

The ecology of Canada Yew (*Taxus canadensis* Marsh.): A review

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Abstract: Canada yew (*Taxus canadensis* Marsh.) is a shade-tolerant 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 accounts suggest that before Euro-American settlement, Canada yew was a common plant across its range in many forest types and 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 during the last century 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 abiotic and biotic conditions, 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. Suggestions for future research are discussed.

Key words: autecology, Canada yew, *Taxus canadensis*, distribution, white-tailed deer, browsing effects.

Résumé : L'if du Canada (*Taxus canadensis* Marsh.), un arbuste nain toujours vert et tolérant l'ombre, est indigène dans les sous-bois de forêts boréales et décidues de nord-est de l'Amérique. L'if du Canada montre une forme de croissance relativement unique, avec ses longues branches traînantes capables de former des groupes de tiges. Les données historiques suggèrent qu'avant l'arrivée des Européens au Canada, l'if constituait une plante commune sur l'ensemble de son aire dans plusieurs types de forêts et qu'il était localement abondant ou dominant dans 5–20 % des peuplements forestiers dans la partie nord de son aire. L'aire de l'if du Canada a décliné au cours du dernier siècle, suite au broutage par les ongulés indigènes, au feu, à l'aménagement intensif des forêts, et au défrichage des sols aux fins de l'agriculture et autres développements. On le considère comme peu commun sur l'ensemble de son aire nord-américaine actuelle, sauf pour des populations souvent isolées dans les régions qui demeurent à l'abri du broutage intensif par les orignaux et les cerfs de Virginie (e.g., îles, régions avec fort couvert de neige, ou régions naturellement à faible abondance d'ongulés). Son déclin a vraisemblablement fait suite à des changements abiotiques et biotiques, incluant la structure et la composition de la végétation de sous-bois, et leurs effets concomitants sur les vertébrés des sous-bois. Une augmentation des populations du cerf de Virginie et une réduction des couverts de neige suite aux changements climatiques dans l'est de l'Amérique du Nord menacent cette espèce d'extirpation sur d'autres parties de son aire au cours du prochain siècle. Les auteurs proposent des suggestions pour les recherches futures.

Mots-clés : autécologie, if du Canada, *Taxus canadensis*, distribution, cerf de Virginie, effet du broutage.

[Traduit par la Rédaction]

1. Introduction

Canada yew (*Taxus canadensis* Marsh.), a formerly widespread evergreen forest shrub, is of conservation interest for several reasons. First, its decline is frequently cited as an ex-

ample of the negative effects of white-tailed deer (*Odocoileus virginianus*) on forest ecosystems (e.g., Leopold et al. 1947; Allison 1990a, 1990b; Waller and Alverson 1997; Soulé et al. 2003; Holmes et al. 2009) and may serve as a case study for other overabundant herbivore–plant systems

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in North America and beyond. Canada yew (or alternatively as “yew”) is often described as being “formerly abundant” or “common” in many forest types in eastern North America before browsing by deer and (or) moose (*Alces alces*) functionally removed it from much of its historic range (e.g., Braun 1950; Curtis 1959). Although anecdotal evidence of this range contraction and decline in abundance is very common, quantitative data on the historic abundance of yew are scarce. Nevertheless, the general perception that yew has disappeared from parts of its historic range and declined where it still persists has raised concern about potential cascading effects of its decline on other ecosystem components (e.g., Braun 1950; Waller and Alverson 1997). In addition to historic and ongoing threats, an incipient industry in eastern Canada based on leaf harvesting for extraction of paclitaxel (Taxol®) and other pharmaceuticals has added an economic component to the ecological rationale for its conservation (Cameron and Smith 2002).

In this paper, we review information on the ecology of 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 for future research aimed at the conservation of yew. This review includes information from published sources, grey literature, and unpublished data. We do not review yew's pharmacological properties and related economics because these subjects have 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 (<3 m), straggling growth form with upright branches that reach 2–4 m (Voss 1972; Pinto and Herr 2005). Needles of Canada yew are linear, flat, attach spirally along the stem, and measure 1–2.5 cm long and 1–3 mm wide (Pinto and Herr 2005). Live stems retain their foliage up to 8 years (Allison 1990a), while dead needles can remain for up to 2–5 years after twig/stem death (Krefting 1974). Canada yew is monoecious and male and female cones are initiated in the leaf axils during the summer and overwinter as buds (Dupler 1919, 1920; Wilson et al. 1996). Ovules are wind pollinated in spring, with fertile female cones developing a single hard seed surrounded by a fleshy red aril (Wilson et al. 1996).

3. Taxonomy and genetics

The genus *Taxus*, which dates from the Jurassic Period (Florin 1958), comprises nine, mostly allopatric species (Price 1990), although Spjut (2007a) recently proposed recognition of 24 species and 55 varieties based on morphology. Members of the genus are generally defined by (i) production of a seed partly surrounded by a loose, cup-like, reddish aril and (ii) the development of stomata in rows (Spjut 2007b). 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 2007a). The phylogenetic relationship of Canada yew to other members of the genus remains equivocal (e.g., Senneville et al. 2001; Collins et al. 2003; Spjut 2007a; Hao et al. 2008).

At the species level, Canada yew demonstrates low overall genetic diversity across its North American range (Senneville et al. 2001; Corradini et al. 2002). Several barriers exist to establishment of disjunct yew populations, including irregular seed crops, low germination rates, and long periods of seed development, and these may limit gene flow between isolated yew populations that likely started from a single seedling (Senneville et al. 2001).

