Death and *Taxus*: the high cost of palatability for a declining evergreen shrub, *Taxus canadensis*

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Abstract: *Taxus canadensis* Marsh., a shade-tolerant evergreen shrub, is in decline as a result of past anthropogenic disturbances and increased cervid browsing. To identify factors that may be influencing establishment for this species, we planted 1080 *T. canadensis* cuttings in a hemlock–hardwood forest in the spring of 2004. Cuttings were planted across a gradient of light environments, consisting of artificial canopy gaps (61–441 m^2) and closed-canopy conditions, and half were protected with deer exclosures. Following four growing seasons, *T. canadensis* survival in exclosures was 92% compared with 75% in controls. A mixed-effects binary logistic regression analysis revealed that deer exclusion had the most influence on the probability of survival; all else being equal an individual was nearly seven times more likely to survive if planted inside an exclosure ($P < 0.001$). Increasing light intensity had a counterbalancing effect on growth and survival; light increased leader growth ($P = 0.019$) but reduced an individual's probability of survival ($P < 0.001$), possibly owing to enhanced herbivory and elevated moisture stress. Consequently, enhancing resource availability and growth may not decrease the impact of biomass loss to herbivory. These results suggest that even with relatively low herbivore densities, exclosures are required for the recovery of highly palatable species.

Résumé : *Taxus canadensis* Marsh. un arbuste sempervirent et tolérant à l'ombre, connaît un déclin à cause de perturbations anthropogéniques passées et du broutement accru des cervidés. Dans le but d'identifier les facteurs qui peuvent influencer l'établissement de cette espèce, nous avons planté 1080 boutures de *T. canadensis* dans une forêt de pruche et de feuillus au printemps 2004. Les boutures ont été plantées le long d'un gradient de luminosité, dans des trouées artificielles dans la canopée (61–441 m^2) et sous couvert fermé. La moitié des boutures ont été protégées des chevreuils par des exclos. Après quatre saisons de croissance, la survie de *T. canadensis* atteignait 92% dans les exclos comparativement à 75 % dans les parcelles témoins. Une analyse de régression logistique binaire à effets mixtes a révélé que l'exclusion des chevreuils avait le plus d'influence sur la probabilité de survie : tous les autres facteurs étant égaux, un individu avait presque sept fois plus de chances de survivre en étant planté à l'intérieur d'un exclos ($P < 0,001$). Le fait d'augmenter l'intensité lumineuse a eu un effet de compensation entre la croissance et la survie : la lumière a augmenté la croissance de la pousse terminale ($P = 0,019$) mais a réduit la probabilité qu'un individu survive ($P < 0,001$), possiblement à cause du broutement accru et de l'augmentation du stress hydrique. Par conséquent, le fait d'améliorer la disponibilité des ressources et la croissance peut ne pas réduire l'impact de la perte de biomasse due au broutement. Ces résultats indiquent que même avec une densité relativement faible d'herbivores, des exclos sont nécessaires pour assurer la récupération des espèces très appétentes.

[Traduit par la Rédaction]

Introduction

In forest ecosystems woody shrubs face many challenges in the struggle for survival and growth. In addition to coping with the high-shade environment of the forest floor (Oliver and Larson 1996), in many systems shrubs have to contend with the presence of mammalian herbivores. Since these understory inhabitants spend their entire existence within the reach of browsers, they must carefully balance the allocation of limited resources among maintenance, growth, and defense (Herms and Mattson 1992). When nutrients and light are readily available, fast-growing species rapidly regrow tissues to compensate for herbivore consumption, but if resources are limited, investment in defense may be the preferred option (Augustine and McNaughton 1998). The production of antiherbivore defenses is advantageous only when the benefits of protection exceed costs (Coley et al. 1985). Therefore, for species with slow foliar turnover rates, such as understory evergreen shrubs, the protection of existing leaves may be more cost effective than simply growing new ones (Coley et al. 1985; Coley and Barone 1996).

With time, herbivore damage can select for (constitutive resistance) or stimulate (induced resistance) protective mechanisms (Strauss et al. 2002) in plants to deter or reduce further herbivore damage. Defenses range from chemical compounds that make foliage toxic or unpalatable (review by Augustine and McNaughton 1998; Hobbs 1996) to mechanical structures that dissuade browsers (e.g., thorns; Gomez and Zamora 2002). For example, in Japan the temperate evergreen shrub *Damnacanthus indicus* C. F. Gaertn.

