000-2001 and 2001-2002 (National Weather Service Marquette, MI Weather Forecast Office 2006). Winter deer densities in the study area are very low ($< 2/\text{km}^2$); under normal snow conditions most deer migrate out of the study area to traditional winter deer yards outside of the Lake Superior Watershed (T. Minzey, Michigan Department of Natural Resources, pers. comm., Potvin et al. 2005). Snowshoe hare densities are relatively low and moose are rare in the study area (J. Belant, National Park Service, pers. comm.).

Twenty-nine (29) mesic northern/mixed hardwood forest stands on moderately to well-drained sandy or sandy loam soil were selected for study (Figure 1). A stand was defined as having a relatively uniform vegetation composition and stand history as determined from a combination of aerial photos, topographic maps, stand compartment maps, and ground-truthing. Stands were selected primarily to represent the range of Canada yew ground cover in the region: low (1-15% ground cover), medium (15-30%), and high (>30%). Stands were also limited to those >70% tree canopy cover. Fifteen of the stands were sampled in 2001 and the remaining 14 in 2002. Twenty-three of these stands were managed for sawtimber at the time of sampling, i.e., selection harvest to reduce tree basal area to approximately 16m²/ha every 10-15 years (M. Wilk, Shelter Bay Forests, pers. comm.); the remaining six were within protected areas free of timber harvest for at least 30 years (B. Leutscher, Pictured Rocks National Lakeshore, pers. comm.; K. Doran, Hiawatha National Forest, pers. comm.).

Within each stand, sampling stations were systematically established along equally spaced transects to ensure uniform coverage of the site (Figure 2). Stations were spaced >175m from each other and >100m from roads and site boundaries to minimize edge effects. The number of stations varied from 8 to 18, depending on the area and shape of the stand.

2.2 Vegetation Measurements

Because Canada yew reproduces vegetatively and below-ground connections between ramets (stems) deteriorate after a few years, it is extremely difficult to delineate genets (genetic individuals). Therefore, the ramet was selected as the basic

sampling unit and defined as an emergent stem not connected to neighboring stems at a soil depth of 2cm (Allison and Stachowicz 1995). A nearest neighbor method was used to collect data on five Canada yew ramets at each station. Starting at the center of the sampling station, the nearest stem was selected and the following measurements taken on each: distance from start point to stem; total stem length (from 2cm above soil to terminal leader); maximum stem height perpendicular to the ground; whether the stem was broken; and whether the stem was live or dead. Each live stem was also scored based on a visual assessment of the proportion of annual growth browsed by deer during any of the three previous winters from the time of sampling (1= <5% twigs browsed, 2= 6-25%, 3= 26-50%, 4= 51-75%, 5= 76-95%, 6= >95%). This scoring system was used for two reasons: 1) consistently differentiating browsing evidence between the most recent winter and previous winters can be problematic for Canada yew (King 1970), and 2) by using a composite measure of browsing over three consecutive winters we compensated for any annual differences in winter deer use a site may have received, i.e., we assume that each site should have received an approximately equal amount of deer use over the three years combined. Although winter browsing by snowshoe hares on Canada yew is relatively rare in the Great Lakes region (King 1970), the roughly crushed stems from deer browsing are easily differentiated from the clean, angular bite characteristic of snowshoe hares.

For each cluster of sampled stems, slope, aspect, and whether or not they were part of a Canada yew patch (>1m diameter cluster of stems at a density greater than $\approx 15/\text{m}^2$) was recorded. Distance (m) to the nearest patch edge was recorded for stems within patches. Sampling stations where Canada yew stems were not recorded were

omitted from analysis leaving 24 stands with at least one sampling station where Canada yew was detected. Analyses were further limited to those clusters containing at least 3 live stems. Means for each of these clusters were determined for stem length and browsing score.

Tree species and number within eight diameter at breast height (dbh) classes (≥ 3 cm dbh) were recorded within a 0.02ha plot at each station to estimate basal area. Canopy cover of deciduous and coniferous trees was estimated with an ocular tube at 21 points along a transect bisecting the station. Canopy cover at each station was then designated as deciduous ($< 25\%$ canopy coverage by conifers) or mixed ($\geq 25\%$).

Areal coverage of Canada yew within each stand was estimated from a uniform grid of 11-m radius plots spaced along and in between vegetation station sampling transects such that each stand had a sampling station:11-m plot ratio of $\sim 1:3$. Cover of Canada yew within 11m plots was visually estimated to the nearest 1% and mean percent cover within each stand was calculated.

2.3 Deer Pellet Counts

To test whether stands received similar browsing pressure, in May 2002, 3-m radius plots were systematically located throughout each stand (range = 22-83) and the number of white-tailed deer pellet-groups deposited that winter were counted in each plot. Pellet-groups deposited in winter can be easily differentiated in spring from those deposited during the previous summer or winter periods (i.e., pellets > 7 months old), and the number of pellet-groups/400m² sampled can be used as a relative index of local winter deer abundance (Potvin et al. 2005). Based on various

reported defecation rates, Potvin et al. (2005) estimated that 6.75 pellet-groups/400m² sampled was equivalent to 2.3-5.8 deer/km².

2.4 Statistical Analysis

Our study is an observational one and is therefore best suited for analysis with an information-theoretic approach to model selection (Burnham and Anderson 2002). We developed nine *a priori* models composed of independent variables that might influence browsing intensity based on a literature review, personal observations, and pilot data from September 2000 from a separate study area >200 km distant. Models incorporated three spatial scales of browse selection: a) at the scale of clusters of individual stems (<0.001ha), b) at an intermediate scale that incorporates spatial heterogeneity in vegetation characteristics within each stand (~0.01-0.1ha), and c) at the scale of individual stands (20-50ha).

Models 1-4 (Table – Models) focused on two variables at the smallest scale, and included combinations of mean stem length (LENGTH) and patch location (LOC). Stem length is related to both apparency to herbivores (e.g., taller stems are more likely to be seen, easier to access, and remain above snow pack) and biomass (King 1970). White-tailed deer may be reluctant to enter dense patches of Canada yew because of increased travel costs (Parker et al. 1994, Forester et al. 2007). Further, severity of browsing on Canada yew may be either positively or negatively related to the amount of conspecific browse biomass available nearby (Frid and Turkington 2001). To simplify interpretation of the models, clusters of stems were placed into one of three patch location categories for analysis: “No Patch” (stems not in a defined patch); “Edge” (<1m from edge of defined patch); and “Interior” (>1m from edge of

defined patch). We justified grouping clusters into the “interior” category after univariate plots suggested that the effect of distance from patch edge on browsing intensity was relatively uniform for values from >1m from the edge (range =1-25m).

Models 5-8 focused on three intermediate-scale habitat variables that may affect browsing intensity on stems: slope/aspect (SLOPE), percent canopy cover (CANOPY), and proportion of canopy comprised of conifer species (CONIFER). These variables may affect browsing by: 1) reducing snow cover (e.g., north facing slopes generally retain more snow than south-facing slopes, and conifer-dominated canopies intercept more snow than deciduous-dominated canopies), or 2) changing the amount of photosynthetically-active radiation reaching the understory and therefore affecting nutritional quality of browse (e.g., greater canopy cover is negatively related to amount of sunlight and carbon content in browse, and north-facing slopes receive less sunlight than south-facing slopes). Stachowicz and Allison (1995) documented higher browsing rates on Canada yew stems on south-facing slopes and under deciduous canopies. Model 9 evaluated the influence of the total amount of Canada yew browse available within a stand, i.e., percent Canada yew cover (YEWCOV), on browsing intensity of individual clusters. Amount of Canada yew at the scale of a deer’s home range (or portion thereof) could affect selectivity of browsing by deer (e.g., Vivas and Saether 1987). Further, there may be a dilution effect in that for a given number of deer, browsing (or probability of browsing) is spread over a greater number of stems as amount of Canada yew increases (Frid and Turkington 2001). A global model containing all of the variables and selected interactions was also included in the model set (Burnham and Anderson 2002).

Each of the nine models was fit to mean cumulative browsing score for each cluster using a generalized linear model with a normal distribution (PROC GENMOD) using SAS 9.1 (SAS Institute, Cary, North Carolina). We used the generalized estimating equations method in GENMOD because it allowed us to account for the non-independence of clusters of stems within a stand, i.e., that clusters within a stand were more likely browsed by the same individual deer than for clusters between stands. Log-likelihood estimates generated by GENMOD for each model were used to calculate Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). To account for overdispersion in the data, the quasi-likelihood AIC (QAIC) was used, derived by dividing AIC by an approximated variance inflation factor ($\hat{c}$; the X^2 statistic divided by the degrees of freedom of the global model). We also used the small sample size adjustment, QAIC_c, due to an n/K ratio <40 (Burnham and Anderson 2002). The model(s) with the smallest QAIC_c value are considered the most parsimonious. We then calculated ΔQAIC_c (the difference between QAIC_c of each model and the best model) and QAIC_c weights (weight of evidence calculated by rescaling ΔQAIC_c scores such that all weights add to 1). Models with $\Delta\text{QAIC}_c < 2.0$ are considered equally plausible given the data (Burnham and Anderson 2002). Variable importance weights were calculated according to Burnham and Anderson (2002).

3. RESULTS

A total of 237 Canada yew stem clusters were sampled in 24 stands. Two-hundred-sixteen (216) clusters had at least 3 live stems, and of these, 208 clusters were included in the model selection analysis due to missing data. Cover of Canada yew (from 11-m radius plots) at the 24 stands ranged from 0.0 to 54.4%; Browsing score ranged from 1.4 to 6.0 (Table 1).

Browsing intensity, as measured by mean cumulative browsing score, tended to decrease as stem length, percent canopy cover, amount of conifer in canopy, and percent Canada yew cover increased (Figure 3). Browsing intensity was greatest for stems not in discrete patches and least for stems >1m from the edge of patches (Figure 3). Browsing intensity appeared similar between slope/aspect categories (Figure 3).

Dead Canada yew stems were unevenly distributed among the three patch location categories (Figure 4); clusters of stems at the edge of or in the interior of discrete yew patches were less likely to contain at least one dead stem than for stems not in patches.

Deer pellet counts confirmed that winter deer densities were low for all study stands, i.e., the number of pellet-groups/400m² observed at each of the sites was less than the 6.75 pellet-groups/400m² value used by Potvin et al. (2005) to represent deer densities of ~2-6/km². The mean number of pellet-groups/400m² ($\pm$ SE) for all stands combined was 1.7 ($\pm$ 0.1).

The global model fit the data well based on the goodness-of-fit analysis ($X^2=148.7$, $df=12$, $P<0.001$; Olsson 2002). The best supported model in the model

set was Model 2, the single variable model for patch location (LOC; Table 2). QAIC_c for this model was 505.1 and had a QAIC_c weight of 0.49, i.e., this model has a 49% likelihood of being the best model in the initial 10 model set. Parameter estimates for patch location indicated that browsing intensity was greatest for isolated clusters of stems, intermediate for clusters at the edge of Canada yew patches, and least for clusters greater than 1m from the edge. Models 3 and 4, which included both mean stem length and patch location, were also supported with ΔQAIC_c scores of <2 . However, for Model 3, 95% confidence intervals for the parameter estimate for mean stem length (LENGTH) included zero, suggesting that patch location was driving model results. The global model and Model 9, the single variable model of percent Canada yew cover in the stand, were less supported (ΔQAIC_c scores between 4 and 8). All other models were poorly supported, with $\Delta\text{QAIC}_c >25$.