Canada yew is most often found in patches and is considered a clonal plant, which is defined as individual, often interconnected, ramets (stems), constituting a genet (individual). Both Senneville et al. (2001) and Corradini et al. (2002) confirmed that 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 Postglacial history

The postglacial history of Canada yew in eastern North America is not well understood and the difficulty of distinguishing yew pollen from similar species makes clear conclusions difficult. However, the oldest occurrences of macrofossils and (or) pollen of Canada yew in North American sediment cores are as follows (range of years BP): central Minnesota (ca. 13 600 – 12 500) (Birks 1976); northeast Iowa (ca. 12 500 – 9300) (Baker et al. 1996); northern Maine (ca. 10 500 – 8800) (Anderson et al. 1986); New Hampshire (ca. 8400–7100) (Spear et al. 1994); and southwestern Quebec (ca. 8400) (Carcaillet et al. 2001). Carcaillet et al. (2001) suggest that yew was the dominant understory shrub in white pine (*Pinus strobus* L.) forests in southwestern Quebec by ca. 6500 years BP. Therefore, it appears that 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 constituting the current northern hardwood and mixed hardwood forests of northeastern North America — sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britt.), and white pine — migrated into the region between 9000–4000 years BP. (Davis 1983; Pielou 1991). Canada yew's migration during glacial retreat was faster than expected based on some aspects of its life history, including relatively slow growth and dependence on moist, organic soils (Martell 1974). However, several authors have suggested that some Canada yew populations may have persisted in refugia during glaciation in rocky cliffs or steep ravines and subsequently acted as local sources for reestablishment (Gonsoulin 1975; Larson et al. 2000).

4.2 Historic distribution

At the time of Euro-American settlement, Canada yew's range likely spanned the forested regions of northeastern

North America, from southeastern Manitoba to Newfoundland and south as far as northeastern Iowa, eastern Kentucky, and western Virginia (Fig. 1; Little 1971; Martell 1974). It has been documented in 19 US 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 7 Canadian provinces (Labrador, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Islands, and Quebec), (Little 1971; NatureServe 2007).

Although Canada yew's northern limit is relatively imprecise, its southern limit is well defined. Canada yew's pre-Euro-American settlement distribution was limited to cool, mesic forest areas, with mean annual precipitation ranging from 550 to 1650 mm, and mean annual temperature between -5.1 and 13.0 °C (Table 1; Thompson et al. 1999). The core of its range also roughly overlaps with an area of relatively high mean winter snow depth (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 its pre-Euro-American settlement distribution at finer spatial scales, namely its frequency of occurrence at the landscape scale (i.e., among forest stands), and its frequency, percent cover, and relative dominance within forest stands. This lack of a precise historic picture of yew in North America has caused confusion about its relative importance in forests across its range that has, in our opinion, hampered prioritization of yew for conservation. To partly address this issue, we compiled data from anecdotal accounts and published sources to better describe its historic distribution and role in North American forests ²). Observations in these accounts range from 1822 to 2007. However, because of yew's sensitivity to overbrowsing by herbivorous mammals, fire, and forest disturbance, this plant likely experienced the greatest declines from its historic maximum in parts of its range where it has experienced Euro-American settlement the longest. In other words, we suspect that in many cases, Canada yew had already declined by the time its distribution was documented and therefore inferences made here about its historic distribution and abundance should be considered conservative. Below, we summarize what is known about yew's distribution on mainland and island sites, some of which lacked browsing ungulates.

4.2.1 Mainlands

Nichols (1935) and Martell (1974) described yew as "common" throughout the northern and mixed hardwood forests of northeastern North America. Martell (1974) stated that 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. In Wisconsin, Curtis (1959) reported yew as a "characteristic shrub" of mesic northern hardwood

forests, and Braun (1950) listed it as "frequent" in eastern white cedar (*Thuja occidentalis* L.) bogs within beech–maple forests of the southern Great Lakes states.

Some quantitative data on frequency of occurrence within landscapes are 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). At finer landscape scales, Curtis (1959) found it in 27% of northern mixed hardwood forest plots across northern Wisconsin and Ohmann 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, it was present in 20% of boreal forest stands in north central Minnesota (Buell and Niering 1957), 14% of hemlock stands in New Hampshire (L. 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 appears unlikely that it 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 its patchy and erratic distribution at the landscape level is related to yew's limited ability to colonize by seed (See Section 5.1), but other factors such as disturbance regimes (e.g., fire and blowdown events), land use legacies, and local population dynamics of browsing mammals are also likely involved.

Where Canada yew is present in mainland habitats, however, there are numerous cases of it dominating the understory. It is known as *ne'bagandaag* in Ojibwemowin, which can be translated as "laying everywhere on the ground" (J. Meeker, personal communication). Leopold et al. (1947) stated that parts of Wisconsin, Michigan, Pennsylvania, and New York had "accumulated heavy growths of ground hemlock." It 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 Grandpré and Bergeron 1997), and Wisconsin (Braun 1950). It 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., eastern white cedar) stands in Upper Michigan, the General Land Survey noted yew on 33%–75% of survey lines, suggesting it was the dominant understory plant (Van Deelen et al. 1996). Other studies have also suggested that yew was one of the most important components of lowland conifer understories in Ohio (Collins et al. 1979) and Minnesota (Ohmann and Ream 1971).

Some quantitative information regarding the historic importance of yew is also available. Maximum cover values reported for yew in boreal forest stands are 12%–64% in

² See table S1 of Supplementary Material at <http://botany.nrc.ca>.

Fig. 1. Distribution of Canada yew (*Taxus canadensis*) in North America. Map is derived from Little (1971).