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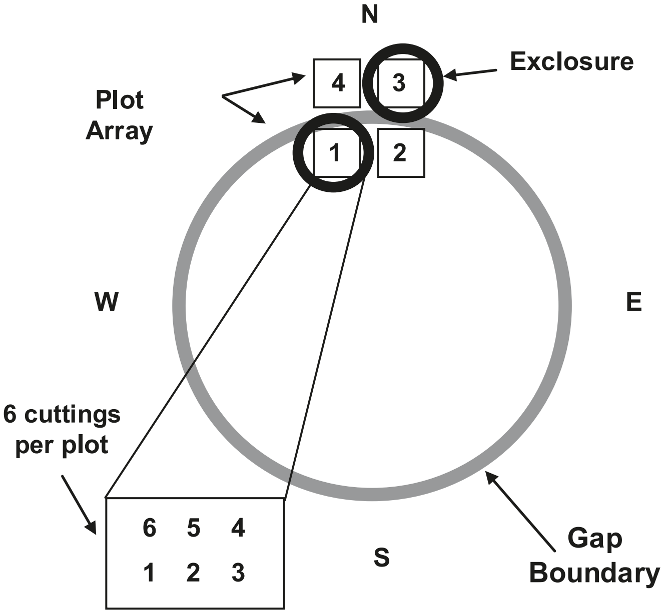
exhibits shorter leaf lengths, thicker spines, and smaller internode distances between spines in regions with Sika deer (*Cervus nippon* Temminck) than in regions without deer (Takada et al. 2001). However, some understory shrubs such as the conifer *Taxus canadensis* Marsh., commonly known as Canada yew or ground hemlock, appear to lack any apparent resistance to ungulate browsers. Despite the presence of the toxin paclitaxel in its foliage (Senneville et al. 2001), this shrub is favored browse for white-tailed deer (*Odocoileus virginiana* Zimmermann) in winter and for moose (*Alces alces americana* Clinton) year-round (Martell 1974).

Several authors (Leopold et al. 1947; Jenkins and Bartlett 1959; Martell 1974; Alverson et al. 1988; Telfer 2004) provide observational evidence to link the decline of *T. canadensis* throughout its natural range, which includes the Midwest and Northeast regions of the United States and southeastern Canada (Martell 1974), to over browsing by white-tailed deer, but experimental data are uncommon. Historically, this species was common to cool and moist sites, including maritime proveniences of the Lake States, until extirpated from many areas with high deer populations (Martell 1974). Undoubtedly, wide-scale logging and subsequent fires that were prevalent at the turn of the last century have also contributed to the decrease in abundance (Jensen 1943; Whitney 1994). Today this species is largely associated with primary and old-growth forests (Tyrrell and Crow 1989; Stachowicz and Allison 1995), sites that typically escaped fires, and areas with high winter snowfall where deer densities are low (Doepker et al. 1995). It has also been associated with some midsuccessional forests that are dominated by *Quercus rubra* L. and *Acer rubrum* L. (Stachowicz and Allison 1995). In addition, once a plant's population is reduced, accelerated rates of extirpation by deer can occur (Côté et al. 2004). Therefore, deer may not only be influencing established populations; they may also be hindering the establishment and recruitment of new individuals dispersing outside these current population zones. While studies have looked at the direct impacts of deer browsing on existing *T. canadensis* populations (Beals et al. 1960; Allison 1990*a*, 1990*b*, 1992; Stachowicz and Allison 1995), to our knowledge none have evaluated the biological or environmental factors that influence the survival and growth of newly established individuals. Restoration of *T. canadensis* is desirable; in addition to contributing to forest understory diversity and structure, this species provides habitat for shrub-nesting songbirds and small mammals (Belant and Windels 2003). Its arils are also eaten by both birds and rodents (Wilson et al. 1996).

To identify environmental factors that may influence the survival and growth of highly palatable understory shrub species, we planted 1080 *T. canadensis* cuttings in a hemlock–hardwood forest in the western Upper Peninsula of Michigan. We planted cuttings inside and outside of deer exclosures located on the edges of artificial canopy gaps and under closed-canopy conditions. Our experimental design provided a gradient of understory light levels for *T. canadensis* growth and allowed us to directly test the impact of herbivory under a variety of environmental conditions. We tested the following hypotheses: (1) elevated understory light levels will increase *T. canadensis* growth; (2) subsequently, higher growth rates will decrease the impact of biomass loss to herbivores and increase long-term survival; and (3) the initial vigor of an individual at the time of planting will also be indicative of its ability to survive, grow, and withstand herbivore damage.

Fig. 1. Experimental planting design.



Materials and methods

Study site

This *T. canadensis* planting experiment was conducted in a hemlock–hardwood forest located at Michigan Technological University's Ford Forestry Center (46°37′N, 88°29′W) near Alberta, Michigan. Alberta is situated in the western portion of Michigan's Upper Peninsula. Soils in our study gaps were dominated by moderately well drained Kallio cobbly silt loams, 1%–20% slopes, with small areas of poorly drained Pickford mucky silt loams in depressions (Berndt 1988). Mean winter and summer temperatures are –9.8 °C and 17.4 °C, respectively (Berndt 1988). Total mean annual precipitation is 87.4 cm, and mean winter snowfall is 382.5 cm (Berndt 1988). Deer densities for the region range from 6.5 deer·km^{-2} in the spring to 9.3 deer·km^{-2} in the fall (Mayhew 2003). Given the spatial extent of the study area, approximately 60 ha, it is unlikely that deer densities varied substantially across the study site.

