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Original Article

Partial cutting favours northern white-cedar regeneration but does not ensure recruitment to canopy: does browsing matter?

Olivier Villemaire-Côté [1,2,*], Jean-Pierre Tremblay [2,3], Laura S. Kenefic[4] and Jean-Claude Ruel[1,2]

[1]Département des sciences du bois et de la forêt, Université Laval, 2405 Rue de la Terrasse, Quebec G1V 0A6, Canada
[2]Centre d'étude de la forêt, Université Laval, 1045 Rue de la Médecine, Quebec G1V 0A6, Canada
[3]Département de biologie, Université Laval, 1045 Rue de la Médecine, Quebec G1V 0A6, Canada
[4]U.S. Forest Service, Northern Research Station, 54 Government Road, Bradley, ME 04411, USA
*Corresponding author: Tel: +1-418-808-8931; E-mail: olivier.villemairecote@gmail.com

Abstract

Gap dynamics facilitate recruitment of late-successional species such as northern white-cedar (*Thuja occidentalis* L.). For this reason, harvests that result in partial rather than complete canopy removal have been suggested for cedar. However, success of regenerating cedar following partial harvests is uncertain, especially where there is heavy browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) or snowshoe hare (*Lepus americanus*). Efforts to understand how partial harvests and browsing interact to affect natural regeneration of cedar have been limited. We inventoried partially harvested stands along a gradient of 1–11 years since harvest in New Brunswick, Canada, in an area where deer frequently overwinter. Cedar regeneration was negatively influenced by browsing, but positively influenced by years since harvest and sapling basal area. Cedar seedling survival was assessed over a 2-year period and found to be primarily a function of height at initial measurement, with little influence of browsing. Annual vertical gain of cedar seedlings (a surrogate for height growth) decreased with increasing years since harvest and was influenced by distance from gap edge. In gaps, vertical gain increased with distance to gap edge, while distance to gap edge had a negative influence on vertical gain of seedlings in the matrix (between-gap areas). Many tagged cedar seedlings disappeared prior to remeasurement. These were likely completely consumed by browsers, limiting our ability to determine relative influences of partial harvest and browsing on cedar regeneration. We conclude that partial harvests, as applied in this study, increase cedar abundance and vertical gain, but browsing may necessitate seedling protection. We suggest monitoring to confirm sufficient cedar regeneration in partially harvested stands, using exclosures where browsing is a concern, and retaining or at least delaying removal of seed-bearing cedar overstory trees until regeneration has reached heights safe from browsing.

Introduction

Northern white-cedar (*Thuja occidentalis* L., hereafter cedar) is an important element of habitat for many wildlife species and a tree of high economic value, with decay-resistant wood used for specialty products such as shingles, log homes and outdoor furniture. Long lived and shade tolerant, cedar is found in pure stands on lowlands and a minor component in mixed-species stands on upland sites of eastern North America (Johnston, 1990). With slow growth in the shade, cedar is commonly a late-successional species for which dominance increases with stand age (Bergeron, 2000). Canopy gaps are beneficial for cedar; growth of established trees reacts positively to low- to moderate-severity canopy disturbances even after prolonged suppression (Hofmeyer *et al.*, 2010; Ruel *et al.*, 2014; Fraver *et al.*, 2020).

Silvicultural practices have been associated with cedar regeneration problems in mixed stands, as they tend to favour companion species with different requirements than cedar (Boucher *et al.*, 2006; Larouche *et al.*, 2010). Silvicultural treatments often fail to protect the advance regeneration of cedar that is essential for successful cedar recruitment (Heitzman *et al.*, 1999; Larouche *et al.*, 2010; Larouche and Ruel, 2015; Fraver *et al.*, 2020). Notably, even-aged management has only been shown to successfully regenerate cedar on lowland sites in the absence of competition and browsing (Verme and Johnston, 1986; Heitzman *et al.*, 1999). Instead, recent studies suggest that partial harvesting may be more appropriate for regenerating cedar (Larouche *et al.*, 2010, 2011; Larouche and Ruel, 2015; Saucier *et al.*, 2018).

At the northern limit of their range, white-tailed deer (*Odocoileus virginianus* Zimmerman, hereafter deer) aggregate in the winter in mixed or coniferous stands known as deer yards. Cedar stands are preferentially selected by deer for this purpose (Morrison *et al.*, 2003) as these stands provide both cover and food. This process leads to high browsing pressure in relatively small areas (Lesage *et al.*, 2000; Messier and Barrette, 1985). Regeneration and recruitment failures of cedar stands (Cornett *et al.*, 2000; Danneyrolles *et al.*, 2017) have been associated with browsing by white-tailed deer (Heitzman *et al.*, 1997; Cornett *et al.*, 2000; Larouche and Ruel, 2015) and to a lesser extent snowshoe hare (*Lepus americanus*, hereafter hare) (Verme and Johnston, 1986; Villemaire-Côté *et al.*, 2017). This problem can be exacerbated by winter harvesting operations that further attract deer by

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providing accessible foliage on harvest residues at a time when other food sources are scarce (St-Louis *et al.*, 2000).

The time period during which cedar regeneration remains vulnerable to browsing is highly variable. Cedar can establish and survive for extended periods of time in a suppressed state (Hofmeyer *et al.*, 2010; Ruel *et al.*, 2014; Fraver *et al.*, 2020). Growth to a height that is safe from browsing (3 m) varies widely depending on growing conditions, i.e. from 9 years in productive conditions (Villemaire-Côté *et al.*, 2017) to over 75 years when suppressed (Hofmeyer *et al.*, 2010). Because cedar regeneration can be eliminated by a single browsing event (Heitzman *et al.*, 1999), its slow growth increases the likelihood that consequential browsing events will occur. In many locations where deer overwinter, the goal of forest management is to maintain cedar in the canopy. In some jurisdictions, cedar harvests are limited or prohibited for this reason. Yet, harvesting moratoria can exacerbate problems with sustainability of the cedar resource if they preclude canopy disturbances that promote regeneration and recruitment (Allogio *et al.*, 2021; Larouche *et al.*, 2011; Saucier *et al.*, 2018; Villemaire-Côté *et al.*, 2022). Furthermore, because dense cedar stands provide cover for overwintering deer, they concentrate the browsing pressure that prevents successful ascension of new trees to the canopy. In contrast, partial harvests could promote cedar regeneration and recruitment while maintaining some cover for deer (Larouche *et al.*, 2011; Saucier *et al.*, 2018). It is unknown whether this will be successful because canopy openings that positively affect seedling and sapling growth also increase browse availability and thus can attract deer (St-Louis *et al.*, 2000; Kuijper *et al.*, 2009). This effect could be both short term due to the influx of foliage on harvest residues and long term due to increased abundance of regeneration. It is not clear whether the overall effect of partial harvests on cedar regeneration and recruitment will be positive in light of interactions with browsing.