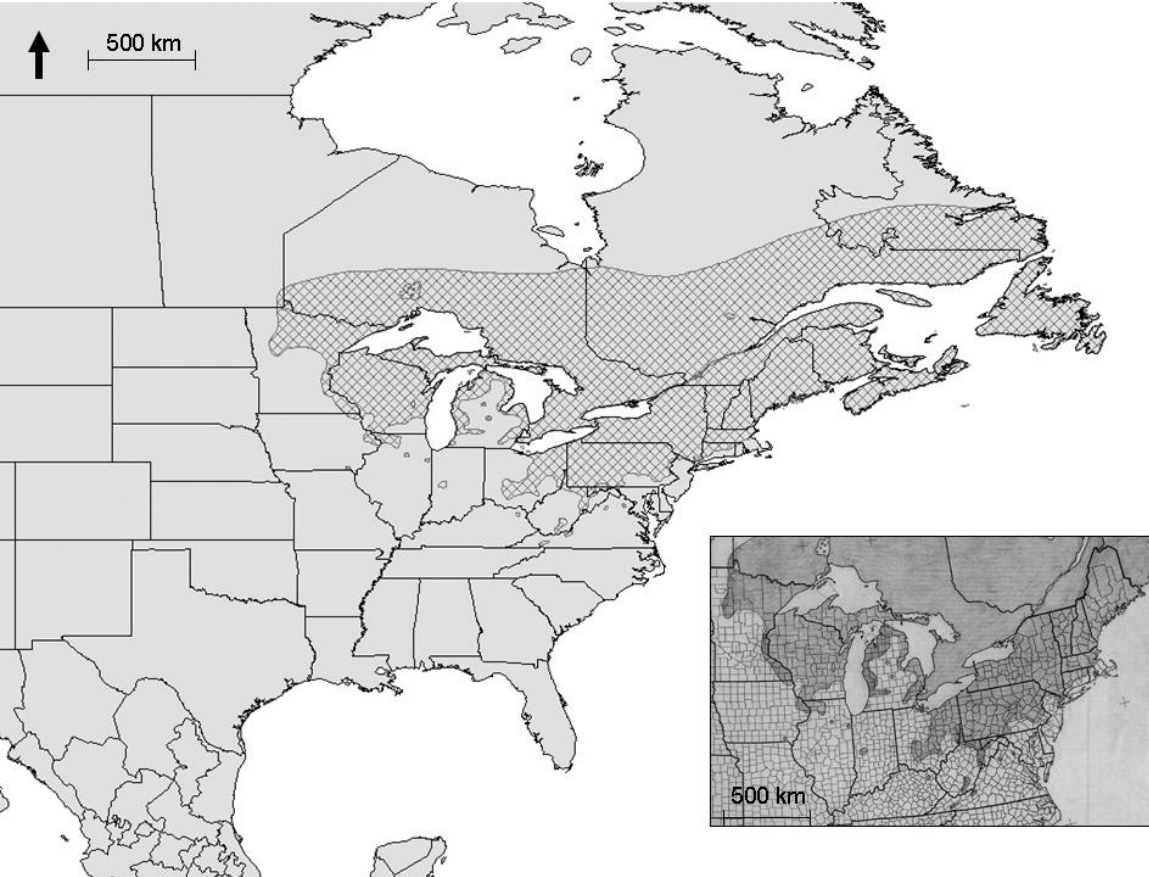


Table 1. Climatic variables for Canada yew within its North American range as described by Little (1971).

Climate variable	Minimum	Median	Maximum
Mean annual temperature (°C)	−5.1	2.6	13.0
Mean Jan. 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 Jan. precipitation (mm)	17	68	163
Mean July precipitation (mm)	60	98	212
Growing degree days ^a	0.3	1.3	3.2
Average Dec. snow depth (cm)	0.0	21.8	49.0
Average Jan. snow depth (cm)	0.0	39.3	71.2
Average Feb. snow depth (cm)	0.0	50.6	90.2
Average Mar. snow depth (cm)	0.0	44.8	97.1
Average Dec.–Feb. snow depth (cm)	3.9	37.0	69.5
Average Nov.–Mar. snow depth (cm)	3.6	34.5	65.1
Average no. of days ≥ 50 cm snow depth	0	38	114

Note: Temperature, precipitation, and growing degree days are from Thompson et al. (1999). Snow depth data are from D. Kluver (unpublished data) and are based on analysis of North American snow depth data from 1947 to 2001. See Kluver (2007) for more details on how the data were calculated.

^a5 °C base × 1000; represents the total amount of energy available to the plant through the course of the year.

Minnesota (Buell and Bormann 1955; Buell and Niering 1957) and 57% in Quebec (De Grandpré et al. 1993). Rogers (1980) reported a mean cover value of 13% for all 71 hemlock stands sampled in northeastern North America, while

yew represented 2% of the understory in a single hemlock stand in New Hampshire (L. Howard, personal communication). Maximum values for yew cover in northern and mixed hardwood stands are 33%–100% in Massachusetts (Egler

1940), 1%–54% in Michigan (S. Windels, unpublished 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 ungulate-free islands (particularly in the Great Lakes and the Atlantic Provinces), it appears that yew attained its highest frequency of occurrence and coverage. Holt (1905 in Krefting 1974) stated that yew was “everywhere abundant in the upland forest” of Isle Royale (Lake Superior) and McMurray (1933, cited in Krefting 1974) estimated that, prior to the arrival of moose (*Alces alces*), it covered one third of the island (or approximately 18 000 ha) based on the 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 the 1992 surveys, it was still described as “dominant” or “dense” on 11 of the 22 islands, with cover values ranging from 24% to 83%. Beals et al. (1960) further describes the likely historic state of 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.” On other Great Lakes islands it has been described as forming “a dense impenetrable ground cover” (Manitou Island, 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 many islands in the Atlantic Provinces. During an expedition across Newfoundland Island in 1822, Cormack (1928) described 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 yew. Glen (1999) reported yew occurred in 12% of northern and mixed hardwood forest plots across Prince Edward Island, with coverage values ranging from 1% to 100%.

4.3 Current status and distribution

At this time, Canada yew can be found in all of the states or provinces listed as part of its native range (NatureServe 2007). Its global status was last reviewed in 1983 and was ranked as G5 (globally secure; NatureServe 2007). It is ranked as N5 (nationally secure) in the United States and Canada. As of 2007, it was considered “vulnerable”, “impaired”, or “critically imperiled” in 12 states and 1 province in eastern North America (NatureServe 2007). It is also a Regional Forester Sensitive Species in five National Forests in the eastern US: Monongahela National Forest (West Virginia), Allegheny National Forest (Pennsylvania), Huron-Manistee National Forest (Michigan), Superior Na-

tional Forest (Minnesota), and the Chippewa National Forest (Minnesota), (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. One difficulty in describing the spatial nature of this decline is that it has not occurred uniformly across time or space. Nevertheless, there is convincing evidence from across the native range of Canada yew that the decline has been spatially broad and ongoing for much of the last century. Factors including overbrowsing, intensive forest management, land use change, and direct harvesting for pharmaceutical products continue to affect the current status of Canada yew.