Study design and data collection

Rooted stem cuttings of *T. canadensis* were planted in the last 2 weeks of June 2004, on the edges of artificial canopy gaps and under closed-canopy conditions. Cuttings were grown at the J.W. Toumey Nursery and were fertilized and hardened off prior to planting. Artificial canopy gaps were created in hemlock stands during the winter of 2002–2003 through the removal of low-quality hardwoods. In total, 21 gaps were installed and were categorized as small, medium, and large: 50–150, 151–250, and 251–450 m^2, respectively. Of these, three small, four medium, and three large gaps were randomly chosen for *T. canadensis* planting. Cuttings

Table 1. Environmental attributes of sample plots and initial dimensions of *Taxus canadensis* cuttings.

	Taxus canadensis[a]		Understory light[b,c]			Competition percent cover by functional group[b]						
	Height (cm)	Diameter (mm)	Direct	Diffuse	Total	Forbs	Graminoids	Woody	*Rubus*	Fern	Fern allies[d]	Total
Control												
Mean	16.4	2.3	9.7	1.4	11.1	7.7	9.4	6.8	2.7	5.1	0.6	32.2
Median	16.0	2.2	8.5	1.4	9.9	4.0	1.5	4.0	0.0	0.0	0.0	19.0
Min.	5.0	0.7	1.7	0.7	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Max.	40.0	4.9	23.3	2.2	25.1	85.0	100.0	54.0	55.0	48.0	10.0	148.0
SD	4.9	0.7	4.8	0.2	4.8	12.3	20.5	8.2	9.8	8.6	1.6	35.2
Exclosure												
Mean	16.3	2.3	9.6	1.4	11.0	10.1	4.8	10.0	4.2	7.8	1.3	38.1
Median	16.0	2.2	9.0	1.4	10.3	6.5	1.0	6.5	0.0	2.0	0.0	26.8
Min.	5.0	0.8	1.5	0.9	2.5	0.0	0.0	0.0	0.0	0.0	0.0	1.5
Max.	40.0	5.2	23.3	2.1	23.6	50.0	52.0	54.0	95.0	70.0	50.0	153.0
SD	4.6	0.7	4.6	0.2	4.7	10.0	8.6	10.7	15.5	13.3	5.7	34.7

[a] Initial dimensions measured in 2004, $n = 1080$.

[b] Measured in 2007 for each subplot ($n = 180$). Descriptive statistics were calculated for control plots ($n = 90$) and exclosure plots ($n = 90$).

[c] Direct and diffuse under-canopy radiation: photosynthetically active flux density under-canopy average for the growing season (mol·m^{-2}·day^{-1}) (WinSCANOPY 2005).

[d] Fern allies include club mosses and *Equisetum* spp.

were planted in four arrays within each gap; arrays contained four, 1 m^2 plots, two of which were randomly chosen for deer exclosures and were located at the north, east, south, and west edges of each gap (Fig. 1). In addition, five randomly placed closed-canopy arrays, hereafter referred to as null gaps, were also established for comparison. Each null gap contained four, 1 m^2 plots, two of which were randomly chosen for deer exclosures. Our mini-hoop deer exclosures (1 m radius, 1.52 m high) were constructed from heavy gauge, 15 cm^2 wire mesh. This mesh size excludes white-tailed deer but not snowshoe hare (*Lepus americanus* Macfarlani). We planted six *T. canadensis* cuttings within each plot for a total of 1080 cuttings. All individuals were watered for the first 2 weeks following planting.

At the time of planting (June 2004), the initial condition of each yew cutting was documented. Leader length, hereafter referred to as height, and stem diameter, measured at ground level with digital calipers, were recorded (Table 1) along with the initial vigor of each plant. Height was determined by outstretching the dominant leader and measuring the distance between its terminal and the plant's base. Each cutting's vigor was visually assessed and assigned to one of three categories: fair, good, or excellent (Fig. 2). Several attributes were considered for assigning vigor class: diameter, height, foliage color and density, and amount of branching. Pearson's χ^2 test verified that individuals in the three vigor classes were evenly distributed between control and exlcosure treatments (Fig. 3) at the time of planting ($\chi^2 = 0.282$, df = 2, $P = 0.868$). *Taxus canadensis* survival was tallied after two, three, and four growing seasons.