A post-hoc analysis of model parameters suggested that even though the single variable model that included percent cover (YEWCOV) did not perform well against Models 2-4, it was the next ranked model in the model set and the 95% confidence intervals for the YEWCOV parameter estimate did not include zero. If included in a model with patch location (LOC) overall predictive power might be increased. Therefore, two extra models were added to the model set: a two variable model with patch location (LOC) and percent cover (YEWCOV) and a three variable model with patch location, percent yew cover, and an interaction term (LOC*YEWCOV). This post-hoc analysis demonstrated that the two-variable model was overwhelmingly the best model, lowering the QAIC_c to 494.5 (Table 2). This model is 91% likely to be the best model based on its QAIC_c weight of 0.91. No other model had a QAIC_c

weight of <4. Parameter estimates for the variables LOC and YEWCOV suggest that two forces are acting independently to affect browsing intensity on clusters of Canada yew stems at two spatial scales. A model term measuring interaction between these two factors was not in the top ranked model, suggesting that these factors operate independently. Variable importance weights for all variables in the post-hoc model set (calculated as the sum of QAIC_c weights for each model in which the predictor appears) suggest that LOC (1.000) and YEWCOV (0.990) are equally important in affecting browsing intensity. All other variables, including LENGTH, had variable importance weights less <0.079 and therefore had relatively less effect on browsing intensity. At the intermediate scale (or a scale representing within-stand heterogeneity), location of stems within a patch affected browsing intensity. In relation to stems in the interior of patches (>1m from edge), mean browsing score was 0.63 units higher for stems at the edge of Canada yew patches and 1.53 units higher for stems not associated with patches. At the stand scale, mean browsing score decreased 0.27 units for every 10% increase in stand-level Canada yew cover.

4. DISCUSSION

Browsing intensity on Canada yew in this study was related to two factors operating independently at two spatial scales: a local (patch) scale pattern in which deer browsing intensity was least in the interior of Canada yew patches and a stand scale pattern in which browsing intensity decreased linearly with increasing amount of Canada yew cover. The local scale pattern we observed is consistent with observations in northern Wisconsin where deer appeared to focus browsing activity on stems immediately adjoining deer trails bisecting large patches of Canada yew,

eventually widening and creating new trails over a period of years until nearly all Canada yew within the patch was heavily browsed (J. Meeker, personal communication). Hester and Baile (1998) observed similar patterns of browsing on heather (*Calluna vulgaris*) by domestic sheep (*Ovis aries*) and red deer (*Cervus elaphus*) in Scotland. Browsing was focused almost exclusively within 3m of the edge of heather patches by both species and the gradual expansion of trails eventually resulted in increased fragmentation of existing heather patches.

Canada yew is considered the most preferred browse item by deer in the Great Lakes states, so much so that it is often browsed disproportionately more than other highly preferred browse items such as white cedar (*Thuja occidentalis*; Beals et al. 1960, King 1970). However, despite its high preference by deer, it may be energetically expensive for deer to penetrate deeply into dense or wide patches of Canada yew to browse. Based on models derived from travel through snow, Parker et al. (1984) estimated that energetic costs expended by elk and mule deer to travel through slash increased with increasing height and density of the slash piles.

Canada yew's propensity to reproduce by layering produces roughly circular-shaped patches comprised of dense tangles of intermingling stems; this patchy growth form is especially evident in high-density areas with large individuals (Allison 1990). Mean height and length of stems in most discrete patches of Canada yew observed in this study were greater than 40cm and 55cm, respectively (S. Windels, unpublished data). We suggest that this patchy growth form may physically inhibit deer penetration into patches of Canada yew >2m in diameter, thus creating a refugia to browsing deer in the interior of these patches. Examples of physical refugia are

relatively common in plant-ungulate systems (Borgmann et al. 1999, Garcia et al. 2000, Anderson et al. 2002). However, we are unaware of other instances of a physical refugia created by individuals of the same species. Allison (1990a, b) demonstrated that white-tailed deer can directly and indirectly affect sexual reproduction in Canada yew, a wind-pollinated species. The refugia created by dense patches of Canada yew may act as seed and pollen sources for Canada yew populations subjected to deer browsing.

The pattern of decreasing browsing intensity on Canada yew stems as Canada yew abundance increased at the stand scale is consistent with a Holling Type II functional response as described by Noy-Meir (1975). Beals et al. (1960) observed a similar negative relationship of deer browsing intensity to Canada yew cover in the Apostle Islands archipelago in Lake Superior. This Type II response has also been observed in other plant-herbivore systems, including white-tailed deer and nettle (*Laportea canadensis*; Augustine et al. 1998) and ground squirrels (*Spermophilus parryii*) and lupine (*Lupinus arcticus*; Frid and Turkington 2001). Under a uniform deer density (or number of deer-use days) and therefore uniform level of absolute biomass consumption, the amount of impact per stem is reduced as density (cover) increases. In our study, this pattern was not observed temporally within a stand, but was apparent across the entire set of study stands sampled.

A Type II functional response also theoretically allows for two alternate stable states of plant abundance under a constant herbivore density (Augustine et al. 1998). In our study system, Canada yew would be extirpated when its abundance at the site-level falls below some threshold value, i.e., over time, Canada yew will be extirpated

when the amount of biomass removed annually by deer exceeds the amount of biomass produced at the site level. Above the threshold value, the amount of browse removed by deer does not exceed the amount produced and Canada yew abundance increases over time. Under the very low deer densities in our study area, we believe that this theoretical threshold occurs between 15-30% areal cover for stands in the snow belt of the Lake Superior Watershed. For many of the stands sampled with <15% cover of Canada yew, the mean browsing score approached 4, which equates to 50-75% of its available twigs browsed. These stands also had proportionally more dead stems in the sample clusters (S. Windels, unpublished data), suggesting that deer browsing was exceeding the capacity of the Canada yew population to maintain itself. Conversely, all of the stands in our study area with Canada yew cover >30% appeared vigorous and relatively unaffected by browsing.

There are two larger scale trends, outside the scope of our original objectives, that likely affect the threshold of cover we observed. First, white-tailed deer densities throughout the Great Lakes region are generally increasing (McCabe and McCabe 1997, Rooney et al. 2002). Second, climate change predictions for the Great Lakes region suggest trends towards milder winters with less lake-effect snowfall (Kunkel et al. 2000). Early snowfall events often cover yew stems and protect them from browsing. Deep snows also force some deer populations to migrate to traditional deer yards and away from upland areas containing Canada yew. A change in the timing or amount of annual snowfall therefore may expose Canada to deer browsing for more days in the late-fall/early winter browsing period. Together, these trends suggest that the total number of deer-use days will increase within the Lake Superior Watershed.

Increased use of coastal forests by white-tailed deer may shift the threshold towards a higher value of Canada yew cover.

A complete understanding of the stand level relationship we describe is complicated by the apparent physical barrier to stem access that large diameter patches may provide. The effect of decreasing browse pressure with distance from a patch edge we observed reduces the amount of Canada yew available to browsing deer below what is present at the site. Further, as patch radius increases, the ratio of edge (i.e., the area of the outer portion of circular patch most susceptible to browsing) to the total area of the patch decreases (logarithmically for a circular patch) so that only a fraction of the total patch would be most susceptible to browsing by deer. Total cover of Canada yew at the site level is basically comprised of the sum of the cover of individual patches. For illustrative purposes, if we assume a constant average patch size as Canada yew ground cover increases within a site, the amount of patch edge susceptible to browsing would be linearly related to total Canada yew cover. However, if average patch size increases as Canada yew cover increases within a site, then the amount of patch edge would increase logarithmically as Canada yew cover increases. In either case, a site with a high abundance of Canada yew made up of many small patches would be more susceptible to browsing by deer than a high abundance site made up of a smaller number of large patches.

McLaren et al. (1996) speculated that chronic browsing pressure on balsam fir by moose caused a stunted growth form that ultimately resulted in a breakdown in the plant's chemical defense, thereby increasing both its palatability and net nutrient gain for moose. That is, even though instantaneous dry matter intake rates were likely

very low for moose browsing on these stunted trees with little available forage biomass, the relatively low chemical defense concentrations in the fir trees resulted in a higher net instantaneous nutrient intake rate than on neighboring forage plants. Canada yew, however, is poorly defended chemically from browsing mammals. Therefore a change in concentration of defensive compounds from overbrowsing is likely not a factor in Canada yew's susceptibility to deer or other browsing mammals.

5. CONCLUSION

White-tailed deer have been implicated as one of the main drivers in the dramatic decline in range and importance of Canada yew in forest understories in the eastern United States. Results from our study suggest that intensity of deer browsing on Canada yew in the Lake Superior Watershed was affected by two factors operating independently at two spatial scales relevant to white-tailed deer. Our results suggest that as the size of individual Canada yew patches increases, the likelihood of the patch persisting under a constant deer browsing pressure also increases. Moreover, we speculate that the extirpation of Canada yew from a stand occurs on a patch-by-patch basis rather than a steady decline across all stems within a stand. As stems at the edges of patches gradually die from heavy browsing, functional patch size decreases and new stems nearer the interior become susceptible to browsing. Due to the logarithmic relationship between amount of edge and area of circular patch, the rate at which patches shrink from chronic intensive browsing accelerates as patch size decreases until this "death spiral" culminates in the functional loss of that patch from the site. Further, stands with a greater abundance of Canada yew browse are also more likely to persist than stands with lower abundances. Though we did not find a

significant interaction between these two factors in our models, intuitively stands containing only small patches of Canada yew should be more prone to local extirpation than stands containing mostly large patches.

Our study stands were all located within zones of traditionally low white-tailed deer density and maximum snow depth during this study was close to or above long-term averages. However, it is unknown if the patterns and processes of deer-induced Canada yew decline we observed are found elsewhere in Canada yew's range. Future research should examine deer browsing patterns on Canada yew under higher deer densities.

ACKNOWLEDGEMENTS

We thank Richard Posey, Adam Kavalunas, Dan Oberg, Marcel Potvin, and Anne Chouinard for assistance with field work. Assistance with study site selection and site access was provided by Jerry Belant (Pictured Rocks National Lakeshore), Kevin Doran (Hiawatha National Forest), and Marty Wilk (Shelter Bay Forests). We thank Casey Huckins, Brian McLaren, Jim Meeker, Linda Nagel, and Chris Webster for comments that improved earlier drafts. This research was supported by The Nature Conservancy of Michigan, Michigan Department of Natural Resources Natural Heritage Program, Michigan Technological University's Graduate School and the Department of Forest Resources and Environmental Science, and the U.S. National Park Service.