However, areas remain where yew is still a dominant component of northern forest understories. In general, these are areas where winter white-tailed deer or moose abundances are low or where access to yew is restricted as on islands or steep slopes, rocky terrain, or where deep snowfall covers the plants (Stachowicz and Allison 1995; Waller and Alverson 1997). At least 25 islands in the US portion of the Great Lakes contain significant populations of yew (Ewert et al. 2004).

5. Life history

5.1 Growth and reproduction

Canada yew typically grows as a low, straggling shrub but often produces upright branches up to 2 m tall. Individuals up to 4 m tall and 9 cm 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; Martell 1974; Holmes et al. 2009). Mean annual mortality rate for individually marked ramets over a 9 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, unpublished data).

Densities of live stems from northern mixed hardwood forest stands in the Upper Peninsula of Michigan ranged from 0.10–20.0 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. Percent foliar cover of yew, as often cited in the literature, is closely correlated with stem density across its range and can be converted using the following formula: percent cover = 4.6042 + 2.895(stems/m²) ($R^2 = 0.844$, $P < 0.001$; Fig. 2).

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, woody debris, or soil), produces adventitious roots, and grows as a trophically and physiologically autonomous ramet (Wilson et al. 1996; Corradini et al. 2002). Long, prostrate stems are more likely to be pressed against the ground and produce adventitious roots than are short, erect stems (King 1970; Windels 2008). Data on rates of vegetative reproduction are lacking, particularly in relation to site conditions or geography. In northern Wisconsin, mean production of new ramets per square metre per

Table 2. Selected attributes and growth rates for natural populations of Canada yew (*Taxus canadensis* M.) in North America.

Character	Mean	Range	N	State/province	Source
Stem attributes					
Length (cm)	48	12–228	1172	Michigan	S. Windels, unpublished data ^a
Height (cm)	na	5–326	262	Wisconsin	Foster (1993)
	35	10–157	1172	Michigan	S. Windels, unpublished data ^a
Diameter (mm)	73	4–250	262	Wisconsin	Foster (1993)
	5.7	1.4–22.2	515	Michigan	S. Windels, unpublished data ^a
Age (years)	9.9	1.0–34.0	262	Wisconsin	Foster (1993)
	14	3–41	262	Wisconsin	Foster (1993)
	18	11–25	40	Michigan	Danz (1998)
	na	9–30	na	Quebec	Senneville et al. (2001)
Growth rates					
Twig length (cm/year)	4.3	1.1–11.6	126	Michigan	S. Windels, unpublished data ^b
	3.4	0.6–10.5	429	Michigan	S. Windels, unpublished data ^c
Stem height (cm/year)	na	1–8	na	Massachusetts	Wilson et al. (1996)
	~7.0	na	262	Wisconsin	Foster (1993)
	2.6	na	477	Michigan	S. Holmes, unpublished data ^d
Stem diameter (mm/year)	~0.7	na	262	Wisconsin	Foster (1993)

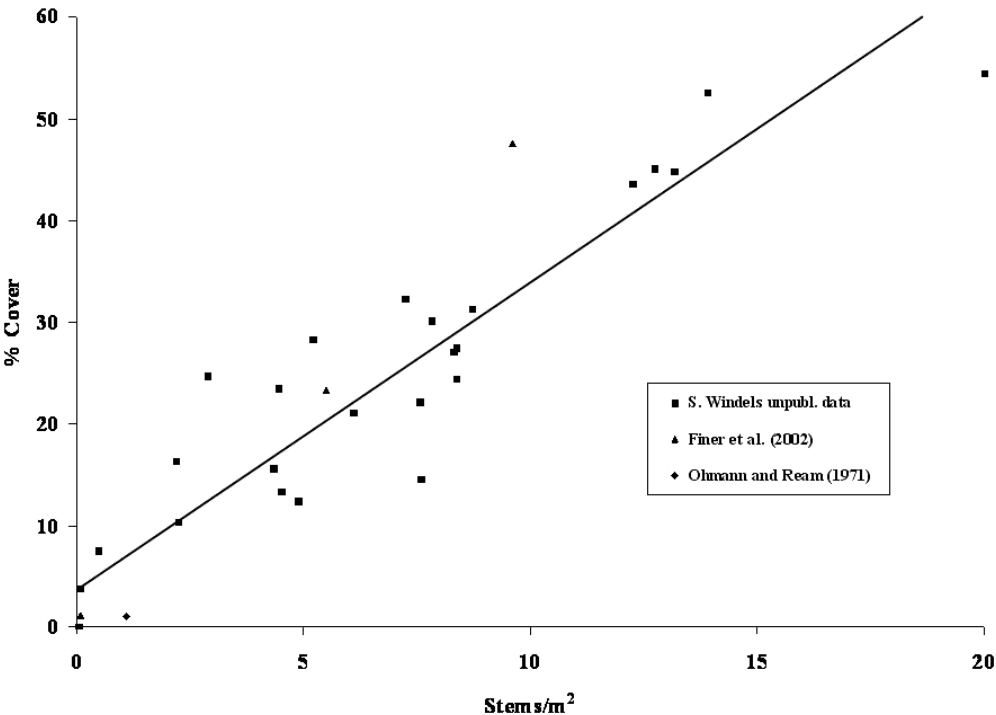
^aOnly stems >10 cm in length were measured.

^bTerminal twigs.

^cLateral twigs.

^dTransplanted cuttings protected in exclosures.

Fig. 2. Relationship of stem density (stems/m²) to % cover for Canada yew in Michigan, Minnesota, and Quebec. % cover = 4.6042 + 2.895(stems/m²) ($R^2 = 0.844$; $P < 0.001$). Data from S. Windels, unpublished data; Finer et al. 1999; and Ohman and Ream 1971.



year was 0.056 in fenced enclosures and 0.004 in adjacent sites exposed to deer browsing (S. Windels and D. Foster, unpublished data).