In September 2007 we remeasured the height and diameter of each individual and visually estimated the percent cover of competing vegetation by functional group (graminoids, ferns, club moss, *Equisetum* spp., forbs, woody, and *Rubus* spp.) for each plot (Table 1). To quantify the understory light environment at each plot, we took a digital hemispherical photograph 70 cm above each plot's center. When combined with spatial location, percent slope, and aspect, hemispherical photography can be used to model local light availability at various points within a given canopy gap (WinSCANOPY 2005). Digital hemispherical photographs were analyzed with the software WinSCANOPY (WinSCANOPY 2005) to determine the levels of direct and diffuse below canopy radiation for each plot. Radiation was measured as the mean direct and diffuse photosynthetically active flux density for the growing season (mol·m^{-2}·day^{-1}; Table 1). WinSCANOPY's default growing season period was used, which is 1 May – 30 September.

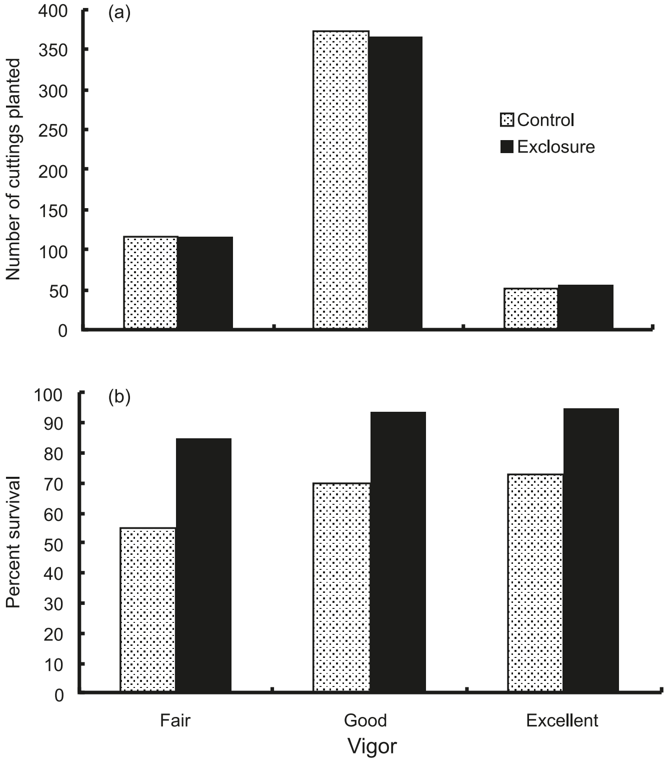
Data analysis

Our experimental design had a hierarchical structure; yew cuttings were planted in arrays, and arrays were clustered within artificial canopy gaps. This design did not allow us to assume independence among individual *T. canadensis* cuttings growing within the same spatial unit (arrays or gaps). Therefore, we used mixed-effects statistical methods that accounted for this hierarchical structure in our data (Schabenberger and Pierce 2002).

Binary logistic regression models with mixed effects, implemented in the statistical environment R (R Development Core Team 2008), were used to identify *T. canadensis* cutting and environmental variables that best predicted survival ($n = 1080$) after four growing seasons. We also explored dimensional changes in *T. canadensis* with multiple linear mixed-effects regression models in the same statistical environment. We calculated relative change in height as the percent change in height between the initial height measurement (June 2004) and the final height measurement (September 2007). Absolute change in height was calculated by subtracting the initial height measurement (June 2004) from the final height measurement (September 2007). These methods were also used to calculate diameter change. First, we sought to determine the influence of treatment on dimensional change for all surviving individuals ($n = 857$). Then

Fig. 2. Initial vigor classes for *Taxus canadensis* cuttings (from left to right): fair, good, and excellent.

Fig. 3. Number of *Taxus canadensis* cuttings (n = 1080) planted in control plots and exclosure plots (*a*) and percent survival after four growing seasons (*b*) by initial vigor class.



we explored the influence of environmental variables and initial *T. canadensis* size on the height growth of extant individuals that escaped herbivory in exclosures (n = 445). For the later two height models, we used a square-root transformation to normalize the response variable.

Both types of methods, binary logistic regression with mixed effects and multiple linear mixed-effects regression, were used to analyze the effect of initial cutting characteristics and environmental variables (fixed effects) on the response variable (survival and height growth, respectively) while fitting a nested random effect to each array and gap. The random effect accounts for the spatial correlation within arrays and gaps and the variation among arrays and gaps (Schabenberger and Pierce 2002). For all three models (survival, relative height growth, and absolute height growth), we first fitted a full model, which included as fixed effects the initial dimensions of *T. canadensis*, environmental variables (see Table 1) and associated interaction terms, and random effects for gap and array. We then tested the significance of the random effects; after which nonsignificant fixed effects were removed one at a time until only significant terms remained. Nonsignificance was further verified by readdition of the removed variables to the reduced model. Akaike's information criterion and Akaike weights were used to select the most parsimonious and biologically meaningful models, and likelihood ratio tests (LRT) were used to assess statistical significance. Finally, we calculated a generalized R^2 following the procedure outlined by Nagelkerke (1991).