Previous work on cedar regeneration following partial harvests has focused on areas with either nearly absent or very high and constant browsing pressure (Larouche *et al.*, 2010; Larouche *et al.*, 2011; Larouche and Ruel, 2015; Saucier *et al.*, 2018). Other studies used retrospective dendrochronological analyses to investigate natural recruitment dynamics of cedar trees, but were conducted where browsing was relatively limited (Hofmeyer *et al.*, 2010; Ruel *et al.*, 2014; Fraver *et al.*, 2020). Little is known about cedar regeneration following partial harvests under low to moderate browsing pressure. In this study, we aimed to identify biotic (herbivory, competition) and abiotic (site, harvesting) factors affecting cedar regeneration following operational partial harvests in an area where deer frequently overwinter. We predicted that abundance of regenerating cedar would increase with years since harvest, and with increasing distance from residual trees because of greater resource availability, but that these effects would be mitigated by competition (i.e. density of regeneration of other tree species) and browsing. We further predicted that these biotic factors (i.e. herbivory, competition) would have greater influence on survival of regenerating cedar than abiotic factors (i.e. drainage, years since harvest, distance from residual trees). Lastly, we predicted that growth of cedar seedlings would increase after harvest, with the magnitude of the response relating positively to distance to residual trees and negatively to years since harvest, competition and browsing. To test our predictions, we inventoried partially harvested stands over 2 years along a gradient of years since harvest (1–11 years) in New Brunswick, Canada.

Methods

The study area was located on privately owned and managed forestland in Victoria County, north-western New Brunswick, Canada (46.79°–47.00° N, 67.43°–67.21° W), with a mean annual temperature of 4.4°C and mean annual precipitation of 1050 mm between 1980 and 2010 (Environment and Climate Change Canada, 2023). We selected 16 pure or mixed cedar stands (pre-harvest proportion of cedar basal area, hereafter BA, >25 per cent) that were partially harvested within the last 15 years and had slopes <20 per cent. All sites showed clear signs of deer presence, including faeces, trail networks, browsing, antlers, bones and rubs. Apart from cedar, stands were mainly composed of balsam fir (*Abies balsamea* L.), red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* Mill.), with some trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* [L.] Carr.).

In New Brunswick, deer population estimates are provided at the wildlife management zone level (>100 km^2). The study area fell at the border between three wildlife management zones (6, 10, 11; Department of Natural Resources and Energy Development, 2021). Average estimated deer densities (including forested and non-forested areas) over the last 10 years, representing the time since forest harvesting in the study area, were 1.23 ± 0.22 deer/km^2 (zone 6), 1.68 ± 0.27 deer/km^2 (zone 10) and 0.89 ± 0.16 deer/km^2 (zone 11). Deer yards located on private land were not delineated, but the study stands were in a 'habitat management area' where cedar was subject to lower harvesting intensity to maintain deer habitat. Deer were known to use portions of the study area following winter harvesting operations (D. Corey, personal communication), which occur in January or February to reduce soil and regeneration damage on lowland sites.

Harvesting was done using a whole-tree method; trees were felled with a tracked feller-buncher, yarded using a grapple skidder and delimbed roadside. Winter harvests in cedar stands leave abundant winter food in the form of cedar branches and tops from felled trees, especially roadside. Prescriptions specified that machinery trails be 5- to 6-m wide and 20-m apart on centre. All sites were partially harvested following relatively broad criteria that focused on maintaining cedar. In cedar-dominated stands, all trees were harvested from machinery trails with no harvesting in the areas between the trails (hereafter the matrix). In spruce- or fir-dominated stands, all trees were harvested from machinery trails and merchantable trees (≥9.0 cm in diameter 1.3 m above the ground, d.b.h.) other than cedar were harvested in the matrix; in some of these stands, light harvesting of cedar was also conducted along trail edges (one out of every four cedar trees within machine reach, ≈6 m). This resulted in a range of residual BA (Table S1) depending on pre-harvest composition and density, but increased cedar abundance in the stands. In portions of stands where cedar was absent, harvests sometimes created small clearcut areas (<0.15 ha), but these were excluded from our study because they did not represent partially harvested conditions.

The 16 study stands were selected from ≈40 candidate sites using stratified random sampling to ensure a range of years since harvesting. Drainage ranged from good (slow but sustained drainage) to poor (water table at or near the surface year-round) and years since harvest ranged from 1 to 11 at first measurement. BA in the matrix averaged 36.7 m^2/ha ± 13.5 SD (Table S1). In each stand, we tallied saplings (1.0–8.9 cm d.b.h.) and merchantable

trees (≥9.0 cm d.b.h.) by species on 2- and 3-m-wide belt transects centred on two random 50-m linear transects placed perpendicular to the machinery trails. The transects included both matrix conditions and the approximately linear gaps created by the machinery trails and selective removal of trail-adjacent trees.