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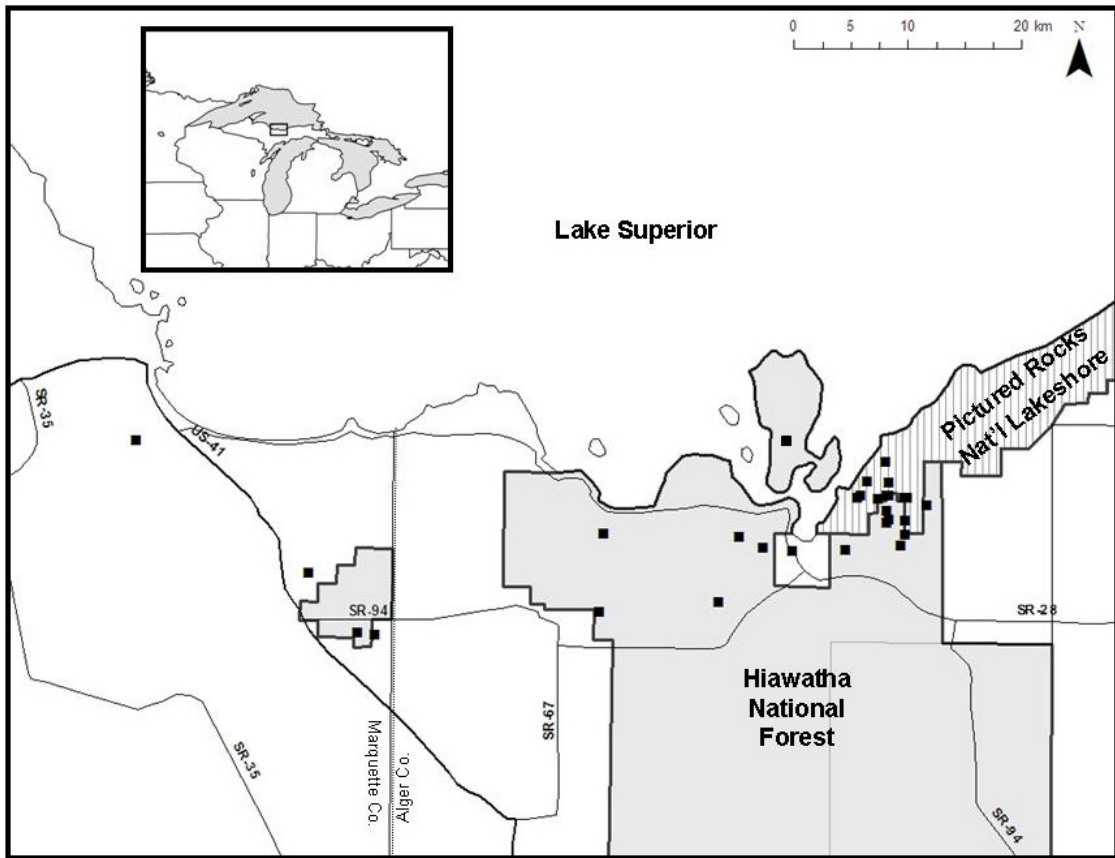
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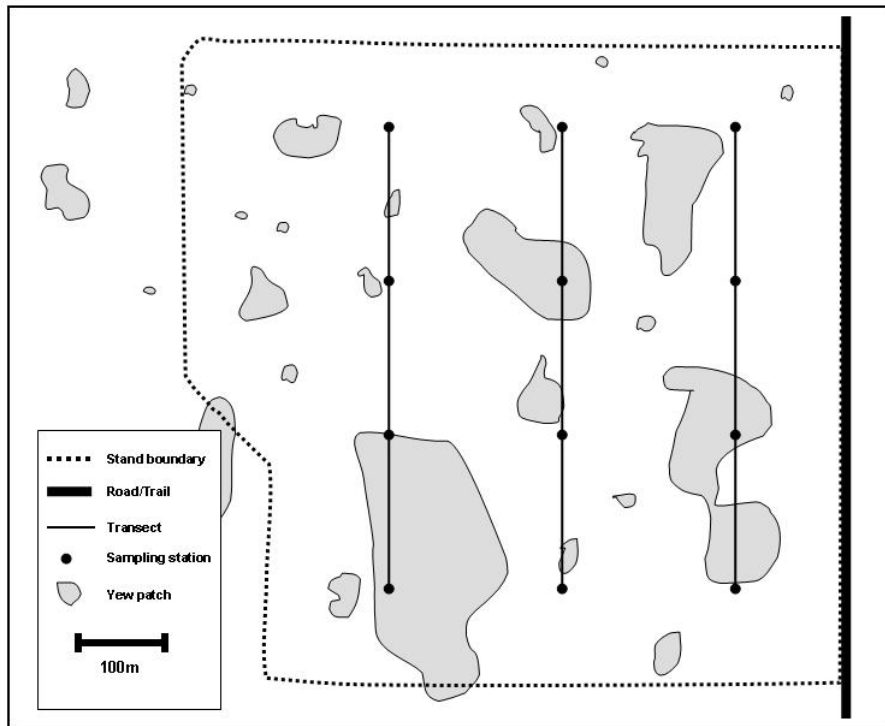
Figure 1. Distribution of study sites (black squares) in Marquette and Alger counties, Michigan, USA. Inset shows location of study area in relation the Great Lakes.

Figure 2. Typical arrangement of sampling transects and stations in relation to patches of Canada yew for 30 forested stands sampled in Marquette and Alger counties, Michigan, USA.

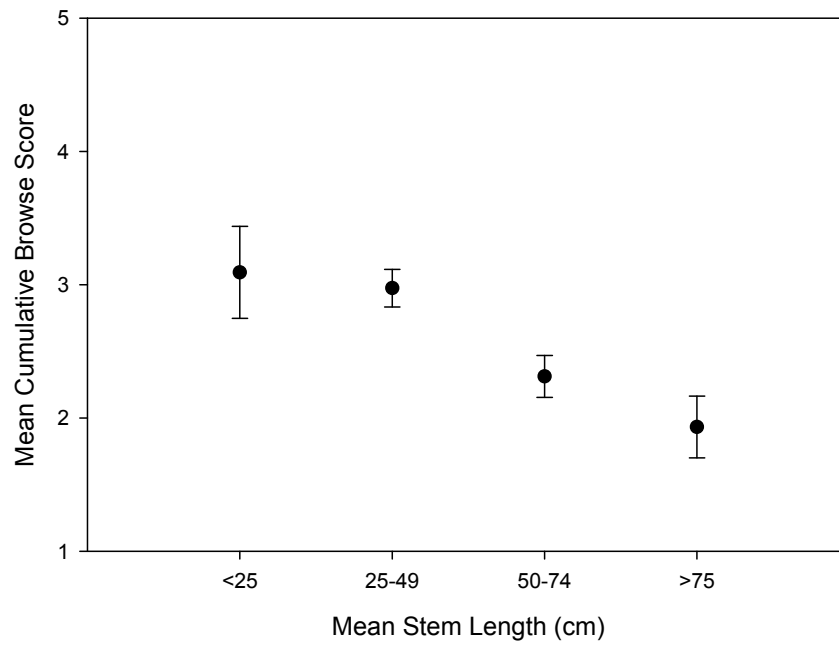
Figure 3a-f. Mean cumulative browsing score (± 1 SE) for clusters of Canada yew stems in relation to various predictor variables from 24 stands in Marquette and Alger counties, MI, 2001-2002. Cumulative browse scores were based on the proportion of twigs browsed by deer during the previous three winters for each stem in a cluster (1= <5% twigs browsed, 2= 6-25%, 3= 26-50%, 4= 51-75%, 5= 76-95%, 6= >95%).

Figure 4. Proportion of sampled Canada yew clusters (minimum 5 stems) containing ≥ 1 dead stems in relation to distance from yew patch edge from 24 stands in Marquette and Alger counties, MI, 2001-2002. Numbers above each category represent total number of clusters sampled.

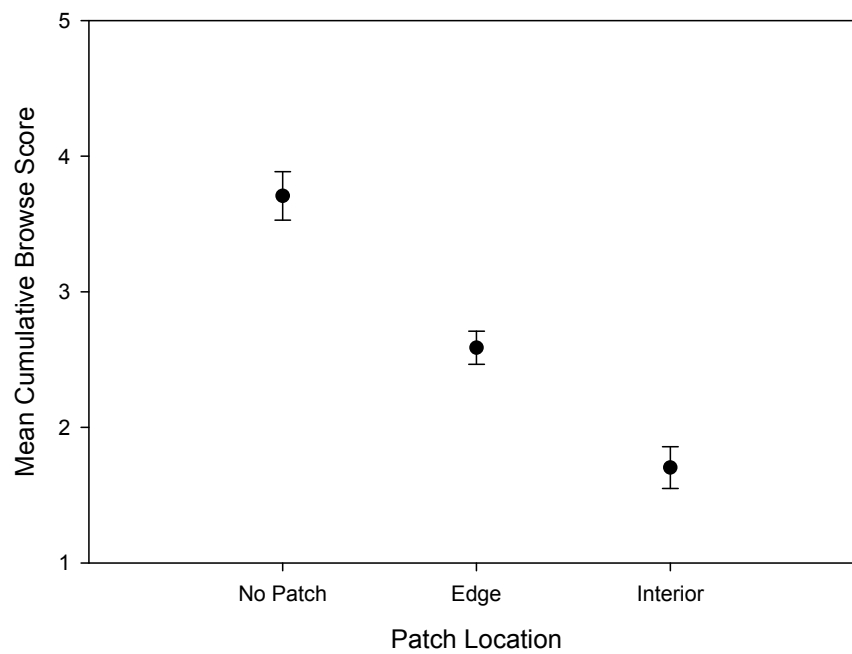




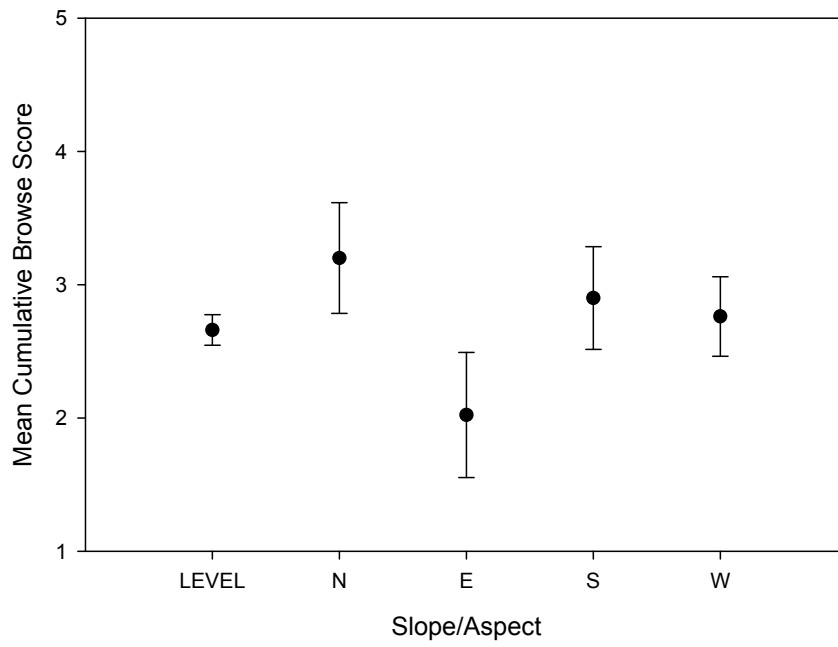
a.



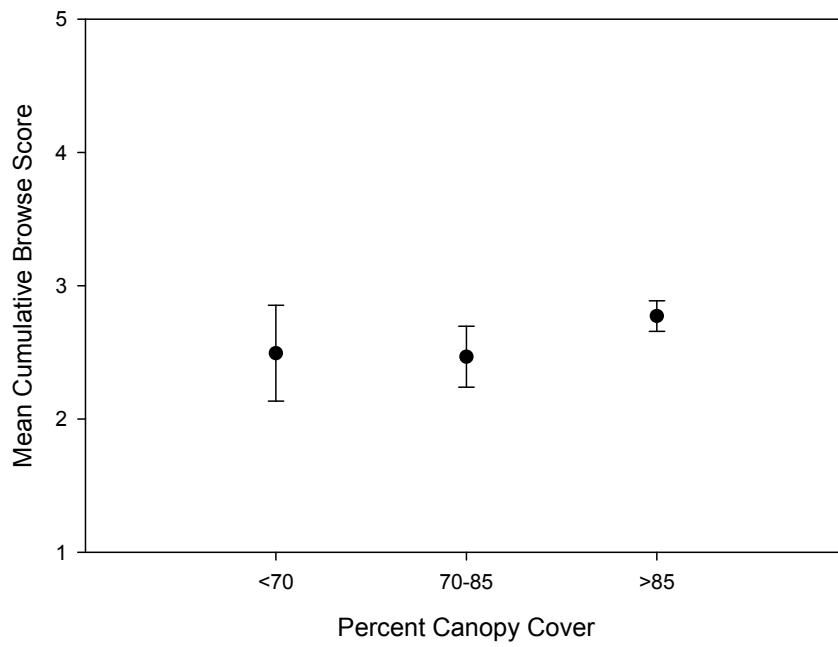
b.



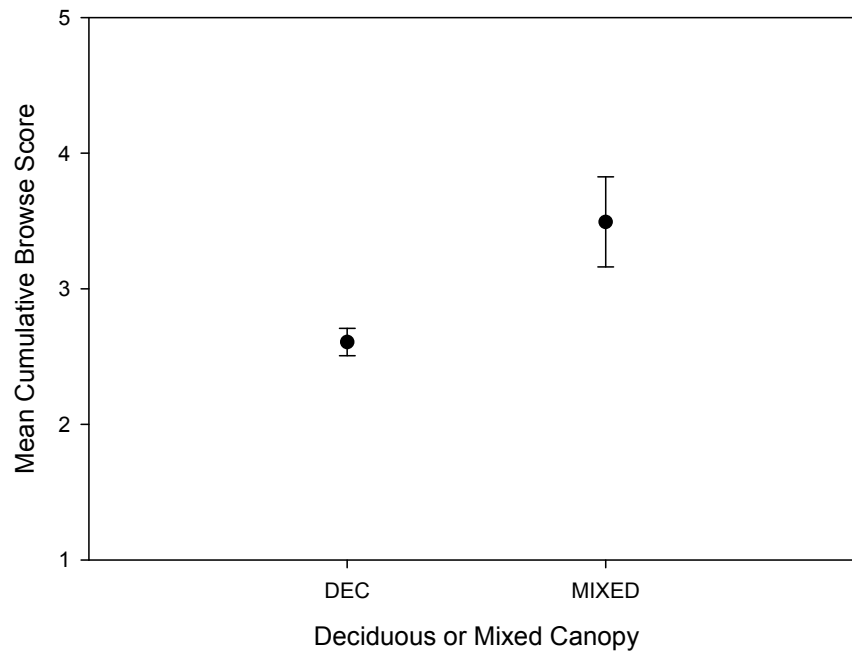
c.