Results

Taxus canadensis survival was significantly associated with deer exclusion. After four growing seasons, 91.9% of individuals in exclosures (n = 540) were alive, compared with just 75.0% of cuttings planted in control plots (n = 540). Most of the surviving control plot cuttings were in poor condition, as discussed below. The survival model (Table 2) revealed that the presence of an exclosure had the most influence on *T. canadensis* survival. All else being equal, an individual was 6.61 times more likely to survive if it was planted within an exclosure (Table 2). In addition to treatment, the model also revealed that light environment, competition, and vigor class influenced survival (Table 2). Higher levels of under-canopy direct radiation reduced an individual's probability of survival, mean (±SD) direct radiation for survivors (n = 857) and nonsurvivors (n = 223) was 9.24 ± 4.49 and 11.14 ± 5.12 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, respectively; higher levels of forb and fern coverage increased a cutting's probability of survival. An initial vigor classification of fair reduced an individual's chance of survival, whereas good and excellent vigor increased it (Table 2).

The presence of exclosures greatly reduced the amount of herbivore damage on cuttings in treatment plots. In 2007, 93.9% of all control plot individuals were browsed compared with just 3.8% of *T. canadensis* planted in exclosures. Damage in the exclosure plots was attributed to snowshoe hare. Although initial heights and diameters of *T. canadensis* cuttings planted in control and exclosure plots were very similar (Table 1), after four growing seasons large differences in height and diameter growth between the two treatments were observed. Diameters increased for almost all of the surviving individuals (Fig. 4) regardless of treatment, but the increases were greater in exclosures (n = 857, df = 811, t = 12.97, P < 0.001). While *T. canadensis* cuttings planted within exclosures increased in height, change in height was

Table 2. Binary logistic regression model using mixed effects to analyze the influence of environmental factors on the probability of *Taxus canadensis* survival (1, live; 0, otherwise).

(A) Survival model.

				Odds ratio	
Fixed effect	Estimate	SE	*P*	Estimate	95% CI
Intercept	1.39	0.35	<0.001		
Exclosure	1.89	0.21	<0.001	6.61	4.42–9.88
Vigor (fair vs. good)	–1.06	0.21	<0.001	0.35	0.23–0.52
Vigor (excellent vs. good)	0.58	0.35	0.088	1.80	0.92–3.55
DirUnd[a]	–0.08	0.02	<0.001	0.92	0.88–0.97
Forbs	0.02	0.01	0.032	1.02	1.00–1.05
Ferns	0.05	0.02	0.002	1.05	1.02–1.08

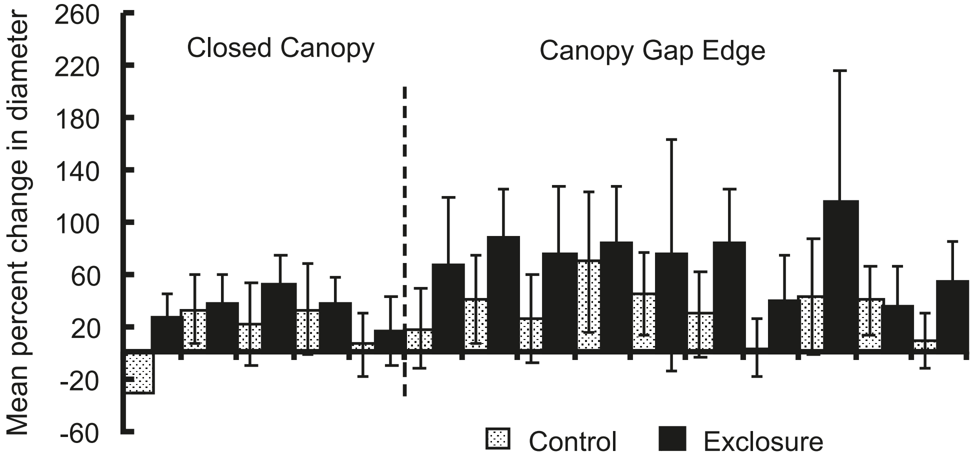
(B) Model fit.

	χ^2	df	*P*
Hosmer–Lemeshow	13.23	8	0.104
Likelihood ratio	220.07	8	<0.001

Note: The fixed effects are treatment (exclosure or control), vigor (fair, good, excellent), competition (percent cover forbs and ferns), and light (under-canopy direct radiation). Arrays nested in gaps (45 levels) were treated as the random effect. For the Hosmer–Lemeshow goodness-of-fit test, a significant *P* value indicates a lack of model fit.

[a] Direct under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season (mol·m^{-2}·day^{-1}) (WinSCANOPY 2005).