We placed ten 4-m^2 circular regeneration plots along each line transect, with 5 m between plot centres. We noted the location of the plot centre (matrix or gap) and recorded distance to the nearest gap edge (defined by the gap-facing sides of residual tree boles) in metres with 0 for plot centres on the edge and positive and negative numbers for plot centres in the gap or matrix, respectively. We measured apparent height (distance from ground to apex, perpendicular to ground) of every cedar with d.b.h. < 1 cm with mature (scale-like) foliage within the regeneration plots. We considered apparent height to better reflect accessibility to deer browsing than stem length due to the tendency of cedar seedlings and saplings to have a form other than strictly vertical due to their flexibility. We also tagged up to 15 cedar seedlings in height categories <15 and ≥15 cm in height, each, starting from plot centre, for repeated measurements. When cedar seedlings were scarce within a plot, we widened the plot radius to 2 m. We tagged seedlings <10 cm using wooden sticks inserted at the base of the seedling, and seedlings ≥10 cm using aluminium tags attached with a metal wire to the base of the seedling and tucked under the litter. We photographed the seedlings and drew detailed plot maps to facilitate remeasurement. Overall, we tagged 1220 cedar in 320 plots.

We attempted to measure apparent height and browsing on tagged seedlings twice a year (Spring and Fall) to discriminate between browsing occurring during periods of dormancy or active growth. However, early snowfall and logistical issues prevented access to the sites and limited us to three measurements: Spring 2019 and Falls 2019 and 2020 (i.e. two full growing seasons). Average temperature was 3.98°C for 2019 and 5.78°C for 2020, while total precipitation was 1225 mm for 2019 and 983 mm for 2020 (Environment and Climate Change Canada, 2023). We evaluated browsing as (1) apex removal (yes or no) and (2) number of first-order lateral branches browsed and unbrowsed. We recorded the herbivore responsible for the damage based on appearance of the browsed stem: ripped (deer), clipped (hare) or unknown. We tallied competing woody regeneration (trees and shrubs other than cedar with d.b.h. < 1 cm, hereafter low competition) within plots by species and height categories (1–10 cm, 11–30 cm, 31–130 cm, >130 cm), and assigned them a browsing score (0, 1–25 per cent, 26–50 per cent, 51–75 per cent, >75 per cent of foliage browsed) per herbivore (deer, hare or unknown).

Cedar generally has low abundance but high browse selectivity, making it a poor indicator of overall browsing pressure. We therefore used a browsing index as a proxy for deer and hare browsing pressure following Frelich and Lorimer (1985). Specifically, we calculated the proportion of stems browsed for browse-indicator species other than cedar. We used the four most abundant companion species as indicators: balsam fir, red maple, paper birch and fly honeysuckle (*Lonicera canadensis* Bartram ex Marsh). No single species was abundant enough on each site to provide a suitable metric on its own. For each site, we calculated the proportion of stems of these four species that were browsed by hare and by deer (Table S2). Given the generally low abundance of companion species and their variation within site, we calculated this index at the site level.

Statistical analyses

All statistical analyses were performed using R v.4.0.2 (R Core Team, 2020). We used a negative binomial abundance model (negative binomial family, log link, package *glmmTMB*, Brooks *et al.*, 2017) to evaluate the potential effect of partial harvest on the establishment of new cedar regeneration. Because pre-harvest data were not available, we used seedlings ≤30 cm in height as a surrogate for post-harvest regeneration. This height threshold was chosen as it focused the assessment on likely newly established regeneration given the slow growth of cedar seedlings (Bombardier-Cauffopé, 2018). We only used cedar located within the 4-m^2 circular plots for these models.

Predictive covariates included drainage, years since harvest, deer and hare browsing indices, overstory BA (d.b.h. ≥ 9.0 cm), proportion of cedar overstory BA, distance to gap edge, deciduous sapling BA, coniferous sapling BA and density of woody competition by height category (1–10 cm, 11–30 cm, 31–130 cm, >130 cm). We included a random effect for multiple transects nested in site; we removed site from the models as its variance was estimated near 0 and its removal improved goodness-of-fit without considerably changing model coefficients (Bates *et al.*, 2018).

We used binomial generalized linear mixed-effects models to evaluate the 2-year cumulative survival of regenerating cedar (binomial family, logit link, package *glmmTMB*, Brooks *et al.*, 2017). We compared three suites of models representing differing assumptions about the fate of the tagged seedlings that could not be located at the time of remeasurement: (1) dead due to factors other than browsing, (2) dead due to browsing and (3) missing data (this scenario is the most conservative and omits all trees that could not be relocated). None of these assumptions accounted for potential detection error. We included a random effect for plots nested in transects nested in sites. We removed transect from all models and plot from scenario 3 models as their variances were estimated near 0 and their removal improved goodness-of-fit without considerably changing model coefficients (Bates *et al.*, 2018). Predictive covariates included initial (i.e. at the time of first measurement) height, drainage, years since harvest, presence of browsing on the cedar, distance to gap edge, browsing indices for hare and deer, as well as a suite of competition variables (deciduous sapling BA, coniferous sapling BA, overstory BA and woody plant density at heights 11–30 cm, 31–130 cm, >130 cm). We also included interactions between initial height and either years since harvest, browsing or woody plant density at heights 11–30 cm, 31–130 cm and >130 cm.

We used linear mixed-effects models to evaluate the 2-year vertical gain of regenerating cedar (gaussian family, identity link, package *lme4*, Bates *et al.*, 2015). We defined vertical gain as the difference between final and initial apparent height over two growing seasons. To facilitate model fitting, we rounded vertical gain values between 0 and −1 cm to 0 (deemed within measurement error) and eliminated all remaining negative vertical gain values for unbrowsed cedar. We square-root transformed the response variable to satisfy underlying model assumptions. We included a random effect for plots nested in transects nested in sites. The full model included the following predictive covariates: initial cedar height as a covariate, drainage, distance to gap edge, presence of browsing on the cedar, years since harvest and the same competition metrices as in the survival models. We also included interactions between initial height and sapling BA or years since harvest.

We used the Akaike Information Criterion (AIC) to select the most parsimonious of each set of models (Burnham and Anderson, 2002) using package *AICCmodavg* (Mazerolle, 2016): models without competition predictors, models with only overstory competition predictors, models with overstory and sapling competition predictors, and models with all competition predictors, with and without browsing variables (Table 1). When multiple models

Table 1. Description of predictive covariate categories and associated hypotheses included in model selection for all three suites of models (abundance, survival and vertical gain) in partially harvested northern white-cedar stands in New Brunswick, Canada.