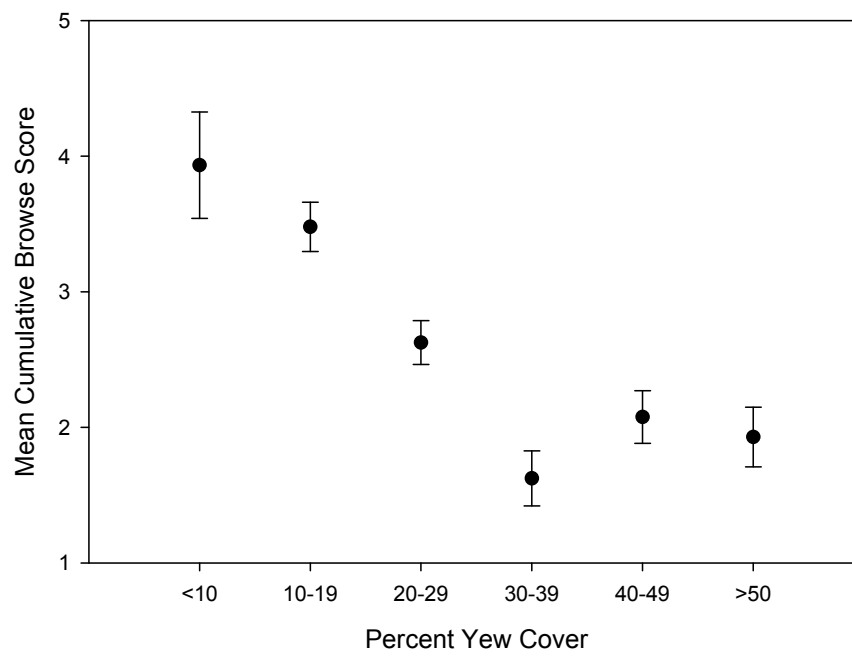
d.



e.



f.



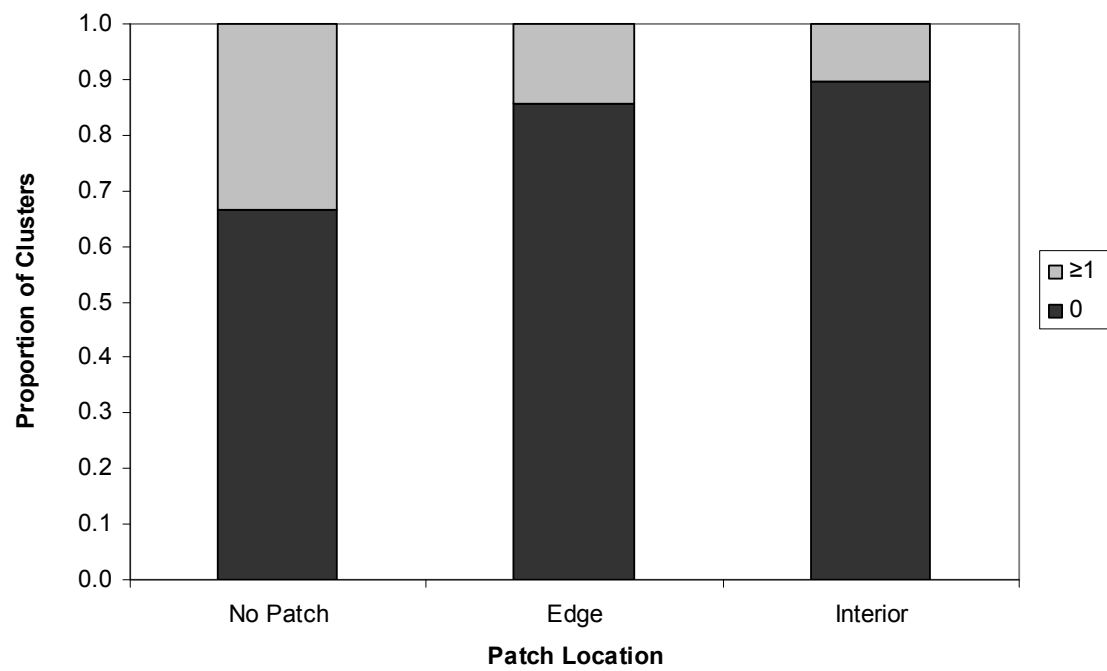


Table 1. Characteristics of 24 forested stands sampled for Canada yew browse in 2001-2002 in Marquette and Alger counties, Michigan. Only those stands with at least one cluster of ≥ 3 live stems were included in model selection analyses and are shown below.

Stand Name	Year Sampled	Management Status	Canopy Cover (%)	Decid / Conifer Basal Area (m ² /ha)	Yew Cover (%)	Yew Stems		
						N ^a	Cumulative Browse Score	Length (cm)
CWC	2001	Protected	92.6 $\pm$ 2.8	40.0 / 0.0	0.0 $\pm$ 0.0	1	6.0 $\pm$ na	19.2 $\pm$ na
Section 33	2001	Managed	86.3 $\pm$ 6.3	21.9 / 0.0	10.3 $\pm$ 1.7	7	3.9 $\pm$ 0.4	45.2 $\pm$ 4.5
HillTop	2001	Managed	80.6 $\pm$ 4.1	22.9 / 0.1	13.3 $\pm$ 2.2	15	2.8 $\pm$ 0.4	47.3 $\pm$ 2.9
Carmody West	2001	Protected	96.0 $\pm$ 1.1	22.7 / 0.0	14.5 $\pm$ 2.9	8	2.5 $\pm$ 0.4	44.6 $\pm$ 4.8
Dukes West	2001	Managed	87.1 $\pm$ 3.7	27.4 / 0.1	16.3 $\pm$ 3.7	10	5.2 $\pm$ 0.2	32.7 $\pm$ 2.3
Carmody East	2001	Managed	79.8 $\pm$ 6.4	19.1 / 0.1	23.9 $\pm$ 3.6	11	2.1 $\pm$ 0.4	60.1 $\pm$ 4.6
Monette	2001	Managed	96.4 $\pm$ 2.5	24.8 / 0.1	27.1 $\pm$ 2.6	8	2.2 $\pm$ 0.3	50.1 $\pm$ 6.4
SuperThick	2001	Managed	76.5 $\pm$ 4.5	16.4 / 0.0	28.3 $\pm$ 3.1	14	2.5 $\pm$ 0.4	47.2 $\pm$ 2.8
Chatham Ski Hill	2001	Managed	93.8 $\pm$ 2.2	22.6 / 5.3	43.6 $\pm$ 2.5	18	2.7 $\pm$ 0.3	47.7 $\pm$ 3.7
Section 28	2001	Managed	86.4 $\pm$ 4.8	17.1 / 0.1	45.1 $\pm$ 2.7	13	1.4 $\pm$ 0.2	60.6 $\pm$ 8.4
Miners NE	2001	Managed	88.7 $\pm$ 3.3	15.6 / 0.5	52.6 $\pm$ 2.6	11	1.9 $\pm$ 0.3	60.2 $\pm$ 5.9

Table 1. (Cont.)

Stand Name	Year Sampled	Management Status	Canopy Cover (%)	Decid / Conifer Basal Area (m ² /ha)	Yew Cover (%)	Yew Stems		
						N ^a	Cumulative Browse Score	Length (cm)
Miners Control	2002	Protected	96.3 ± 2.2	36.3 / 0.0	0.0 ± 0.0	4	3.5 ± 0.7	21.4 ± 3.0
Abe Lk.	2002	Managed	91.1 ± 2.0	25.1 / 3.1	3.8 ± 1.4	4	4.0 ± 0.7	33.8 ± 4.2
Munising Ski Hill	2002	Managed	95.2 ± 2.6	10.6 / 9.5	7.5 ± 2.4	3	3.8 ± 0.8	38.1 ± 8.4
Miller Road	2002	Managed	86.9 ± 3.2	25.3 / 0.0	12.4 ± 4.0	6	3.3 ± 0.5	39.3 ± 6.7
Perch Lk. North	2002	Managed	96.7 ± 1.8	14.2 / 8.5	15.6 ± 2.5	12	3.4 ± 0.4	43.4 ± 5.1
HW Island	2002	Managed	85.7 ± 3.4	19.9 / 0.2	22.2 ± 2.9	9	2.5 ± 0.4	50.4 ± 6.0
PIRO	2002	Protected	96.3 ± 1.3	29.1 / 0.1	24.4 ± 3.9	9	3.3 ± 0.4	45.4 ± 5.7
553	2002	Managed	94.3 ± 2.5	21.3 / 0.7	24.8 ± 5.0	5	3.8 ± 0.7	58.6 ± 4.7
H-58	2002	Managed	89.9 ± 2.0	21.9 / 0.1	27.5 ± 4.1	6	2.6 ± 0.4	47.3 ± 8.8
Perch Lk. East	2002	Managed	85.2 ± 2.4	14.2 / 1.8	31.3 ± 3.5	9	1.6 ± 0.2	45.4 ± 5.3
Big Tree	2002	Managed	91.7 ± 2.5	22.5 / 0.1	32.3 ± 4.3	8	1.7 ± 0.4	59.0 ± 10.6
Miners Basin	2002	Managed	93.3 ± 1.9	26.7 / 0.0	45.1 ± 3.2	9	1.7 ± 0.3	52.1 ± 4.2
Miners North	2002	Managed	85.7 ± 5.8	22.8 / 0.7	54.4 ± 4.3	8	2.0 ± 0.3	49.7 ± 3.7

^aNumber of clusters of sampled yew stems with ≥ 3 live stems.

Table 2. Model selection results from analysis of white-tailed deer browsing intensity on Canada yew in relation to local and site-level factors in northern/mixed hardwood forests in the Upper Peninsula, Michigan, 2001-2002. A *post hoc* model selection analysis was conducted after results from the *a priori* exercise suggested model fit could be improved.

Model	Predictors	Parameter	LCI	UCI	k	Deviance	<i>A priori</i>				<i>Post-hoc</i>			
							QAIC _c	Δ_i	Rank	Weight	QAIC _c	Δ_i	Rank	Weight
1	INTERCEPT	3.7407	2.9895	4.4919	3	380.46	530.76	25.70	6	0.00	530.76	36.05	8	0.00
	LENGTH	-0.0222	-0.0325	-0.0119										
2	INTERCEPT	1.7033	14.4577	1.9488	5	312.74	505.06	0.00	1	0.49	505.06	10.35	4	0.01
	LOC (1)	2.0034	1.4081	2.5988										
	LOC (2)	0.8835	0.6398	1.1272										
3	INTERCEPT	1.8983	1.4834	2.3132	6	312.19	506.92	1.86	3	0.19	506.92	12.20	6	0.00
	LENGTH	-0.0033	-0.0096	0.0030										
	LOC (1)	1.9150	1.3254	2.5046										
	LOC (2)	0.8506	0.6014	1.0998										
4	INTERCEPT	2.7588	2.2187	3.2989	5	315.41	506.36	1.30	2	0.26	506.36	11.65	5	0.00
	LENGTH*LOC (1)	0.0280	0.0109	0.0451										
	LENGTH*LOC (2)	-0.0040	-0.0130	0.0049										
5	INTERCEPT	2.7617	2.0863	3.4371	7	407.62	549.71	44.65	10	0.00	549.71	55.01	12	0.00
	SLOPE (E)	-0.7394	-1.6222	0.1433										
	SLOPE (LEVEL)	-0.1012	0.4036	-0.8922										
	SLOPE (N)	0.4383	-0.4976	1.3743										
	SLOPE (S)	0.1383	-0.5895	0.8662										
6	INTERCEPT	1.5243	0.2587	2.7900	3	409.24	541.88	36.82	9	0.00	541.88	47.17	11	0.00
	CANOPY	0.0131	-0.0004	0.0267										
7	INTERCEPT	3.4921	3.1468	3.8374	4	401.98	541.23	36.17	7	0.00	541.23	46.52	10	0.00
	CONIFER (1)	-0.8855	-1.3771	-0.3938										
8	INTERCEPT	2.4838	1.0486	3.9190	5	397.90	541.77	36.71	8	0.00	541.77	47.06	9	0.00
	CANOPY	0.0107	-0.0029	0.0243										
	CONIFER (1)	-0.8184	-1.3294	-0.3075										

Table 2. (cont.)