Fig. 4. Mean percent change in diameter (±1 SD) of surviving *Taxus canadensis* after four growing seasons. Each control–exclosure pair represents a single canopy gap or closed-canopy array. Study gaps are ordered from smallest to largest along the *x* axis. Of the initial 1080 planted cuttings, 857 cuttings were still extant following four growing seasons.



negative for almost all of the individuals within control plots (Figs. 5*a* and 5*b*); relative height change and absolute height change varied significantly between exclosure and control plots for surviving individuals (n = 857; t = 26.61, df = 811, $P < 0.001$ and t = 28.80, df = 811, $P < 0.001$, respectively). Given the reduced condition of control plot individuals, we expect that mortality will increase with time, since high rates of browsing are likely to continue.

For individuals surviving inside of exclosures with no evidence of browse damage (n = 445), both relative and absolute change in height over four growing seasons could be predicted by initial *T. canadensis* dimensions and diffuse under-canopy radiation, which ranged from 0.86 to 2.14 mol·m^{-2}·day^{-1} (Table 3). Taller initial heights ($P < 0.001$) decreased relative change in height growth, while larger initial diameters (P = 0.031) and higher levels of diffuse under-canopy radiation (P = 0.047) increased it (LRT = 96.21, $P < 0.001$, R^2 = 0.19; Table 3). Absolute height growth over four growing seasons was also associated with larger initial diameters and higher levels of diffuse under-canopy radiation (P = 0.007 and 0.019, respectively), which explained 10% of the variation (LRT = 46.89, $P < 0.001$, R^2 = 0.10; Table 3). Initial height was not a significant variable (P = 0.370) in the absolute height growth model.

Arils, which are the red, fleshy berry-like reproductive structures that encase single seeds (Soper and Heimburger 1982), were observed on five exclosed *T. canadensis*, but none were found on control plot plants. Mean (±SD) aril production was 1.2 ± 0.4 arils·plant^{-1}. Four of these individuals were growing in the southern array of a small gap (96 m^2). The fifth individual was located on the eastern edge of a medium gap (174 m^2). Mean (±SD) height and di-

Fig. 5. Mean percent change in height (±1 SD) of *Taxus canadensis* planting following four growing seasons for all *T. canadensis* present (n = 1080), dead and alive (*a*), and for all individuals alive (n = 857) 4 years postplanting (*b*). Each control–exclosure pair represents a single canopy gap or closed canopy array. Study gaps are ordered from smallest to largest along the *x* axis.