Contiguous patches of stems that are several hectares in size have been reported (Beals and Cottam 1960; Judziwicz and Koch 1993; S. Windels, personal observation). Corradini et al. (2002) reported patch sizes at their study site in Quebec ranged from 3 to 20 m 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 yew patches (m^2/year) are lacking. Allison (2006) estimated growth rates (in cross-sectional leaf area) for individual ramets to extrapolate areal growth of a single population on the Apostle Islands, Wisconsin. Growth rates ranged from 39 cm^2/year for small plants ($<1000 \text{ cm}^2$) to 197 cm^2/year for large plants ($>2500 \text{ cm}^2$).

Individual stems (ramets) are relatively short lived (Table 2), but individuals (genets) may live for hundreds of years (Corradini et al. 2002). Individual or groups of intertwined genets tend to occupy the same space or even migrate slightly over time (Hansen et al. 1973) through vegetative reproduction focused around radially symmetrical “founder” genets that are produced from seed (Senneville et al. 2001; Corradini et al. 2002).

The decumbent, or prostrate, portions of branches of 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 it is adapted to understories with deep organic layers, e.g., climax conditions. Berliner and Torrey (1989) reported that roots were “heavily colonized” by vesicular-arbuscular endomycorrhizal fungi during the entire growing season but found no evidence of ectomycorrhizae. A more detailed description of its root physiology is contained in Bannan (1942).

Several aspects of the reproductive ecology of Canada yew have been relatively well studied, including sex expression (Allison 1991, 2008), self-fertility (Allison 1993; Wilson et al. 1996), and pollination success (Allison 1990c; Wilson et al. 1996). The effects of herbivory on various aspects of the reproductive ecology of yew are also well known (Allison 1990a, 1990b, 1992).

Recruitment of new Canada yew stems via sexual reproduction appears rare in most populations, which has been attributed to bottlenecks at the seed production and (or) germination stage. Seeds begin ripening in mid-summer and most are mature by the early fall (Wilson et al. 1996). Densities of mature ripening seeds ranged from 0.03 to 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 depredated 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. 1998; 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), although mammalian seed predators consume all or part of the seed in addition to the aril in some parts of its range (Wilson et al. 1996).

Like other yews, seeds of Canada yew have relatively low germination rates (Young and Young 1992; Foster 1993; Hulme 1996; Senneville et al. 2001). Seeds require 60–120 d of cold stratification and temperatures of $\sim 15^\circ\text{C}$ for germination (Rudolf 1974). Microsite requirements for germination are unknown. 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; García et al. 2000).

5.2 Habitat

Canada yew can be found in mesic to wet-mesic forests $<1500 \text{ m}$ 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. See Table S1² for frequency and abundance of 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; Glen 1999 but see Stachowicz and Allison 1995) and is rarely found in old fields or other nonforested habitats (Egler 1940). It occurs on most soil types found within its range but appears to grow 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).

Canada yew is a highly shade tolerant species and therefore does not require substantial amounts of light 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 1 m (Aubin et al. 2000). Conversely, as a highly shade tolerant species, yew does not grow well in open environments; growth rates on south-facing slopes in Massachusetts were one quarter of those on level or north-facing slopes (Stachowicz and Allison 1995). Martell (1974) noted that it grows in open sites provided its roots are kept moist and cool. Optimal growth and survival of yew appears to be 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, 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 4 year experiment in Michigan where yew cuttings were transplanted into deer-proof enclosures suggest optimal growth rates occur in small canopy gaps, such as those created by individual tree falls (Holmes et al. 2009). Stem growth rates (cm/year) were greatest in small canopy gaps (50–150 m^2 in area; $\bar{x} = 3.0$),

intermediate in medium (151–250 m²; $\bar{x}$ = 2.5) and large (251–450 m²; $\bar{x}$ = 2.8) gaps, and least in closed canopy sites ($\bar{x}$ = 1.7). Yew decreased in abundance after 400 m² canopy gaps were created above yew patches in closed-canopy forests in Quebec (De Grandpré and Bergeron 1997). Likewise, Canada yew has been documented to be eliminated or reduced in abundance following deforestation (Egler 1940; Glen 1999) or intensive forest management (Nichols 1913; Egler 1940; Leopold et al. 1947; Stachowicz and Allison 1995; Glen 1999), presumably from a reduction in soil moisture and understory humidity below the tolerance level of Canada yew.

Although forest structure and soil characteristics are important, presence and abundance of yew may be most closely tied to moisture conditions at and below the soil surface owing to its relatively shallow root system. Growth rates of adventitious roots have been related to soil moisture in other plant species (e.g., Briske and Wilson 1978), and therefore layering by Canada yew is likely also related to available soil moisture. Canada yew is generally more abundant in late versus early successional forests (Whitney and Foster 1988; Glen 1999), north-facing versus south-facing aspects (Stachowicz and Allison 1995; Glen 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 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 with a maritime climate (e.g., the Canadian Maritime Provinces, 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 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 ungulate-free 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 yew appear to reach its greatest abundance and stature on islands rather than on mainland habitats? We suggest four factors unique to islands that provide optimal conditions. First, islands tend to support less stable populations of ungulates, and often lack herbivore species found on mainlands (e.g., Caughley 1970). As a result, islands are more likely to become ungulate free through stochastic population processes or avoid colonization and remain so for greater periods. Net annual growth rates for yew are greatest in the absence of browsers (See Table 3). Second, the cool and moist conditions associated with island maritime climates allow yew to grow faster than in most mainland habitats. This maritime effect would also essentially expand its

realized niche into areas where it may otherwise be limited by available microclimates. Third, frequencies of intense fires are generally lower on islands than on mainlands in boreal systems (e.g., Bergeron 1991). 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 yew grows best. Trees growing on islands tend to be more exposed, experience greater windspeeds, and grow in shallower soils than their mainland counterparts (Kramer et al. 2001; Elie and Ruel 2005).