Model	Predictors	Parameter	LCI	UCI	k	Deviance	<i>A priori</i>				<i>Post-hoc</i>			
							QAIC _c	Δ_i	Rank	Weight	QAIC _c	Δ_i	Rank	Weight
9	INTERCEPT	3.8626	3.2372	4.4881	3	337.42	512.46	7.40	5	0.01	512.46	17.76	7	0.00
	YEWCOV	-0.0425	-0.0607	-0.0243										
10 (Global)	INTERCEPT	1.6726	0.0513	3.2939	18	266.08	509.76	4.70	4	0.05	509.76	15.05	3	0.00
	LENGTH	0.0002	-0.0120	0.0125										
	LOC (1)	0.5431	-0.8939	1.9800										
	LOC (2)	0.8426	-0.2707	1.9559										
	LENGTH*LOC (1)	0.0292	-0.0019	0.0604										
	LENGTH*LOC (2)	-0.0043	-0.0220	0.0134										
	SLOPE (E)	-0.4194	-1.4496	0.6108										
	SLOPE (LEVEL)	0.1925	-0.3621	0.7470										
	SLOPE (N)	-0.0014	-0.7242	0.7215										
	SLOPE (S)	0.1482	-0.5265	0.8230										
	CANOPY	0.0163	0.0065	0.0261										
	CONIFER (1)	-0.5958	-1.1676	-0.0240										
	YEWCOV	-0.0271	-0.0400	-0.0143										
Model 11	INTERCEPT	2.6906	2.1004	3.2809	6	288.17	na	na	na	na	494.71	0.00	1	0.91
	LOC (1)	1.5258	0.9015	2.1502										
	LOC (2)	0.6323	0.3750	0.8897										
	YEWCOV	-0.0265	-0.0420	-0.0109										
Model 12	INTERCEPT	2.2263	1.3067	3.1459	9	285.16	na	na	na	na	499.60	4.89	2	0.08
	LOC (1)	1.8630	0.5694	3.1566										
	LOC (2)	1.3375	0.4074	2.2676										
	YEWCOV	-0.0140	-0.0344	0.0064										
	LOC (1)*YEWCOV	-0.0058	-0.0496	0.0379										
	LOC (2)*YEWCOV	-0.0211	-0.0448	0.0027										

Chapter 3:

**Patterns in Understory Vegetation and Vertebrate Community Structure
Along a Gradient of Canada Yew Density:
Implications for the Decline of a Dominant Understory Plant**

This chapter is written according to the style of:

Journal of Wildlife Management

Abstract: Many small forest vertebrates rely on understory vegetation for foraging habitat, reproductive substrate, or concealment from predators. Canada yew (*Taxus canadensis*), an evergreen shrub, may provide unique habitat features for understory vertebrates such as small mammals and songbirds because of its patchy growth form and evergreen nature. Historically, Canada yew was an important ground cover component in northern forests of the northeastern United States and adjacent Canada but during the last century it has since declined through most of its prior range due to anthropogenic disturbance and overbrowsing by white-tailed deer (*Odocoileus virginianus*). The loss of Canada yew from forest understories may therefore have cascading impacts on some faunal groups in northern forests. To investigate the potential for this phenomenon, we compared understory habitat characteristics in northern forest stands across a gradient of Canada yew density and examined how the abundance and community structure of small mammals and songbirds related to Canada yew density and other understory vegetation characteristics. Canada yew had a direct effect on the abundance of hardwood seedlings <1m tall and forb cover but did not affect recruitment of hardwoods into taller height classes. We found no strong direct relationships between Canada yew abundance and indices of abundance and diversity for either small mammals or songbirds. Instead, abundances of several individual species as well as diversity measures for both small mammals and songbirds were related to measures of understory structure. Our results suggest that the loss of Canada yew from eastern forests will not always result in a decrease in understory structure because plants released from competition with Canada yew may replace it. The loss of Canada yew from forest stands appears most likely to result in

a decline in the abundance and diversity of small mammals and understory songbirds in relatively undisturbed forests with characteristically low levels of general understory structure.

INTRODUCTION

Waller and Alverson (1997) speculated on the cascading effects white-tailed deer have on eastern deciduous forests, suggesting that change in a structural forest component resulting from intensive deer browsing can affect taxa in other trophic levels. Canada yew (*Taxus canadensis*), also known as ground hemlock or American yew, is an evergreen shrub native to the mixed conifer-hardwood forests of the northeastern United States and southeastern Canada (Martell 1974). Prior to Euro-American settlement, it was a major ground cover component in some late-successional mesic forests of the region, comprising up to 70% or more of total ground cover in some forests (Braun 1950, Martell 1974). Canada yew has been extirpated from many parts of its range as a result of overbrowsing by white-tailed deer (*Odocoileus virginianus*) and other wild ungulates during the first half of the 20th century (see Chapter 1 and references therein). To our knowledge, almost no research has explicitly sought to identify potential cascading effects of the loss of Canada yew on other components of forest ecosystems (but see Belant and Windels 2003).

Understory vegetation cover is generally inversely related to overstory vegetation cover (Constable and Lieffers 1996, Aubin et al. 2000). However, Canada yew's high shade tolerance allows extremely dense patches to populate forest understories in undisturbed forests where near continuous canopy cover precludes dense growth of other woody and herbaceous plants. In some closed-canopy northern hardwood forests in Michigan, Canada yew can comprise more than 90% of total woody stem

density and up to 27% cover in otherwise sparse understories (S. Windels, unpubl. data). Similar conditions were observed by Finér et al. (1997) in old-growth boreal forest stands in Quebec. Under optimal conditions Canada yew grows in dense patches with stem densities of Canada yew approaching those of all other woody stems combined (Finér et al. 1997, S. Windels, unpubl. data).

Considering the dense nature in which Canada yew is capable of growing, it seems intuitive that at high abundances it can affect stratification of understory vegetation by limiting establishment and growth of other species within or below patches of yew. Several authors have observed that abundance of Canada yew is often negatively correlated with abundance of other understory species. For example, Nichols (1913) observed that Canada yew frequently grew in dense patches “to the exclusion of all undergrowth” and Egler (1940) stated that “unless yew is absent, an herb layer is not present.” Other authors have specifically noted the inhibitory effect of dense yew on species richness and abundance of herbaceous plants (Buell and Bormann 1955, Judziewicz and Koch 1993, Balgooyen and Waller 1995, De Grandpre and Bergeron 1997).

Dense Canada yew inhibits establishment of seedlings of woody plants such as eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*; Braun 1950, Risenhoover and Maass 1987, Tyrell and Crow 1994, Danz 1998). Interestingly, sapling density and tree recruitment appear generally unaffected by dense Canada yew (Risenhoover and Maass 1987, Danz 1998). Changes in abundance of Canada yew as a result of

overbrowsing by deer and other factors therefore should be expected to change other components of forest understory structure.

There are many reasons to believe that the presence and density of Canada yew could influence bird and small mammal abundance and species richness. Songbird species that use forest understories for nesting and/or foraging are often closely associated with understory structural characteristics including horizontal cover and foliage height density. Likewise, presence or abundance of small mammals, such as deer mice (*Peromyscus* spp.) and red-backed voles (*Myodes gapperii*), are also often associated with understory structural characteristics. At within-stand spatial scales, however, some bird species may respond more closely to the presence or abundance of certain plant species rather than to the general structure they provide (Wiens and Rotenberry 1981, Fleishman et al. 2003). Some understory songbirds may be more closely associated with Canada yew *per se* rather than general understory structure. Anecdotal accounts suggest that black-throated blue warblers (*Dendroica caerulescens*), in particular, demonstrate a high preference for building nests within patches of Canada yew or in areas with abundant yew (Bent 1963). Some small mammal species may behave similarly; several species of small mammals were more abundant in forests with Canada yew than those without it (Belant and Windels 2003). The decline of Canada yew therefore may have cascading effects on some regional faunal groups, e.g., ground- or shrub-nesting songbirds or small mammals that directly use the understory for foraging, cover, or reproduction.

We investigated potential cascading effects of the loss of Canada yew on forest understories and associated small mammals and songbirds using an observational approach. Specifically, we asked the following questions:

- 1) Does abundance of Canada yew affect the physical structure (physionogonomy) of understory vegetation?
- 2) Is the abundance of Canada yew directly related to abundance of individual species or community-level patterns such as richness and diversity?
- 3) Is the abundance of Canada yew indirectly related to the abundance of individual species or community-level patterns through its influence on physiognomy of understory vegetation?

This information is necessary to assess the potential trophic-level impacts resulting from the wide-spread loss of Canada yew throughout its range.

METHODS

Study Area

This study was conducted in Marquette and Alger Counties, Michigan, USA, within the Lake Superior watershed. Vegetation is predominantly upland forest dominated by the deciduous sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and American beech (*Fagus americana*) with patches of codominant eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), and balsam fir (*Abies balsamea*). Climate is greatly moderated by Lake Superior, with cool summers and mild yet snowy winters.

Twenty-eight mesic northern/mixed hardwood forest stands in Marquette and Alger Counties, Michigan, USA were selected as study sites (Figure 1). A site was

defined as having a relatively uniform vegetation composition and stand history as determined from a combination of aerial photos, topographic maps, stand compartment maps, and ground-truthing. Sites ranged from 25-40 ha and were selected to represent the range of Canada yew ground cover present in the region in each of three ranges: low (trace -15% ground cover), medium (15-30%), and high (>30%). Sites were also limited to those with >70% tree canopy cover and moderately to well-drained sandy or sandy loam soil. Eleven of the sites were sampled in 2001 and the remaining 17 in 2002. Twenty-three of these sites were managed for sawtimber at the time of sampling, i.e., selection harvested to reduce tree basal area to approximately 16m²/ha every 10-15 years. The remaining five sites were within protected areas free of timber harvest for at least 30 years prior to sampling.

Songbird and Small Mammal Sampling

During the summers of 2001 and 2002, we gathered data relating stand-level indices of abundance and diversity of understory songbirds and small mammals to Canada yew abundance within northern forest understories. Sampling stations were systematically established along uniformly spaced transects within each site. Stations were spaced at least 175m from each other and at least 100m from roads and site boundaries to minimize edge effects. The number of stations per site ranged from 6 to 11 depending on the area and shape of the site.

Songbird abundance and species richness were assessed with 5-minute fixed-radius (50m) point count surveys at each sampling station. Two surveys were conducted at each site, at least 3 weeks apart. Sites were each surveyed in one year

between June 1- July 10 in 2001 and May 28 - July 10 in 2002. All birds seen or heard were recorded, although we focused on a suite of common species that utilize the lowest 3m of the understory for either nesting or foraging were considered species most likely to be associated with Canada yew or other understory variables that may be related to Canada yew abundance. These species included: American redstart (*Setophaga ruticilla*), American robin (*Turdus migratorius*), black-throated blue warbler, hermit thrush (*Catharus guttatus*), ovenbird (*Seiurus aurocapilla*), Swainson's thrush (*Catharus ustulatus*), veery (*Catharus fuscescens*), and white-throated sparrow (*Zonotrichia albicollis*).

Small mammal abundance and species richness were assessed using Sherman live traps. Seven 8.0 x 8.8 x 23.4 cm folding traps were placed in an array with a single trap at the sample point and six traps placed at the corners of a hexagon such that all traps were 15m from each other. Traps were placed in "most likely runway" positions, baited with a mixture of rolled oats and peanut butter, and checked twice daily for three consecutive days during either August 2001 or 2002. Traps that were sprung, whether successful or not, or were disturbed in any way (e.g., disturbed by bears or raccoons) were adjusted to represent 0.5 trap nights (Belant 1992). Individuals were not marked and therefore data represent total number of captures/100 adjusted trap nights (ATN) for each species and not number of individuals.