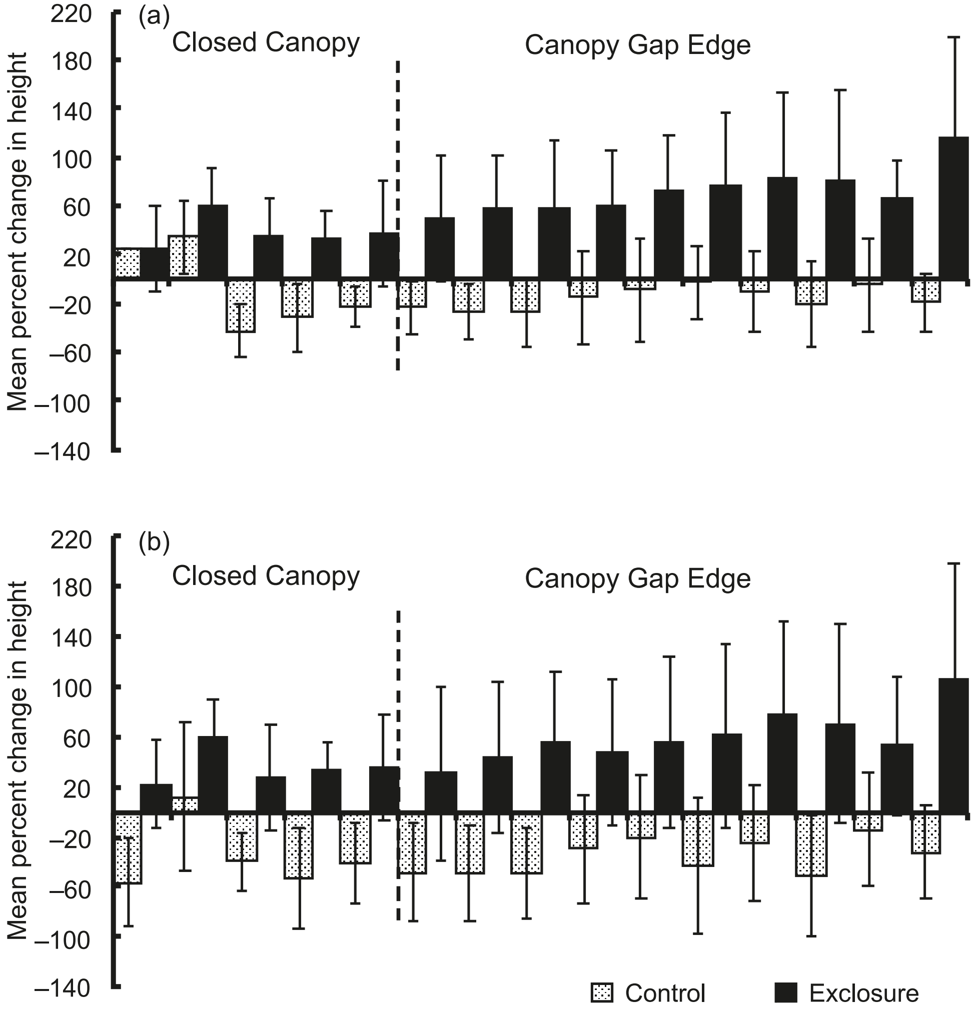


Table 3. Linear mixed-effects models for relative and absolute *Taxus canadensis* height growth (RHG and AHG, respectively) over four growing seasons as a function of initial yew dimensions (height and diameter) and light (DiffUnd; diffuse under-canopy radiation).

					Likelihood ratio		
Response variable	Fixed effect	Estimate	SE	*P*	Value	*P*	R^2
sqrt(RHG)[a]	Intercept	8.72	1.23	<0.001	96.21	<0.001	0.19
	DiffUnd[b] (mol·m^{-2}·day^{-1})	1.53	0.77	0.047			
	Initial height (cm)	–0.24	0.03	<0.001			
	Initial diameter (mm)	0.52	0.24	0.031			
sqrt(AHG)[a]	Intercept	1.74	0.46	<0.001	46.89	<0.001	0.10
	Initial diameter (mm)	0.21	0.08	0.007			
	DiffUnd[b] (mol·m^{-2}·day^{-1})	0.69	0.29	0.019			

Note: Arrays nested in gaps (45 levels) were treated as the random effects. Only surviving, unbrowsed, and exclosed cuttings (n = 445) were included in these analyses. The R^2 applied to the mixed models is a generalization of the classic R^2 (Nagelkerke 1991).

[a] Square-root transformation used to normalize the response variable.

[b] Diffuse under-canopy radiation = photosynthetically active flux density under-canopy average for the growing season (mol·m^{-2}·day^{-1}) (WinSCANOPY 2005).

ameter of the aril producing *T. canadensis* were 33.2 ± 9.8 cm and 4.5 ± 0.7 mm, respectively.

Discussion

In some plant communities, ungulate abundance and overall browsing intensity may be poor predictors of individual species response as a result of contemporary community composition or discontinuities between historic and contemporary ungulate density or habitat associations. In northwestern Pennsylvania, where presettlement deer densities are estimated to be 3–4 deer·km^{-2}, forest herb and shrub species have been negatively impacted at densities as low as 3.7 deer·km^{-2} and lost outright at densities exceeding 7.9 deer·km^{-2} (as reviewed by deCalesta 1997). These densities are much lower than those reported for other locations where ground-layer communities are experiencing deer-induced changes; for example, deer densities reached 43 deer·km^{-2} in the 1970s in Cades Cove, Great Smoky Mountain National Park (Griggs et al. 2006). However, what may appear to be low may still be well in excess of historic levels; deer densities in the western portion of Michigan's Upper Peninsula are twice as high as they were prior to European settlement (Doepker et al. 1995). Deer populations are considered "overabundant" when they alter ecosystem function or decrease the densities of desired species, but this value-laden term must be considered in context (McShea et al. 1997). Plant species vary greatly in their tolerance to deer herbivory. Therefore, systems that appear to be at low risk for over browsing because of relatively low ungulate populations may still be susceptible to damage. In addition, once a plant species becomes rare, even large reductions in deer densities may not facilitate recovery (Balgooyen and Waller 1995; Coomes et al. 2003). For some plant communities, the discontinuity between historical and current densities of plant species and deer may be more important for assessing herbivory risk than actual deer density numbers.

Our results indicate that *T. canadensis*'s ability to persist on the landscape may be threatened by contemporary levels of deer herbivory, and the establishment of new populations in areas with even moderate deer densities will not be possible without deer exclusion. *Taxus canadensis*'s high palatability and low tolerance to browsing suggest that this species may have evolved in the absence of large deer populations; it seems to lack any defense mechanisms to deal with present levels of deer herbivory. At our study site, where deer densities are relatively low compared with other regions in the western Upper Peninsula of Michigan (Mayhew 2003), only 75% of control plot individuals survived after 4 years, and almost 94% of control plot cuttings were browsed. This level of browsing resulted in a significant reduction in leader length over the course of our study and left surviving individuals in poor condition. Our results are consistent with the work of Beals et al. (1960) in the Apostle Islands of Lake Superior. They found that *T. canadensis* was highly susceptible to deer browse damage, and even moderate browse pressure resulted in decreased densities. Since the existence of high-density white-tailed deer populations throughout *T. canadensis*'s range appears to be a rather recent occurrence, within the last century (reviewed by Côté et al. 2004; see also Whitney 1994), the wide-scale distribution and abundance of this species in the past (Martell 1974) coupled with low deer densities may have allowed *T. canadensis* to tolerate high rates of localized browsing.