Predictor categories	Predictors	Hypothesis
Browsing	Presence of browsing on cedar seedling	Browsing on cedar seedling reduces vertical gain and survival
Browsing index	Deer browsing index, hare browsing index	Browsing on competing vegetation serves as a proxy of overall browsing pressure (Frelich and Lorimer, 1985)
Low competition (abundance models)	Abundance of competing vegetation in four height categories: 1–10 cm, 11–30 cm, 31–130 cm, >130 cm	Abundance of low competing vegetation limits abundance (Larouche *et al.*, 2011; Saucier *et al.*, 2018) of regenerating cedar ≤30 cm
Low competition (survival and vertical gain models)	Abundance of competing vegetation in three height categories: 11–30 cm, 31–130 cm, >130 cm	Abundance of low competing vegetation limits survival and vertical gain (Larouche *et al.*, 2011; Saucier *et al.*, 2018) of regenerating cedar
Sapling competition	Basal area of coniferous saplings (d.b.h. 1–8.9 cm) Basal area of deciduous saplings	Abundance of sapling competing vegetation limits abundance, survival and vertical gain of regenerating cedar (Larouche *et al.*, 2011; Saucier *et al.*, 2018)
Tall competition (abundance models)	Total residual basal area of merchantable stems (d.b.h. ≥ 9 cm) Proportion of cedar in total residual basal area of merchantable stems	Abundance of merchantable-sized competition limits abundance (Larouche *et al.*, 2011; Saucier *et al.*, 2018) of regenerating cedar ≤30 cm Increased proportion of cedar in residual canopy indicates favourable conditions for regenerating cedar
Tall competition (survival and vertical gain models)	Total residual basal area of merchantable stems	Abundance of merchantable-sized competition limits abundance (Larouche *et al.*, 2011; Saucier *et al.*, 2018) of regenerating cedar ≤30 cm

had AIC values within 2 of the most parsimonious model, we selected the most parsimonious model but inspected other models to evaluate whether the same parameters were identified as influential using 95 per cent confidence intervals (CI). The vertical gain models were run without restricted maximum likelihood for model comparison, and the selected model was then rerun with restricted maximum likelihood for interpretation (Faraway, 2016: 201). We inspected the data, looking at outliers, normality of distributions, number of zeros and missing data, and multicollinearity using a variance inflation factor threshold of 3 (Zuur *et al.*, 2010). We verified model assumptions (overdispersion, homogeneity of variance, normality of residuals) using packages *performance* (Lüdecke *et al.*, 2020) and *DHARMa* (Hartig, 2020) and used partial residuals as a regression diagnostics tool with the *visreg* package (Breheny and Burchett, 2017). We performed *post hoc* tests using *emmeans* (Lenth, 2022). Model visualization was done using package *sjPlot* (Lüdecke, 2020) and Nakagawa pseudo-R^2 values were calculated with the *performance* package (Lüdecke *et al.*, 2020).

Results

Post-harvest overstory composition strongly favoured cedar (Figure S1) in that the proportion of overstory cedar was consistently higher after harvest than before harvest. Only two stands had an overstory not dominated by cedar (Figure S1), likely due to low pre-harvest cedar abundance. However, except in lowland stands composed nearly entirely of cedar, pole-sized trees (9–19 cm d.b.h., Figure S1) were largely dominated by other species, mostly fir and spruces. Saplings were mostly dominated by deciduous species and fir with few cedar (Figure S2). Abundance of regenerating cedar varied among and within sites: stocking ranged from 10 to 90 per cent and averaged 54 per cent ± 25 SD (Figure S3). In gaps, we found increasingly taller seedlings as we moved away from gap edges (i.e. towards the centre of gaps); taller seedlings in the matrix were located closer to gap edges (Figure S4, Table S1).

Between measurements, 78 cedar died (6.4 per cent) and 159 disappeared (13 per cent). There was infrequent new browsing during the timeframe of the study (2 years). Of the 1220 initially tagged cedar, 224 had been browsed in the past: 129 by deer (108 with apex removals), 70 by hare (51 with apex removals) and 28 by an unknown species (21 with apex removals). The sum of stems browsed by deer, hare and unknown exceeds total number browsed because some were browsed by multiple herbivores. Sixty cedar showed signs of browsing during the study period: 27 by deer (all with apex removals), 24 by hare (22 with apex removals) and 9 by unknown (all with apex removals). Excluding seedlings that could not be relocated and may have died, only five cedar were browsed and died between measurements.

Abundance

The most parsimonious abundance model (Table 2) included browsing parameters as well as sapling and overstory competition, but not low competition (marginal $R^2 = 0.354$, conditional $R^2 = 0.364$, Table S3). It also included distance to gap edge, drainage, years since harvest, coniferous and deciduous sapling BA, overstory BA, proportion of cedar in the overstory, and deer and hare browsing indices.

Indices of deer and hare browsing both had negative effects on abundance of cedar ≤30 cm (Figure 1A,B). Moderately drained sites had lower abundances than sites with good or imperfect drainages, but poorly drained sites had the same abundance as other drainages (Figure 1C). Increases in coniferous and deciduous sapling BA as well as years since harvest positively affected cedar abundance (Figure 1D–F). Residual overstory BA, distance to gap edge and the proportion of cedar in the overstory did not have a detectable effect in the model.

Survival

We were unable to record the fate of 13 per cent of tagged seedlings. Assignment of an assumed fate (dead due to factors other than browsing, dead due to browsing, missing data) resulted

Table 2. AIC model selection results for models predicting abundance of northern white-cedar regeneration ≤30 cm height in New Brunswick, Canada.