Vegetation Measurements

Overstory and understory vegetation parameters were measured to categorize vegetation structure relevant to understory songbirds and small mammals at each

vertebrate sampling station. Vegetation measurements were also taken at additional sampling stations placed within the grid of vertebrate sampling stations to better represent any heterogeneity of the site; total number of sampling stations where vegetation measurements were recorded ranged from 8-18 per site. Data was averaged across sampling stations to produce site-level means. Number and species of trees (≥ 3 cm diameter at breast height [dbh]) were recorded within a 0.02-ha plot at each station to estimate basal area. Canopy cover of deciduous and coniferous trees was estimated with an ocular tube at 21 points along a transect bisecting the station. Number of woody stems (< 3 cm dbh) in 5 height classes (< 0.5 m, 0.5-1.0 m, 1.0-2.0 m, 2.0-3.0 m, and > 3.0 m) were counted for each species present in 5-m² rectangular plots at each station. Percent cover of ferns, forbs, and grasses was estimated in five 1-m² plots placed in a cross pattern at each station. An index of coarse woody debris volume (cm³) was estimated by recording diameter and length of all coarse woody debris > 8 cm max diameter that intersected an 11-m long transect through the center of the station. An index of foliage height density (FHD) was estimated using a 0.05 x 3 m cover board divided into three 1-m segments comprised of 10 cells each. The number of cells obscured by vegetation ($\geq 50\%$ covered) from a distance of 11 m as recorded in the each 4 cardinal directions and averaged to produce an index of total FHD and for three height strata (0-1 m, 1-2 m and 2-3 m). Areal coverage of Canada yew within each site was estimated from a uniform grid of 11-m radius plots spaced along and in-between vegetation station sampling transects such that each site had a sampling station: 11-m plot ratio of $\sim 1:3$.

Analysis

Vegetation

To account for variability in understory structure associated with overstory characteristics, we assigned stands one of three classes based on knowledge of stand history, where available, and visual observation of bivariate plots of total basal area and canopy cover. These three classes generally corresponded to time elapsed since last forest harvest: OPEN sites were harvested 2-5 years before sampling; INTERMEDIATE sites were harvested approximately 6-15 years before sampling, and CLOSED sites were harvested approximately 16-30 years before sampling.

Mean values for vegetation variables for each site class are shown in Table 1.

Density of Canada yew stems is highly correlated with per cent cover of Canada yew ($r = 0.92$; Chapter 1) and therefore Canada yew stem density was used exclusively in analyses because it allowed us to make more logical comparisons with stem density of other woody species. We used the proportion of total woody stems comprised of Canada yew as an index of Canada yew domination of understory vegetation. We tested for differences in vegetation characteristics between overstory classes using one-way analysis of variance. We tested for relationships between abundance and dominance of Canada yew to understory vegetation structure using correlation and multiple regression.

Understory Vertebrates

Species-area accumulation curves demonstrated that >85% of understory songbird species at a site were recorded by the 6th sampling station at the majority of sites (S. Windels, unpubl. data). Species included in the analyses were limited to those with at least five total detections across all sites in each of the two years. The maximum

number of individuals recorded between the two surveys conducted was used to represent species abundance at each sampling station. Mean abundance for each focal species was calculated as the mean no. individuals/sampling station/site. Species richness was defined as the total number of species detected/site. Species diversity was estimated using the Shannon-Weiner index (H'), where $H' = -\sum p_i \ln p_i$ and p_i is the proportion of the total abundance of birds in the i th species.

For small mammals, data analysis was limited to those species with ≥ 10 total captures in each of the two years. Total captures of each species was used to represent species abundance at each sampling station. Mean abundance for each species was calculated as the mean # captures/100 adjusted trap nights/site. Species richness was defined as the total number of species detected/site. Species diversity was also estimated using the Shannon-Weiner index (H').

Univariate regressions were used to test for simple linear and quadratic relationships between Canada yew abundance and bird and small mammal abundance, richness, and diversity. Single species analyses were limited to those small mammal and bird species detected in at least 50% of the sampled sites.

Results

Vegetation

As expected, understory vegetation structure differed between overstory classes. Total density of hardwood stems differed between overstory classes; density of hardwood stems decreased as overstory density increased (Table 1). Most of this difference was in the two lowest height strata ($<0.5\text{m}$ and $0.5\text{-}1\text{m}$) of hardwood stems. Densities of hardwood stems in the $1\text{-}2\text{m}$, $2\text{-}3\text{m}$, and $>3\text{m}$ height classes were

greatest in the INTERMEDIATE class, though these differences were not significant (all $P > 0.05$). Ferns and forbs comprised the majority of herbaceous cover at nearly all sites, and cover of ferns, forbs, grasses, and all herbaceous plants combined were similar between overstory classes (all $P > 0.05$; Table 1). The indices of foliage height density (FHD) were similar between sites though the CLOSED sites had lower values for total FHD and for each of the 1m strata than the other two overstory classes (all $P > 0.05$; Table 1).

The density of all hardwood stems combined ($R^2 = 0.34$, $P = 0.02$) and for the lowest strata only ($<0.5\text{m}$; $R^2 = 0.31$, $P = 0.03$) were negatively related to Canada yew density when accounting for overstory composition (Figure 2). Hardwood stems $<0.5\text{m}$ tall accounted for 74-82% of total hardwood stem density for sites within each overstory class, and therefore associations between Canada yew density and hardwood stems in this strata strongly influenced the significant results seen for all hardwood stems combined. Densities of hardwood stems in the remaining height strata ($>1.0\text{m}$) were not significantly correlated with Canada yew density. The density of conifer stems, primarily comprised of balsam fir, was much lower than either hardwoods or Canada yew and was unrelated with Canada yew density. Cover of ferns, grass, or all herbaceous plants combined were not significantly related to Canada yew density. Percent cover of forbs was weakly and non-significantly related to Canada yew density ($R^2 = 0.11$, $P = 0.09$). Percent cover of forbs also showed a significant negative relationship with total stem density ($R^2 = 0.21$, $P = 0.01$).

Canada yew density was significantly correlated with total stem density ($r = 0.47$, $P = 0.01$). However, as Canada yew density increased it comprised a greater

proportion of total stems ($R^2 = 0.71$, $P < 0.001$). Extrapolation of the regression line suggests that Canada yew will comprise >90% of all stems above densities of 15 yew stems/m². An interaction term between overstory class and Canada yew stem density was significant, suggesting that Canada yew was less dominant at higher yew densities in OPEN sites than in INTERMEDIATE or CLOSED sites (Figure 3).

Foliage height density (FHD) was not linearly or quadratically related to Canada yew density when all understory strata were combined (0-3.0m) or for the three individual strata (all $P > 0.05$). Total density of woody stems, however, in the <1m, 1-2m, and >3m height classes were significantly correlated with FHD in the corresponding the height strata ($r = 0.44$ - 0.80, all $P < 0.02$). Canada yew dominance (i.e., yew density/total stem density) was quadratically related to total FHD (0-3.0m; $R^2 = 0.20$) and FHD in the 0-1m strata ($R^2 = 0.21$), i.e., FHD was greatest for intermediate values of yew dominance, though these relationships were marginally significant ($P = 0.065$ and 0.053, respectively).

Small mammals

We tallied 1416 total captures in 4694 adjusted trap nights (ATN) in 2001 and 2002 combined. We trapped five species of small mammals with ≥ 10 captures in each year: deer mouse, red-backed vole, short-tailed shrew (*Blarina brevicauda*), masked shrew (*Sorex cinereus*), and eastern chipmunk (*Tamias striatus*; Table 2). Three other species, woodland jumping mouse (*Napaeozapus insignis*), northern flying squirrel (*Glaucomys sabrinus*), and red squirrel (*Tamiasciurus hudsonicus*), were captured in low numbers (<8 individuals in both years combined) and excluded from habitat analyses. We also excluded these three species from calculations of

species richness and diversity because of possible biases in capture probability; northern flying squirrels and red squirrels are mostly arboreal rodents and therefore are likely undersampled using Sherman traps placed on the ground. Captures of woodland jumping mice were less than expected (one individual in two years) based on knowledge of their relative abundance in the Upper Peninsula of Michigan (Kurta 1995) and suggests there was some unknown bias against capture of this species in our study.

Deer mice were captured at all sites and were the most abundant common species, accounting for >60% of total captures. Abundance of deer mice (captures/100 ATN) was significantly greater in 2002 than 2001 ($P = 0.03$). Abundance of short-tailed shrews was significantly lower in 2002 than 2001 ($P < 0.01$), while red-backed voles, eastern chipmunks, and total small mammal captures were not significantly different between years. Species richness of small mammals was similar between years. However, Shannon-Weiner diversity, H' , was significantly lower in 2002 than in 2001 ($P = 0.01$), primarily because deer mice increased and short-tailed shrews decreased in abundance in 2002.

Abundances of individual small mammal species were not significantly correlated with Canada yew stem density or most other measures of understory structure (Table 3). Deer mice were negatively related to FHD in 0-1m strata ($r = -0.51$) whereas short-tailed shrews showed a positive correlation to this same variable ($r = 0.48$). Small mammal species richness ($r = 0.41$) and diversity ($r = 0.48$) were also significantly positively related to FHD in the 0-1m strata. Multiple regression models that incorporated year effects for deer mice, short-tailed shrew, and species diversity

improved the fit of these models. Regression models that tested quadratic effects for Canada yew density (and year effects where appropriate) against species abundance or diversity measures were not significant (all $P > 0.05$). Species richness and diversity showed a quadratic relationship with yew dominance, but this was likely correlated with the quadratic effect of yew dominance on FHD.

Red-backed voles were captured in 22 of 28 sites. Mean percent yew cover of sites where red-backed voles were present ($\bar{X}=25.9\%$) was significantly greater than for sites where they were not captured ($\bar{X}=4.7\%$; $P < 0.001$).

Songbirds

Focal understory songbird species that were detected >5 times in both years were: American redstart, American robin, black-throated blue warbler, hermit thrush, veery, and white-throated sparrow. Hermit thrushes and white-throated sparrows were only observed at seven and nine of the 28 sites, respectively, and in low abundances (generally one per site) and so were excluded from habitat analyses. Of the three detections of Swainson's thrush (both years combined), all of them occurred at sampling stations with several large conifer trees, suggesting that this species was selecting for an overstory character which was rare in our study sites. We therefore eliminated these species when calculating species richness and diversity.

Black-throated blue warblers were the most abundant species detected followed by ovenbirds, veerys, American redstarts, and American robins in descending order of abundance (Table 4). Mean relative abundances of all understory species were similar between years except for white-throated sparrows which were more abundant

in 2002 than in 2001 ($P = 0.05$). Understory bird richness and diversity measures were also similar between years.

Understory songbird abundance and diversity were not significantly correlated with Canada yew variables, except for American Redstarts, which were negatively correlated with Canada yew abundance ($r = -0.38$; Table 5). American redstarts were also negatively correlated with forb abundance ($r = -0.44$). Black-throated blue warbler abundance was positively correlated with total stem density ($r = 0.51$), total FHD (0-3m; $r = 0.51$), and FHD in the 0-1m strata ($r = 0.66$), and negatively related to forb abundance ($r = -0.47$). Ovenbirds were negatively correlated with FHD in 0-1m strata ($r = -0.38$). Understory bird richness and diversity showed no significant correlations with other measures of understory structure. Multiple regression models that incorporated quadratic effects for Canada yew abundance or dominance were not significant for any individual species or diversity measure.

Discussion

Canada yew is clearly an important component of understory structure in our study area. Dense Canada yew appears to decrease seedling density of deciduous woody species and forbs. Foliage height density was not related to Canada yew stem density directly, apparently because the presence of other woody and herbaceous plants also provide understory structure. However, importance of Canada yew was quadratically related to FHD, particularly in the 0-1m strata. In other words, FHD was greatest when Canada yew was of intermediate importance in forest understories. Essentially, the structure provided by Canada yew is additive to structure provided by other species at intermediate values of Canada yew abundance. At greater abundances, it

appears that structure provided by Canada yew is compensatory in nature: it provides some structure under <1m but may also reduce understory plant structure that would have been provided by other hardwood species and forbs. In stands where Canada yew was the principal understory structural component, it was particularly important in providing FHD.