5.3 Diseases and pests

Little information is available on diseases and pests affecting Canada yew. Its 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* L.) also appears well defended through various antifeedant compounds (Daniewski et al. 1998). Three species of exotic weevils, black vine weevils (*Otiorhynchus salcatus*), strawberry root weevils (*O. ovatus*), and an unnamed weevil (*Polydrusus impressifrons*), have been observed feeding on twigs (bark-feeding adults) or roots (larvae) of Canada yew in the Great Lakes Region, causing mortality of ramets when insect populations are high (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: (i) understory plant biomass/density, (ii) stratification of understory vegetation, (iii) plant species richness, (iv) nutrient cycling and belowground processes, and (v) fire frequency. Understory vegetation cover is typically inversely related to overstory vegetation cover (Constabel and Lieffers 1996; Aubin et al. 2000). However, 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, it can comprise more than 90% of total woody stem density and up to 27% of total ground cover in otherwise sparse understories (S. Windels, unpublished data). Similar conditions were observed by Finér et al. (1997) in old-growth boreal forest stands in Quebec. Additionally, under optimal conditions, yew grows in dense patches with stand level (i.e., 20–60 ha) stem densities of 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, unpublished data).

Canada yew can affect stratification of understory vegetation by limiting establishment and growth of other species within or underneath it. Several authors have observed that abundance of yew is often negatively correlated with abundance of other understory species. For example, Nichols (1913) observed that yew frequently grew in dense patches “to the exclusion of all undergrowth” and Egler (1940)

Table 3. Selected effects of deer browsing on individual and population level parameters from Michigan and Wisconsin. *P* values are from standard or paired *t* tests of differences in characters being protected and browsed (control) plots.

Character	Protected	Browsed	<i>P</i> value	No. of years protected	Source
Annual mortality rate (%) ^a	1.7	4.1	<0.001	9	S. Windels and D. Foster, unpublished data
	2.6 ^b	5.7	0.4	2	King (1970)
Annual production rate (ramets/ (m ² ·year))	0.056	0.004	<0.05	9	S. Windels and D. Foster, unpublished data
Horizontal growth rate (Δ % cover/ year)	1.7	-4.0	<0.001	9	J. Meeker, unpublished data
Stem height (cm/year)	0.4	-0.9	<0.01	9	S. Windels and D. Foster, unpublished data
	2.5 ^c	-0.2	<0.001	4	S. Holmes, unpublished data
Maximum stem height (cm) ^d	44.3	29.5	<0.05	9	S. Windels and D. Foster, unpublished data
	62.6	22.6	<0.001	9	J. Meeker, unpublished data
Diameter growth (mm/year)	0.10	0.01	0.2	9	S. Windels and D. Foster, unpublished data
	0.20	0.21	0.8	1	King (1970)

^aCalculated as total no. stems died per total no. stems marked per 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.

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 Grandpré and Bergeron 1997). Aubin et al. (2000) determined light extinction coefficients, *k*, for components of understory vegetation in southern boreal forests in Quebec, including Canada yew. Yew (*k* = 0.54) intercepted more light reaching the forest floor than deciduous seedlings (*k* = 0.49), conifer seedlings (*k* = 0.45), and herbaceous vegetation (*k* = 0.37), but less than deciduous shrubs (*k* = 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; Iszkuło 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; Tyrrell and Crow 1994; Windels 2008). Danz (1998) compared seedling and sapling densities of sugar maple and American beech within patches of yew with open areas between patches. Densities of small and large hardwood seedlings were 100 times and 2 times lower, respectively, inside yew patches compared with adjacent open areas, though it is unclear if dense 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 yew did not affect recruitment to sapling or tree stages, similar to observations made by Risenhoover and Maass (1987) and S. Windels (unpublished data).

Plant species richness also appears to be affected by the patchy growth form of Canada yew. Native herb species richness was negatively related to abundance of yew in the Apostle Islands in northern Wisconsin (Judziewicz and Koch 1993; Balgooyen and Waller 1995; Mudrak et al. 2009). Canada yew likely inhibits growth of exotic species too, causing Mudrak et al. (2009) to speculate that the loss of yew from Madeline Island in the Apostles may have contributed to a simultaneous increase in exotic species. Interestingly, Braun (1950) suggested that some herbaceous plants are able to escape competition from dense deciduous seedlings by growing in small gaps within yew patches. Thus, establishment and persistence of some species may be facilitated by the presence of yew.

Belowground processes and nutrient cycling are also likely affected by yew. 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), potentially resulting in a shift of nutrients from outside patches to within patches of Canada yew. Conversely, its 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 yew patches 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, Hély et al. (2000) speculated that in closed-canopy deciduous and coniferous forests in southern Canada, yew likely increases fire risk over stands without yew because (i) it typically grows in higher stem densities than other woody plants and (ii) it generally displaces nonflammable herbaceous plants. However, considering how poorly adapted

yew is to fire (e.g., shallow roots, slow growth, limited dispersal ability), it seems unlikely that it would have co-evolved with frequent fire.

6.2 Wildlife

Taxus spp. contain relatively high concentrations of taxine alkaloids and are generally toxic to grazers such as domestic cattle, sheep, and horses (reviewed by Wilson et al. 2001 but see Piovesan et al. 2009). Wild cervids, however, readily browse on yews and toxic effects have rarely been documented (e.g., Handeland 2008). Besides white-tailed deer and moose, mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and Sika deer (*Cervus nippon*) show a high preference for *Taxus* spp. and can negatively affect yew population traits such as recruitment and mortality (Mitchell 1988; Parks et al. 1988; Mysterud and Østbye 1995, 2004). Leporids such as snowshoe hare (*Lepus americanus*) and rabbits (*Sylvilagus* spp.) also browse on *Taxus* spp. but generally in insignificant amounts (Sweetman 1944; King 1970; Martell 1974; S. Windels, unpublished data).

There are several factors unique to Canada yew that together explain why it is heavily browsed by wild ungulates. In contrast to many other conifer species, it appears to be poorly defended against wild cervids. While most yews can contain high concentrations of toxic alkaloids (Wilson et al. 2001), Weaver and Brown (2004) suggest that white-tailed deer and other wild cervids have adapted mechanisms to detoxify these compounds. Canada yew 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 rarely outgrows the reach of browsers.