Model	K	AIC	ΔAIC	AIC weight
No low competition	**14**	**1276.3**	**0**	**0.64**
Full model	**18**	**1277.8**	**1.5**	**0.31**
No browsing index	16	1283.7	7.4	0.02
No low competition, no sapling competition	12	1284.1	7.8	0.01
No competition	10	1284.1	7.7	0.01
No browsing index, no low competition	12	1286.5	10.2	0
No browsing index, no low competition, no sapling competition	10	1292.6	16.3	0
No browsing index, no competition	8	1292.3	16.0	0
Null model	3	1305.9	29.6	0

K shows the number of model parameters. All models in bold font (ΔAIC < 2 from most parsimonious model) were inspected; within each scenario, all models shared the same influential parameters with the selected models.

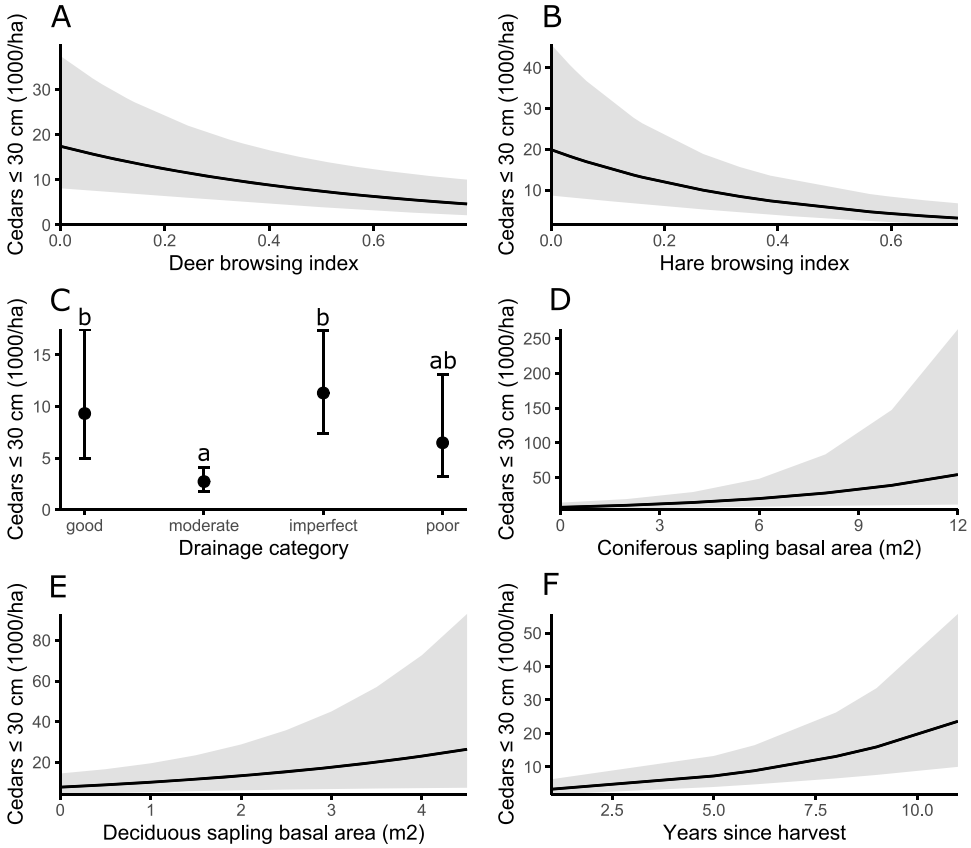

Figure 1. Predicted mean abundance and 95% CIs for the principal variables affecting abundance of northern white-cedar ≤30 cm in New Brunswick, Canada. (**A**) Deer browsing index (larger values represent higher browsing pressure); (**B**) hare browsing index (larger values represent higher browsing pressure); (**C**) drainage; (**D**) coniferous sapling basal area; (**E**) deciduous sapling basal area; (**F**) years since harvest. Different letters within the panel indicate contrasts between means for which the 95% CI does not include 0. Note the different *Y*-axis scales between panels. $n = 320$.

in some differences in identification of the most parsimonious model for each dataset (Table 3). When assuming that missing seedlings were dead due to other factors (scenario 1), the most parsimonious model included covariates for years since harvest, initial height of tagged cedar, distance to gap edge and drainage (marginal $R^2 = 0.484$, conditional $R^2 = 0.577$, Table S4). When assuming that missing seedlings were dead due to browsing (scenario 2) or missing data (i.e. omitting them from the analysis, scenario 3), the most parsimonious models included years since harvest, initial cedar height, browsing, distance to gap edge, drainage, deer and hare browsing indices, as well as interactions between initial cedar height and years since harvest or browsing (scenario 2 marginal $R^2 = 0.700$, conditional $R^2 = 0.722$; scenario 3 marginal $R^2 = 0.540$, conditional $R^2 = 0.550$, Table S4).

For scenario 1, only initial cedar height positively affected cedar survival (Table S4, Figure 2). For scenario 2, only browsing negatively affected cedar survival (Table S4, Figure 2), and we observed a large but variable positive effect of initial height (95 per cent CI odds ratio 0.92–4.46, Table S4). For scenario 3, we only observed initial height as having a large but variable effect on cedar survival (95 per cent CI odds ratio 0.73–9.60, Table S4).

The survival of cedar over the 2-year measurement period increased considerably with seedling height. In fact, all cedar >53 cm in height survived for the duration of the study. Under the

Table 3. AIC results for models predicting the survival of tagged northern white-cedar seedlings in New Brunswick, Canada, according to three scenarios regarding the fate of seedlings that could not be located for remeasurement.