At higher densities, Canada yew comprised the majority of woody plant biomass. Only a small portion of Canada yew stems in our study stands exceeded 1m in height. At these high yew densities, there tends to be little woody plant biomass in the 1-3m strata in the understory. Correlations between Canada yew abundance and density of stems >1m were negative, although not significant. The effect of Canada yew on recruitment of small hardwood seedlings into taller strata therefore appears minimal. This is consistent with observations reported by others for northern hardwood and boreal forests in the Great Lakes region (Braun 1950, Risenhoover and Maass 1987, Danz 1998). It is possible that the negative effects of interspecific competition between Canada yew stems and hardwood seedlings is compensatory to competition between deciduous woody species such as sugar maple and beech.

Many studies have suggested that most small mammal species in eastern forests are habitat generalists and therefore, while they may be loosely associated with particular plant species, they are more often associated with physiognomy (e.g., Brower and Cade 1966, Healy and Brooks 1988, Bowman et al. 2001). Our results are consistent with this pattern; we detected few significant correlations between habitat variables and individual species abundance. Belant and Windels (2003) documented higher abundance, species richness, and diversity of small mammals at

sites with abundant Canada yew compared with adjacent sites without it in the Upper Peninsula of Michigan. Their study design was limited because it did not allow comparisons between sites populated by similar densities of Canada yew and other substrates such as deciduous stems, and thus they could not test if small mammals were responding to floristics or physiognomy. Further, Belant and Windels (2003) measured abundances at a finer scale where there was more contiguous coverage of Canada yew than was present at the stand-level scale in our study. Thus, the same patterns they found may not be true at larger spatial scales where horizontal structure, and therefore small mammal abundance, is more heterogeneous.

Though abundance of red-backed voles was not related to Canada yew abundance, they were more likely to be present in sites that contained Canada yew versus those without it. Similar results were found in nearby sites by Belant and Windels (2003) and in southern Quebec (C. Maisonneuve, unpublished manuscript). Belant and Windels (2003) speculated that the relatively high moisture requirements of red-backed voles (Gentz 1968, McManus 1974) can be more easily met in patches of dense Canada yew, where the dense growth form intercepts more light (Aubin et al. 2000), collects greater amounts of leaf litter (S. Windels, personal observation), and slows evaporation more than other types of plant growth forms present in northern forests.

Contrary to many studies conducted at the scale of individual forest stands (e.g., Wiens 1981, Willson and Comet 1996, Hobson and Bayne 2000, Fleishman et al. 2003), we did not detect significant relationships between measures of bird diversity and understory vegetation structure. This may be partly explained by the habitat

generalism displayed by the five most common species in our analyses. American redstarts, American robins, black-throated blue warblers, ovenbirds, and veerys were detected in a majority of sampled stands (61-89%), and only black-throated blue warblers and ovenbirds demonstrated any significant correlations with measures of general understory structure such as woody stem density or foliage height density.

Black-throated blue warbler abundance was not correlated with Canada yew abundance in our study. We did detect positive associations between black-throated blue warblers and total woody stem density and FHD at the stand level. These results are similar to those reported for black-throated blue warblers elsewhere (Steele 1992, Kearns et al. 2006). Steele (1992) reported that breeding black-throated blue warblers selected forest stands based on shrub density but that individual territories had similar shrub densities as adjacent unoccupied areas. He hypothesized that black-throated blue warblers selected forest stands that contained a threshold density of shrubs, above which most territories would have access to several patches of shrubs for nesting or foraging. In closed canopy northern hardwood forests in the Great Lakes region with relatively bare understories, Canada yew may be the only species capable of providing this threshold density.

However, Steele (1993) reported that within forest stands, black-throated blue warblers selected nest sites based on total shrub stem density and that selection of foraging sites was more plastic. He also found that density of hobblebush (*Viburnum alnifolium*) was significantly greater at nest sites than random sites but other species of shrubs were not, despite achieving similar stem densities as hobblebush. Steele (1993) argues that because black-throated blue warblers are found outside of the

range of hobblebush that it is more likely that black-throated blue warblers are not selecting for floristics but for a particular type of shrub that provides the required structure. A similar argument could be made for Canada yew, i.e., that black-throated blue warblers are not selecting habitats based on presence or abundance of Canada yew but instead are focusing on the unique structure that this species can provide. We suggest more research is needed to elucidate relationships between Canada yew and black-throated blue warblers at finer spatial scales.

Anecdotal accounts suggest black-throated blue warblers show a high preference for nesting in dense patches of Canada yew (Bent 1953, Holmes 1994, Holmes and Pitt 2007). However, independent evidence suggests that stands with high abundance of Canada yew may also act as sinks for birds that prefer nesting in dense shrubs such as black-throated blue warblers and veerys. Predation rates on artificial nests increased as Canada yew cover increased for 22 forest stands in northern Michigan ($R^2 = 0.56$, $P < 0.01$; S. Windels unpubl. data) even though small mammal abundance was not closely related to Canada yew abundance in that study. Though Canada yew may be a preferred nesting habitat for some bird species, at higher abundances Canada yew may homogenize understory structure and therefore potential nest sites to the point where small mammals can more efficiently predate songbirds nests (Martin 1988).

Canada yew can provide crops of red, fleshy arils (fruits) in some years that may be attractive to small mammals (Wilson et al. 1996) and frugivorous birds (Martell 1974). Arils typically ripen in late August and may remain on the stems until late fall (Wilson et al. 1996). Thus, ripe arils are typically not available during the period we

sampled small mammals and birds in our study and it is not clear if abundance of species documented in our study would be reflective of an attraction to this food source.

We selected sites in our study based on general overstory characteristics and Canada yew coverage, not understory structure *per se*. The abundance (0-55% cover) and height (most <1.0m) within stands in this study is typical of the northern portions of the Upper Peninsula, and therefore, we believe our results are representative of the current forest. However, we are less confident that our results are representative of the entire gradient of Canada yew abundance and physical attributes (e.g., stem height) that was historically present in North America, particularly for islands. Islands in the Great Lakes and elsewhere provide evidence that Canada yew can achieve densities up to 85% at the stand-level and exceed 3m in height in the absence of ungulate browsing and other disturbances such as fire (see Chapter 1). We speculate that Canada yew historically was able to grow to these extremes on mainland sites that remained free of these disturbances for a relatively long period of time. Additional research on the vegetation and understory vertebrate patterns we examined here would be valuable.

Conclusions

Our study examined understory vertebrate associations with a specific taxon (Canada yew) and with physiognomy, i.e., understory structure. In other words, we investigated whether the loss of Canada yew from forest understories was mediated by the presence of other understory vegetation that provides similar structure for individual songbird and small mammal species. We detected no relationships

between Canada yew abundance and the abundance of understory vertebrates, suggesting that the small mammal and songbird species present in our study area do not select habitats at the stand-level based on the presence or abundance of Canada yew. We did detect some relationships between abundance and other structural variables that suggest that Canada yew can have indirect effects on ground and shrub dwelling vertebrates. For example, several species, including short-tailed shrews and black-throated blue warblers were positively related to total FHD. Our data demonstrated that stands with abundant Canada yew tended to have lower values of FHD in these strata. Canada yew abundance had a negative, albeit non-significant, effect on abundance of hardwood stems >1m. Canada yew in our study also rarely exceeded 1m in height, and therefore did not contribute to FHD above 1m.

Taken as a whole, our data suggests that the loss of Canada yew from Great Lakes forests does not necessarily result in a decline in understory structure, as this decline may in fact be mediated by the presence of other plant species, particularly in forests with some canopy disturbance. However, within closed canopy forests that receive relatively low levels of canopy disturbance (e.g., in protected areas such as Pictured Rocks National Lakeshore, Michigan), the reduction or extirpation of Canada yew to chronic deer browsing may result in a decline in understory structure and therefore may negatively affect species richness and diversity of understory vertebrates.

Acknowledgements

We thank R. Posey, A. Kavalunas, D. Oberg, L. Kruger, and J. Belant for assistance in the field, and Pictured Rocks National Lakeshore, Hiawatha National Forest, and Shelter Bay Forests for access to study sites. We thank C. Huckins, J. Meeker, and L. Nagel for comments that improved earlier drafts. This research was supported by grants from Michigan Department of Natural Resources Natural Heritage Grant Program, The Nature Conservancy – Michigan, and the DeVlieg Foundation, and a graduate fellowship from Michigan Technological University. The National Park Service also provided support during manuscript preparation.

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Table 1. Mean values for vegetation variables measured at 28 northern and mixed-forest stands in Michigan, USA.

Variable	OPEN	Site Class	
		INTERMEDIATE	CLOSED
Number of Sites	11	8	9
Tree Basal Area (m ² /ha)	19.7 (0.9)	22.7 (0.9)	30.4 (1.9)
Canopy Cover (%)	83.0 (1.3)	92.1 (1.4)	94.4 (0.6)
Deciduous Species (<3cm d.b.h.; stems/m ²)			
Total	9.0 (2.6)	6.5 (1.5)	2.8 (0.8)
<0.5m	7.4 (2.5)	4.8 (1.2)	2.1 (0.6)
0.5-1.0m	1.2 (0.2)	1.2 (0.3)	0.4 (0.2)
1.0-2.0m	0.25 (0.04)	0.36 (0.09)	0.15 (0.07)
2.0-3.0m	0.05 (0.01)	0.11 (0.04)	0.06 (0.04)
>3.0m	0.02 (0.01)	0.08 (0.02)	0.04 (0.05)
Conifer Species (<3cm d.b.h.; stems/m ²)			
	0.03 (0.01)	0.05 (0.08)	0.08 (0.07)
Canada Yew (stems/m ²)			
Total	8.0 (1.7)	3.8 (1.1)	5.2 (1.8)
<0.5m	7.0 (1.6)	3.2 (1.0)	4.4 (1.5)
0.5-1.0m	0.89 (0.19)	0.49 (0.17)	0.79 (0.36)
1.0-2.0m	0.03 (0.02)	0.04 (0.03)	0.01 (0.01)
Herbaceous Cover (%)			
Total	20.8 (2.7)	18.1 (3.4)	29.5 (5.1)
Forbs	7.7 (2.1)	7.2 (2.0)	14.4 (3.7)
Ferns	10.6 (1.5)	9.3 (2.1)	12.9 (1.5)
Grass	2.4 (0.6)	1.6 (0.6)	2.2 (1.1)
FHD Values			
Total (0-3m)	11.9 (1.4)	11.7 (1.6)	8.2 (1.8)
0-1m	6.2 (0.4)	5.3 (0.6)	3.9 (0.5)
1-2m	2.7 (0.5)	3.2 (0.5)	2.1 (0.7)
2-3m	2.9 (0.5)	3.2 (0.6)	2.1 (0.7)

Table 2. Mean (SD) relative abundance (captures/100 ATN) and diversity indices for small mammals captured in 2001 and 2002 in 28 northern and mixed hardwood stands in Michigan's Upper Peninsula.

Variable	2001		2002	Total
Deer Mouse	14.2 (6.5)	*	20.7 (7.9)	18.1 (7.9)
Red-backed Vole	4.9 (6.1)		3.8 (5.2)	4.3 (5.5)
Eastern Chipmunk	2.9 (2.7)		4.3 (4.2)	3.8 (2.7)
Short-tailed Shrew	3.6 (2.4)	*	0.8 (1.2)	1.9 (2.2)
Masked Shrew	0.7 (1.3)		0.3 (0.9)	0.5 (1.1)
Northern Flying Squirrel †	0.3 (0.6)		0.1 (0.2)	0.1 (0.4)
Red Squirrel †	0.1 (0.3)		<0.1 (0.2)	0.1 (0.2)
Woodland Jumping Mouse †	0.1 (0.2)		0 (na)	0.0 (0.1)
Total Captures	26.7 (8.8)		30.0 (9.9)	28.7 (9.5)
Richness	3.9 (1.1)		3.2 (1.0)	3.5 (1.1)
Diversity (H')	1.00 (0.29)	*	0.69 (0.31)	0.81 (0.34)
No. Sites	11		17	28
Adjusted Trap Nights (ATN)	3745.5		5643	9388.5

† Species not included in richness or diversity indices

* Indices different between years ($P < 0.05$)

Table 3. Correlations among small mammal species abundance and diversity measures with habitat variables from 28 northern and mixed hardwood stands in Michigan's Upper Peninsula, 2001-2002. Bolded values highlight significant results ($P < 0.05$).