Digestible energy is the product of gross energy content and digestibility and is an important factor affecting winter forage selection by moose and deer (Robbins et al. 1987). Nutritional information for Canada yew for browsing 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 browsing species, including favored plants such as eastern white cedar, mountain maple (*Acer spicatum* Lam.), 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 composed almost exclusively of yew (Beals et al. 1960; King 1970). It is not surprising, then, that deer can quickly reduce the local abundance of 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 compiled in Table S2³.

Deer-related decline and recovery (or expansion) in Canada yew undoubtedly occurred across North America as deer populations fluctuated in response to hunting and habitat

change. The best documented cases of deer-caused decline of yew are 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; Mudrak et al. 2009). 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 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; Beals et al. 1960; King 1970).

The effects of deer browsing on sexual reproduction of Canada yew are well documented (Allison 1990a, 1990b, 1992; also see Section 5.1). 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 yew populations. Deer browsing negatively affects stem survival, stem production, stem height, and stem growth rates, even over relatively short time frames (Table 3).

Tolerance levels of yew stems to various amounts of ungulate browsing have not been adequately tested. King (1970) performed artificial clipping experiments to determine the response of 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 2 year study were relatively low (Table 3). Based on his data, King (1970) deduced that 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 2 years (because new buds formed the spring after the browsing occurred typically produce little growth until the next 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 W. Dalton (personal communication) who observed that 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 yew stems was negatively related to its abundance in northern and mixed-hardwood stands in Michigan (Windels 2008). Further, in Upper Michigan, stands that contained <10%–20% cover of 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 yew. Stems that grew outside of discrete patches were browsed more intensively than those within patches. Further, stems on the outer 1 m of patches (ranging up to ~1 ha in area) were browsed more intensively than those in the inte-

³Table S2 of Supplementary Material available at <http://botany.nrc.ca>.

rior portions of patches, perhaps 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. These interactions can create refugia of unbrowsed stems that are able to continue sexual and vegetative reproduction (Allison 1990a; Windels 2008).

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 15 cm 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 and thus 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; Windels 2008). 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 snow depth or number of days with at least 50 cm of snow depth from 1949 to 2001 throughout yew's historic range, suggesting that changes in snowfall over the last half century alone are not responsible for its decline (D. Kluver, unpublished 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 and exposing stems to increased browsing pressure the next winter. 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 on yew will be exacerbated, particularly along the southern edge of its range.

Canada yew also appears to exist in two alternate steady states (Noy-Meir 1975; May 1977; Augustine et al. 1998) in the presence of deer and other large browsers, although experimental research is needed to test this observation. Evidence suggests that yew populations will tend to shift towards one of those states depending on deer density and yew abundance: aggregations of dense patches of healthy stems or scattered patches composed of a few stunted, over-browsed stems. For dense yew populations, 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 a threshold density, at which point biomass removed by browsing exceeds biomass produced by the entire population (King 1970; Noy-Meir 1975). Using data derived from Judziwicz and Koch (1993) and Balgooyen and Waller (1995), it appears that white-tailed deer may have shifted Canada yew between stable states when densities exceeded $\sim 7\text{--}12$ deer/km² on the Apostle Islands, where Canada yew often exceeds 60%–80% ground cover under natural conditions (Fig. 3). Windels (2008) measured deer browsing intensity in 29 forest stands in the Upper Peninsula of Michigan with varying abundance of Canada yew that all

experienced a relatively low but constant deer density (2–6 deer/km²). Deer browsing removal appeared to exceed growth in forest stands with <15% cover of yew, moving it towards rarity or extirpation, while stands with >30% cover remained in a robust state (Windels 2008). The deer densities in that study were similar to those that likely occurred before Euro-American settlement in northeastern North America (McCabe and McCabe 1997; Waller and Alverson 1997). Several of the previously mentioned factors, including patch size and snowdepth, will also interact with deer density to affect thresholds between alternate stable states in other parts of Canada yew's range.

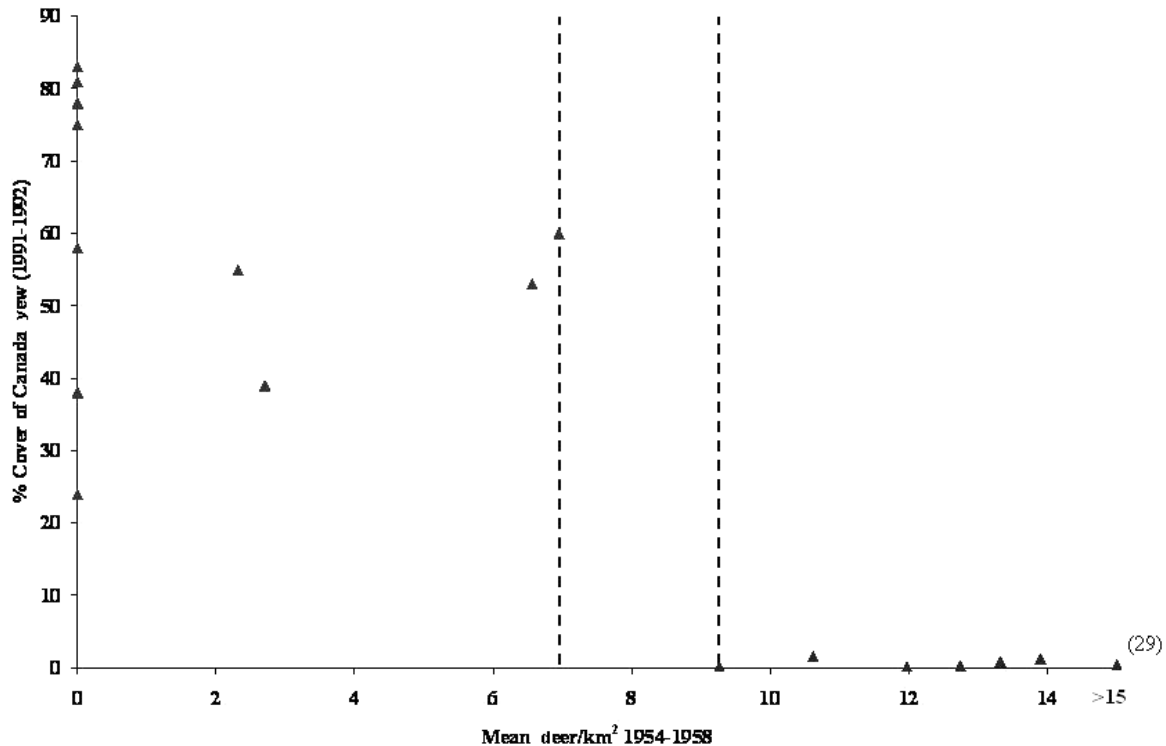
Even in regions with heavy snow, moose may browse on Canada yew year round (Peterson 1955). Canada yew's disappearance from Isle Royale after the arrival of moose in 1909 is well documented (Murie 1934; Krefting 1974; Snyder and Janke 1976; Table S2³). Yew was the dominant ground cover across much of the 52 000 ha island but was functionally extirpated by the early 1930s as moose densities approached 4–10/km² (Murie 1934). It currently only grows well in large moose-proof exclosures on the mainland or on moose-free Passage Island (Krefting 1974; Risenhoover and Maass 1987). Moose also quickly eliminated yew from Newfoundland Island after they colonized the island between 1878 and 1904 (Pimlott 1963). In both cases, continued browsing by moose after the initial reduction in abundance of 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). As in systems with white-tailed deer, Canada yew appears to exist in two alternate stable states when subjected to moose browsing.