	S1: dead, not browsed				S2: dead, browsed				S3: missing data			
Model	***k***	**AIC**	**ΔAIC**	**AIC weight**	***k***	**AIC**	**ΔAIC**	**AIC weight**	***k***	**AIC**	**ΔAIC**	**AIC weight**
Full model	23	974.5	5.0	0.03	23	544.4	4.5	0.06	22	416.1	12.3	0
No browsing, no browsing index	19	970.3	3.5	0.10	19	970.3	430.4	0	18	417.5	13.7	0
No low competition	17	974.0	4.5	0.03	17	542.9	3.0	0.13	16	408.8	5.0	0.04
No low competition, no sapling competition	15	974.7	5.3	0.02	**15**	**541.9**	**2.0**	**0.22**	**14**	**405.8**	**2.0**	**0.16**
No competition	**14**	**973.0**	**0.8**	**0.21**	**14**	**539.9**	**0**	**0.59**	**13**	**403.8**	**0**	**0.43**
No browsing, no browsing index, no low competition	**13**	**970.0**	**0.6**	**0.23**	13	970.0	430.2	0	12	409.5	5.7	0.03
No browsing, no browsing index, no low competition, no sapling competition	**11**	**971.4**	**1.9**	**0.12**	11	971.4	431.6	0	10	406.7	2.9	0.10
No browsing, no browsing index, no competition	**10**	**969.5**	**0**	**0.31**	10	969.5	429.6	0	**9**	**404.8**	**1.1**	**0.25**
Null model	3	1057.6	88.1	0	3	1057.6	517.7	0	2	420.7	16.9	0

Scenario 1 (S1, $n = 1220$): missing seedlings are not considered browsed. Scenario 2 (S2, $n = 1220$): missing seedlings are considered browsed. Scenario 3 (S3, $n = 1074$): missing seedlings are excluded from the models. *k* shows the number of model parameters. All models in bold font (ΔAIC < 2 from most parsimonious model) were inspected; within each scenario, all models shared the same influential parameters with the selected models. AIC values are comparable between scenarios 1 and 2 as they have the same random effect structure and the same data, but not with scenario 3.

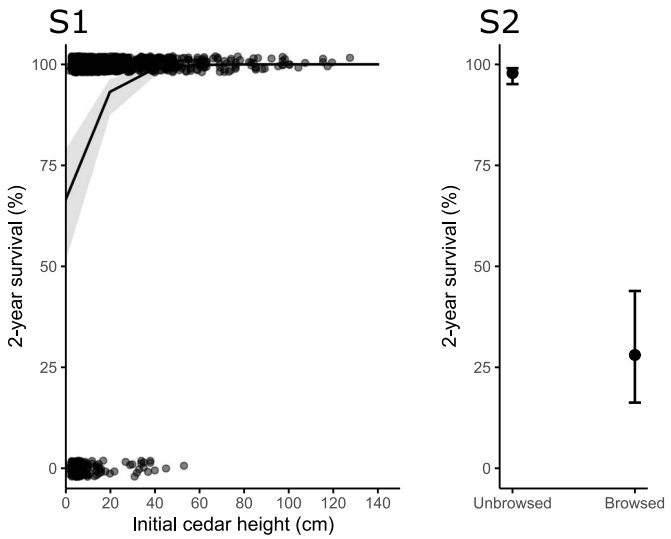

Figure 2. Predicted survival and 95% CIs for principal variables of selected northern white-cedar seedling survival models in New Brunswick, Canada. Scenario 1 (S1): disappeared cedar are not considered browsed. Scenario 2 (S2): disappeared cedar are considered browsed. Datapoints show raw data and are jittered vertically to reduce overlap. $n = 1220$.

first scenario, our model predicted probability of survival >90 per cent once a height of 15 cm has been reached. Under the second scenario, our model predicted survival of 98 per cent (95 per cent CI 95–99 per cent) for unbrowsed cedar, and 28 per cent (95 per cent CI 16–44 per cent) for browsed cedar (Figure 2)**.** Initial height had a positive effect on survival; the scenario 2 model predicted chances of survival >90 per cent once a height of 25 cm has been reached, and the scenario 3 model predicted >95 per cent survival once a height of 11 cm has been reached.

Vertical gain

The most parsimonious vertical gain model (Table 4) included neither browsing, low competition nor sapling competition, but included overstory competition (marginal $R^2 = 0.489$, conditional $R^2 = 0.576$, Table S5). Predictive covariates included initial cedar height, years since harvest and their interaction, distance to gap edge, drainage and overstory BA.

Initial cedar height and distance to gap edge had positive effects on vertical gain, whereas increased years since harvest had a negative but variable effect on vertical gain (95 per cent CI −0.13 to 0.01, Figure 3). Regardless of model estimates for moderate drainage (Table S5), *post hoc* tests revealed no difference between drainage categories (Figure 3). Cedar overstory BA and the interaction between initial cedar height and years since harvest did not influence vertical gain (Table S5).

Discussion

We observed an increase in the abundance of regenerating cedar with increasing years since harvest and decreasing browsing pressure. However, contrary to our expectations, we did not detect an effect of location relative to gap edge and we observed a positive effect of sapling-sized competition on cedar abundance. We also did not observe the predicted effect of competition on cedar seedling survival, and an effect of browsing was only detected

Table 4. AIC results for models predicting vertical gain of northern white-cedar in New Brunswick, Canada.

Model	*k*	AIC	ΔAIC	AIC weight
No browsing, no low competition, no sapling competition	**13**	**2895.5**	**0**	**0.45**
No browsing, no competition	**12**	**2897.0**	**1.5**	**0.21**
No low competition, no sapling competition	14	2897.5	2.0	0.17
No competition	13	2899.0	3.5	0.08
No browsing, no low competition	17	2899.3	3.8	0.07
No low competition	18	2901.3	5.8	0.02
Null model	5	3179.5	284.0	0
Full model	21	2907.0	11.5	0
No browsing	20	2905.0	9.5	0

k shows the number of model parameters. All models in bold font (ΔAIC < 2 from most parsimonious model) were inspected; within each scenario, all models shared the same influential parameters with the selected models. N = 985.