Remnant *T. canadensis* populations, on the other hand, may not be able to cope with the detrimental effects of deer herbivory. Even in an area with comparatively low deer densities, the enhancement of resources for growth did not appear to dampen the impacts of browsing as we had initially hypothesized. Our height change models suggest that increased diffuse light levels increase the rate of height growth, but survival was negatively correlated with direct under-canopy radiation. Although gaps increase the availability of diffuse light, they also increase the daily duration of direct sunlight hitting the forest floor (Paquette et al. 2007). *Taxus canadensis* is typically found in damp and shaded environments (Soper and Heimburger 1982) and is extremely shade tolerant (Martell 1974); therefore, the elevated, gap-edge radiation levels (Canham et al. 1990) may be harmful. In addition, the drier conditions found along the well-illuminated northern edges of gaps (Wright et al. 1998) may have a negative effect on growth. In New Hampshire, Stachowicz and Allison (1995) found that the natural distribution of *T. canadensis* was associated with concave, north- and east-facing slopes, conditions that result in lower solar radiation and higher soil moisture levels. In addition, north-facing slopes tended to produce the most *T. canadensis* biomass (Stachowicz and Allison 1995). Biomass production was also somewhat higher in deciduous forests than in coniferous forests, but the former forest type exhibited higher biomass losses to white-tailed deer browsing (Stachowicz and Allison 1995). Since higher levels of forb and fern coverage increased the probability of *T. canadensis* survival (all else being equal) in our planting, we suggest that these functional groups provide visual protection from deer and (or) their shade enhances soil moisture for growth. Garcia et al. (2000) found that fleshy fruited shrubs protected seedlings of another yew species, *Taxus baccata* L., from herbivory and summer drought in the Sierra Nevada and provided microhabitats for the successful establishment of new seedlings.

We found moderate support for our third hypothesis, since the initial condition of a *T. canadensis* cutting was indicative of its capacity for 4 year survival and height growth but not to produce reproductive structures. Individuals whose vigor classifications were excellent at the time of planting were more likely to survive than good or fair individuals (Table 2), and large initial diameters were positively associated with 4 year height change (relative and absolute; Table 3). Initial height, however, was associated with reduced 4 year relative height change but was not a significant predictor of absolute height change (Table 3). None of the excellent vigor individuals produced arils; three of five aril-producing *T. canadensis* had an initial vigor of good, while the other two were initially classified as fair. To our knowledge, the arils we observed in the fall of 2007 mark the first year of aril production since the time of planting.

Deer herbivory may also be impacting *T. canadensis*'s sexual reproduction. In our study, only protected cuttings produced arils. In a comparative study of natural *T. canadensis* populations in the Apostle Islands, Allison (1990*a*) found that increased levels of deer browsing damage were correlated with lower male strobilus, ovule, and seed production. An exclosure study in the same system also revealed that protected *T. canadensis* produced more male and female strobili than individuals outside of exclosures, but significant differences were not seen until the fourth year of protection (Allison 1990*a*). Although sexual reproduction is important for the exchange of genetic material, this species appears to maintain its populations locally through vegetative propagation rather than seed dispersal (Senneville et al. 2001). *Taxus canadensis* reproduces vegetatively through layering (Allison 1990*a*); therefore, it is likely that this process is also being negatively impacted by deer. Other clonal woody shrubs have exhibited negative responses to mammalian herbivory. Zeigenfuss et al. (2002) reported that elk (*Cervus elaphus* L.) browsing significantly reduced vegetative production for clonal willow species (*Salix* spp.) in Rocky Mountain National Park (Colorado, USA). Likewise, Wang et al. (2007) found that giant panda (*Ailuropoda melancoleuca* David) herbivory reduced new shoot densities for the clonal shrub *Fargesia qinlingensis* Yi et J.X. Shao (arrow bamboo) in China.

In conclusion, it seems that *T. canadensis*'s lack of defenses against white-tailed deer herbivory will prevent its recovery in areas with even low to moderate deer densities. Its high palatability exceeds even that of *Tsuga canadensis* (L.) Carrière and *Thuja occidentalis* L. (Leopold et al. 1947; Beals et al. 1960), two species documented as experiencing widespread recruitment failure because of white-tailed deer (Anderson and Loucks 1979; Frelich and Lorimer 1985; Rooney and Waller 2003). Unlike these tree species, though, *T. canadensis* can never escape the white-tailed deer browse zone through height growth after it is established. The plight of this species raises an important ecological question: How do highly palatable species cope with demographic change? With deer populations on the rise throughout Europe and North America (Côté et al. 2004), the impact of population shifts on plant–herbivore interactions clearly warrants further investigation and a more proactive approach to plant conservation.

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