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 yew versus other woody plants such as mountain maple and mountain ash (*Sorbus americana* Marsh.; Bergerud et al. 2007). In fact, evidence from the Slate Islands (Lake Superior) suggests that yew is a starvation food for caribou (W. Dalton, personal communication). Nevertheless, over-abundant caribou are capable of functionally extirpating yew when other food resources are limited. On the Slate Islands, 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 caribou/km² (W. Dalton, personal communication; Bergerud et al. 2007).

Individual species of understory vertebrates may respond directly to the abundance of Canada yew in forest understories. The abundance and distribution of 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 (Windels 2008; also see Section 6.1). Despite its unique growth form and large geographic range, the relationship of yew with individual taxa of small mammals, birds, and amphibians remains largely unstudied.

Limited information is available regarding interactions between nonbrowsing mammals and Canada yew. Dense tangles of yew stems might create physical barriers or visual

Fig. 3. Abundance of Canada yew on individual islands in the Apostle Islands (Wisconsin) 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) by 5 (Balgooyen and Waller 1995). Data adapted from Judziewicz and Koch (1993).



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 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 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 yew density and abundance of individual mammal species in a broader study across a gradient of yew abundance representative of current forests in the Upper Peninsula of Michigan (Windels 2008). The results do suggest that 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 yew and other species of woody plants, including hobblebush (*Viburnum alnifolium* Marsh.) 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 bird nest predators (e.g., Reitsma et al. 1990). Although patches of Can-

ada yew may be beneficial to these species by providing cover, yew may also provide more opportunities for depre-dating understory and ground-nesting birds. Predation rates on artificial nests increased as yew cover increased for 22 forest stands in northern Michigan ($R^2 = 0.56$, $P < 0.01$; S. Windels, unpublished data). Small mammals were the principal predators identified, even though small mammal abundance was not closely related to yew abundance in that study.

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 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 yew compared with stands with little or no yew cover, and attributed this to the abundance of yew as a nesting substrate. However, a study of stand-level associations between understory songbirds and yew found no such direct relationships (Windels 2008). Some indirect effects were detected though, whereby dense yew affected other measures of understory physiognomy (e.g., hardwood stem density and foliage height diversity) 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 (*Bombocilla 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 them 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 yew may affect the distribution and abundance of leaf litter and the moisture environment, important habitat characteristics for terrestrial salamanders, frogs, and toads (Jaeger 1980). 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 yew.

7. Conclusions

Canada yew appears to have been an important component in many temperate forests in northeastern North America. Its loss from individual 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 precisely known, we suggest its loss from the landscape appears to have few precedents in the postsettlement history of northeastern North America. Solutions to preserving remaining yew populations are neither simple nor perhaps even economically feasible. However, interest in conserving this species appears to be increasing in both the US and Canada.

Canada yew was likely able to persist in its current range (current forest types) over the last 3000–5000 years for three main reasons. First, compared with 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, yew populations likely experienced local extirpations from episodic irruptions of these two species, but enough source populations remained to eventually repopulate areas. Third, the last 5000 years was a relatively cool and moist period and snowfall was likely sufficient to protect yew from browsing. Today, we believe that changes in herbivore densities over the last century and altered climate conditions combine to pose the greatest risk to yew persistence as an important species in North American forests. The prospect of unsustainable commercial harvest of wild Canada yew for pharmaceutical products also remains.

Throughout this review we have identified known gaps in the current state of knowledge regarding Canada yew. While

acknowledging that there are abundant areas for future research related to yew, we suggest the following priorities:

- Modeling the combined effects of forest dynamics, herbivore effects, and Canada yew patch dynamics on the persistence of Canada yew at local scales. We believe that enough information currently exists for various Canada yew life history characteristics to do this. Such modeling efforts may yield valuable insights into the past distribution and abundance of yew in North America and for the future conservation and management of this species.
- Determining 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 yew (S. Windels, personal observation).
- Documenting attributes of stems in older yew populations, on rates of vegetative reproduction and expansion of individual patches, and on belowground 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.
- Experimentally testing the hypothesis that Canada yew can exist in alternate stable states. More research is also needed on the ability of overbrowsed yew populations to respond to removal of browsing pressure and the role of snowdepth or duration of snow cover in protecting yew stems from browsing.
- Determining the role of Canada yew in deciduous forest types in nutrient cycling and soil dynamics. Spatially-dependent habitat relationships between understory vertebrates and Canada yew throughout its natural range also deserve additional study.

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