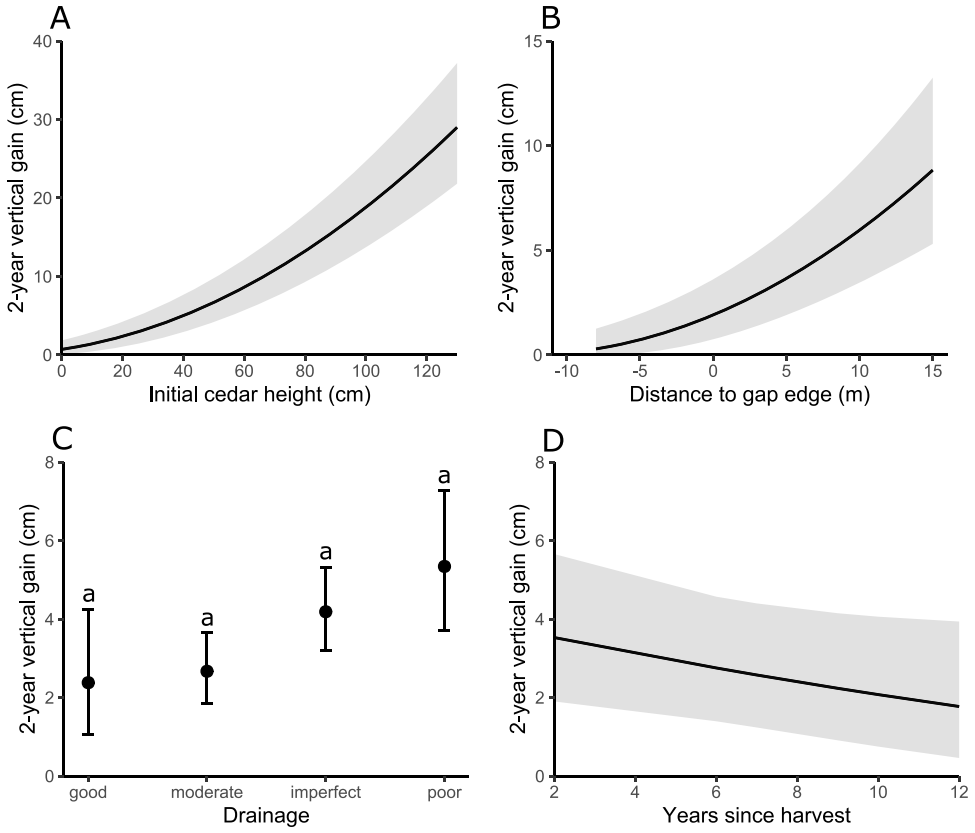

Figure 3. Predicted vertical gain and 95% CIs for the principal variables affecting 2-year vertical gain of northern white-cedar 2-year in New Brunswick, Canada. (**A**) Initial cedar height; (**B**) distance to gap edge (negative values indicate location within the matrix, positive values indicate location within a gap); (**C**) drainage; (**D**) years since harvesting. Matching letters within the panel show contrasts between predicted means with a 95% CI that includes 0. Note the different *y*-axis scales between panels. *n* = 985.

under a 'full browse' scenario in which all missing seedlings were assumed to be browsed. We did observe the predicted decrease in vertical gain with years since harvest and the predicted increase in vertical gain with distance to gap edge, but we did not detect effects of competition or browsing on growth.

We do not have historical data regarding browsing within the study area, apart from the deer and hare browsing indices. However, the absence of cedar saplings (1–8.9 cm d.b.h.) may indicate that past browsing prevented recruitment, as the shade tolerance of cedar should otherwise allow its survival in a suppressed state or recruitment beneath abundant cedar canopies (Cornett *et al.*, 2000; Larouche *et al.*, 2010). This is consistent with studies that have documented a lack of cedar saplings in stands where cedar seedlings are abundant but browsing pressure is high (e.g. Larouche and Ruel, 2015; Villemaire-Côté *et al.*, 2022). This observation is also supported by anecdotal reports of heavy browsing right after harvesting in the study stands (D. Corey, personal communication), a phenomenon that has been documented for cedar in the Great Lakes region (Verme and Johnston, 1986) and in stands with yarded deer in eastern Québec (St-Louis *et al.*, 2000).

For our analyses, we developed indices of deer and hare browsing on plant species less heavily selected by deer. These indices provide valuable information, but do not inform the timing of browsing or selectivity towards regenerating cedar. In addition, the deer browsing index could include browsing by moose (*Alces alces*, also locally abundant), but we concluded that this influence would be minor because moose are generally known to browse cedar only sporadically (Peek *et al.*, 1976) unless preferred food sources are unavailable (Eastman and Ritcey, 1987 for *Thuja plicata*).

Increases in both deer and hare browsing indices had negative effects on the abundance of small cedar seedlings (≤30 cm). While we did not observe extensive new browsing on cedar during our study period, cumulative browsing could have led to lower cedar seedling abundance due to past mortality. Short seedlings could also have been browsed down to a height that prevented their detection. We observed this anecdotally on some tagged seedlings that were eaten by deer or hare and severed a few centimetres from the ground; we would not have detected these if they had not been tagged prior to the browsing event. This underlines how difficult it can be to estimate actual browsing pressure and its effect on the regeneration of highly selected species, as observed for cedar in unmanaged stands in Québec (Villemaire-Côté *et al.*, 2022) and Wisconsin (Reuling *et al.*, 2019).

In stands with good or imperfect drainage, the abundance of cedar ≤30 cm was nearly quadruple that of stands with moderate drainage. The effect of drainage was otherwise not influential on cedar seedling abundance. The BA of coniferous and deciduous saplings also positively affected abundance of cedar ≤30 cm, as observed in the Lake States (Reuling *et al.*, 2019). Although competing vegetation has been found to have a negative impact on the abundance of regenerating cedar elsewhere (e.g. Larouche *et al.*, 2011; Saucier *et al.*, 2018), we did not observe a negative effect from either low (<1 cm d.b.h.) or tall (≥9 cm d.b.h.) competition. It is likely that an abundance of saplings of other species indicates conditions also conducive to cedar regeneration, and that competition in those areas has not been of sufficient intensity or duration to cause mortality of cedar seedlings given their shade tolerance (Johnston, 1990). Furthermore, the absence of a correlation between years since harvest and sapling BA suggests that some stands had established sapling cover prior to harvesting. Consistent with the ability of cedar to form advance regeneration (Heitzman *et al.*, 1999; Fraver *et al.*, 2020), harvesting would therefore only partly explain observed differences in cedar abundance ≤30 cm (e.g. sites B and C, Figures S1–S3).