Variable	Deer Mouse	Red-backed Vole	Short-tailed Shrew	Eastern Chipmunk	Total Captures	Species Richness	Shannon Weiner (H')
Canada Yew Density (stems/m ²)	-0.26	0.08	0.03	-0.25	-0.27	0.21	0.23
Canda Yew Dominance ^a	-0.16	0.03	-0.13	-0.17	-0.23	0.09	0.14
Hardwood Density (stems/m ²)	0.03	0.03	0.13	-0.13	0.03	0.04	-0.14
Total Stem Density (stems/m ²)	-0.17	0.07	0.13	-0.30	-0.18	0.19	0.04
Herbaceous Cover (%)	-0.20	-0.06	-0.06	-0.22	-0.30	-0.26	-0.08
Forb Cover (%)	-0.16	-0.04	0.21	-0.24	-0.28	-0.34	-0.24
Total FHD (0-3m)	-0.32	0.14	0.30	-0.07	-0.10	0.36	0.34
0-1m FHD	-0.51*	0.29	0.48*	-0.03	-0.15	0.41*	0.48*
CWD (cm ³)	-0.08	0.30	-0.13	0.25	0.17	-0.06	0.24

^a Yew dominance was defined as the ratio of Canada yew stem density to total woody stem density

* $P < 0.05$, ** $P < 0.01$

Table 4. Mean (SD) relative abundance (observations/point count station) and diversity indices for breeding forest birds in 2001 and 2002 in 28 northern and mixed hardwood stands in Michigan's Upper Peninsula.

Variable	2001	2002	Total
American Redstart	0.13 (0.13)	0.21 (0.24)	0.18 (0.20)
American Robin	0.16 (0.09)	0.10 (0.15)	0.13 (0.13)
Black-throated Blue Warbler	0.39 (0.31)	0.37 (0.21)	0.38 (0.25)
Hermit Thrush	0.03 (0.05)	0.04 (0.07)	0.03 (0.06)
Ovenbird	0.27 (0.25)	0.34 (0.23)	0.31 (0.24)
Swainson's Thrush †	0.02 (0.04)	<0.01 (0.03)	0.01 (0.04)
Veery	0.33 (0.25)	0.17 (0.18)	0.23 (0.22)
White-throated Sparrow	0.01 (0.04)	* 0.15 (0.21)	0.09 (0.17)
Total Birds	1.34 (0.57)	1.37 (0.65)	1.36 (0.61)
Richness	4.2 (0.8)	3.9 (1.5)	4.0 (1.2)
Diversity (H')	1.08 (0.44)	1.11 (0.30)	1.10 (0.39)
No. Sites	11	17	28

† Species not included in richness or diversity indices

* Indices different between years ($P < 0.05$)

Table 5. Correlations among understory songbird species abundance and diversity measures with habitat variables from 28 northern and mixed hardwood stands in Michigan's Upper Peninsula, 2001-2002. Bolded values highlight significant results.

Variable	American Redstart	American Robin	Black-throated Blue Warbler	Ovenbird	Veery	Total Birds	Richness	Diversity
Canada yew density (stems/m ²)	-0.38*	-0.10	0.32	-0.20	-0.13	-0.19	-0.20	-0.20
Canda yew dominance ^a	-0.32	0.00	0.09	0.07	-0.17	-0.15	-0.13	-0.17
Hardwood density (stems/m ²)	0.20	-0.26	0.29	-0.10	0.10	0.15	0.09	0.14
Total stem density (stems/m ²)	-0.09	-0.30	0.51*	-0.24	-0.01	-0.01	-0.06	-0.02
Herbaceous Cover (%)	-0.44*	0.19	-0.37	0.06	0.02	-0.37	-0.19	-0.34
Forb Cover (%)	-0.29	0.02	-0.51*	0.19	-0.06	-0.32	-0.23	-0.33
Total FHD (0-3m)	0.24	-0.05	0.47*	-0.26	0.27	0.28	0.29	0.33
0-1m FHD	0.09	-0.11	0.66**	-0.38*	0.25	0.23	0.11	0.23

^a Yew dominance was defined as the ratio of Canada yew stem density to total woody stem density

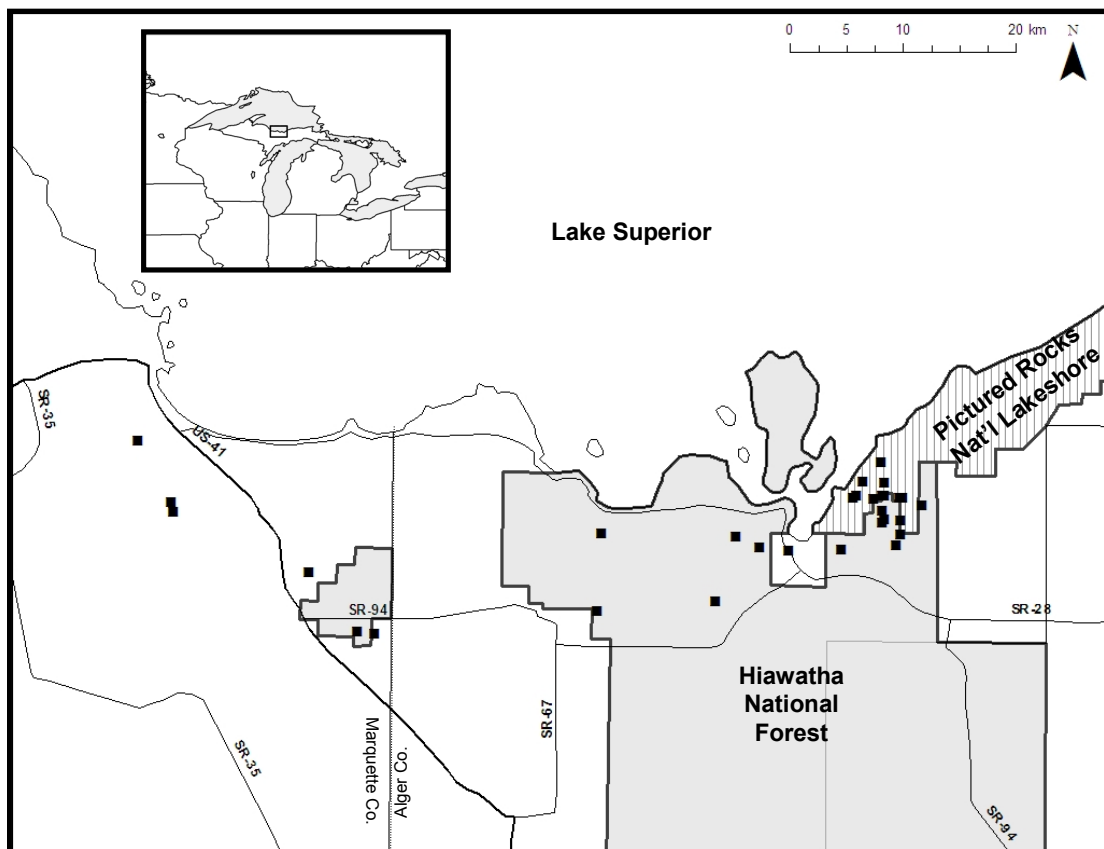
* P < 0.05, ** P < 0.01

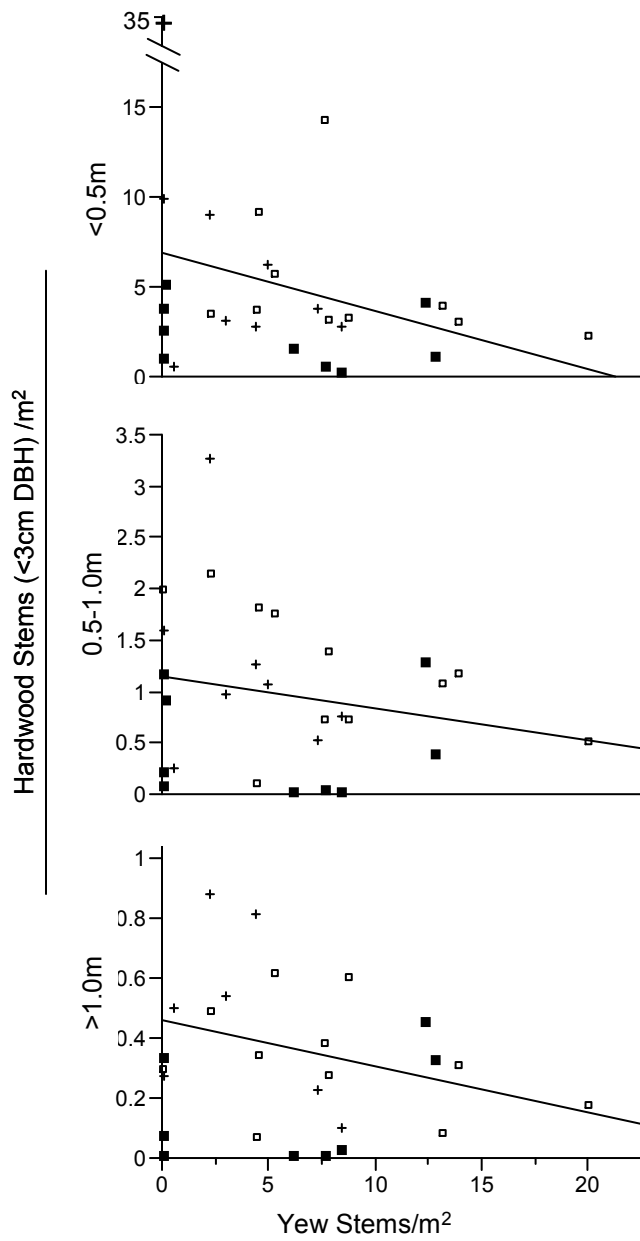
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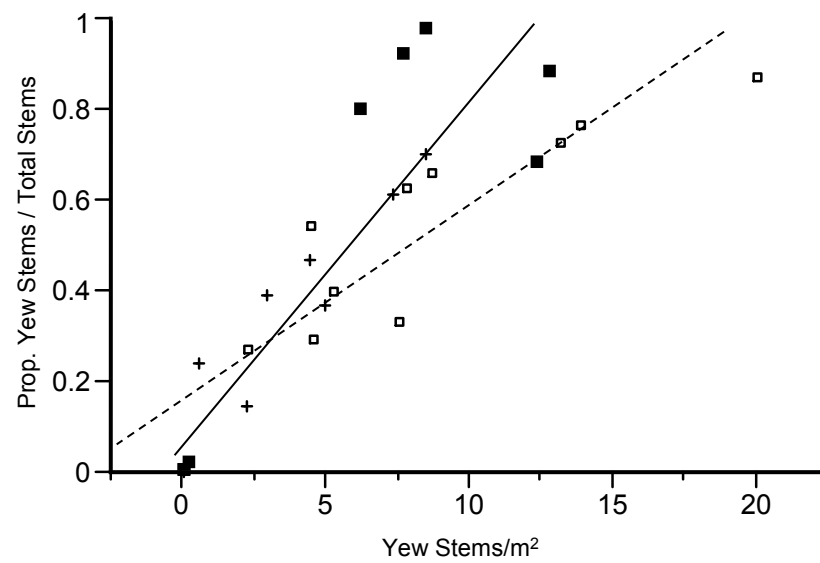
Figure 1. Distribution of study sites (black squares) in Marquette and Alger counties, Michigan, USA. Inset shows location of study area in relation to the Great Lakes.

Figure 2. Scatterplots of Canada yew density (stems/m²) vs. hardwood stem density for stems <0.5m, 0.5-1.0m, and >1.0m tall for 28 northern and mixed-hardwood stands in Marquette and Alger counties, Michigan, USA. Dashed line represents linear fit based on all 28 sites. Symbols for overstory classes are OPEN (open squares), INTERMEDIATE (crosses), and CLOSED (filled squares).

Figure 3. Proportion of total stems comprised of Canada yew stems as a function of Canada yew abundance for 28 northern and mixed-hardwood stands in Marquette and Alger counties, Michigan, USA. The slope of the regression line (dashed) for the OPEN (open squares) overstory sites was significantly different from the slopes for regression lines (solid) for the CLOSED (filled squares) and INTERMEDIATE (crosses) overstory sites.







No copyrighted materials were used in this dissertation.