Years since harvest had a positive effect on the abundance of small cedar seedlings, similar to dynamics observed elsewhere after natural gap formation (e.g. Villemaire-Côté *et al.*, 2022). This suggests that cedar germination is maintained over time after the canopy has been opened, or that germinated seedlings were kept ≤30 cm due to suppression, browsing or snow load. This temporal increase in abundance is likely to slow down after some time due to canopy closure and increased competition (Chimner and Hart, 1996; Larouche *et al.*, 2011).

The results of the survival analyses greatly differed according to how we modelled the tagged seedlings that disappeared between measurements. As such, results should be interpreted with caution. Overall, the survival analyses suggest that cedar seedling survival increases with height; this could be due to reduced browsing or lower susceptibility to other factors such as desiccation (Man *et al.*, 2013). We did not detect an effect of distance to gap edge on survival of 2-year cedar seedlings, suggesting little effect of post-harvest canopy conditions. This is not to say that harvesting has no effect on survival, as the passage of machinery and felling of trees can damage or kill advance regeneration (Pominville and Ruel, 1995) and abundance of cedar seedlings has been found to decrease pre- to post-partial harvesting (Bose *et al.*, 2023). In fact, our survival analyses are in some ways a subset of the abundance analysis; only cedar that existed at the time of inventory could be used for the survival analysis. This could explain why variables such as years since harvest affected abundance but not survival, i.e. processes leading to decreases in cedar abundance occurred before the initiation of the survival measurements.

The other parameters tested for inclusion in the survival models (Table 1) influenced cedar abundance or growth in our study, but seemingly did not affect survival. Initial cedar height and survivorship bias could overshadow some parameters; taller and therefore more established seedlings may have been less susceptible to browsing. Moreover, survival was very high, likely because most browsing pressure happened before the initiation of the study, making it difficult to detect parameters of importance. Variations in climate between years could also have played a role in survival. The first measurement year (2019) had growing season precipitation within normal range, but the second year had growing season precipitation 200 mm below normal (Environment and Climate Change Canada, 2023). This could have led to moisture stress and increased mortality of shorter seedlings (Man *et al.*, 2013, Schulz, 2022) and is consistent with the greater number of dead seedlings and seedlings that could not be relocated after the second year (187) than the first year (54).

As expected, the initial height of cedar seedlings positively affected vertical gain. Taller cedar seedlings have more growth potential, as previously observed after partial harvests (Saucier *et al.*, 2018). Increased years since harvest had a negative effect on vertical gain, contrary to its effect on abundance. This could be an effect of growing conditions (mostly light availability) gradually worsening after harvest and negatively affecting vertical gain. If so, we failed to capture this with the parameters we measured; competition metrics did not affect vertical gain within the timeframe of this study.

With gaps, the positive effect of distance to gap edge on vertical gain is in line with previous studies of cedar regeneration following partial harvesting (Larouche *et al.*, 2011; Saucier *et al.*, 2018). This finding also aligns with studies of the effects of partial harvests on residual tree stems (Montoro Girona *et al.*, 2016; Boivin-Dompierre *et al.*, 2017) and regeneration (Montoro Girona *et al.*, 2018). Within a stand's matrix, growth is generally limited where conditions change little following harvest but increases as one moves closer to gap edges due to an increase in available resources (Beaudet *et al.*, 2011; Kern *et al.*, 2013). This is consistent with cedar regeneration as observed in the present study; seedlings in the matrix were taller closer to gap edges (Figure S4). This analysis has a survivorship bias, as it could only focus on surviving cedar. These results, however, suggest a potential for strip shelterwood regeneration method to benefit growth of regenerating cedar. There is a long history of strip cutting for cedar regeneration in the Lake States, but wide strips (i.e. clearcuts) were predominantly used and often found to be unsuccessful (e.g. Heitzman *et al.*, 1999). Our results suggest that narrower strips (e.g. 1–2 tree heights wide, or oriented to maintain partial shade) may be more successful.

Interestingly, distance to gap edge affected vertical gain but had little to no effect on abundance or survival. This could be due to differences between germination and growth niches (Raymond *et al.*, 2006, Larouche *et al.*, 2011); cedar is able to germinate with or without stand openings but its growth is positively related to canopy openness. As to browsing, it was infrequent over the course of the study and this could partly explain why it was not identified as influential in our models. Moreover, cedar is known to be tolerant of browsing and able to display compensatory height growth following episodes of browsing (Villemaire-Côté, 2023). As with survival, interannual climatic variations might also have affected seedling growth, although our data did not suggest interannual differences in vertical gain.

We found that competition (expressed as density of woody stems in the understory) was positively correlated with cedar

abundance and did not affect 2-year survival or vertical gain following partial harvesting over the 1–11 years since harvest. This result highlights the potential for partial harvest to increase the abundance and vertical gain of cedar regeneration in the short term. However, past research suggests that negative effects of competition may occur later in stand development if overtopping has developed (Larouche *et al.*, 2011; Saucier *et al.*, 2018; Villemaire-Côté *et al.*, 2017). Moreover, the composition of stems 1–19 cm d.b.h. suggests that cedar recruitment to taller height classes was very infrequent, if not absent, both before and after harvesting. This is often observed following partial harvests not focused on creating conditions favourable to cedar (e.g. Larouche *et al.*, 2010). In such cases, partial harvests can increase the number and initial growth of cedar seedlings, but later growth can be constrained by faster growing competitors (Larouche *et al.*, 2011, Saucier *et al.*, 2018).

Moreover, our results highlight the large variation in cedar regeneration that can occur within partially harvested stands. This is common for shade-tolerant, late-successional species such as cedar, red spruce, yellow birch, eastern hemlock and balsam fir (Matonis *et al.*, 2011; Kern *et al.*, 2019). These species can establish under a canopy but often need openings to be recruited to taller height classes and can be outcompeted by faster growing species after canopy opening (Raymond *et al.*, 2018; Kenefic *et al.*, 2021). This leads to slower growth, which equates to more time spent within browsing reach and therefore increased risk of recruitment failure due to browsing. Slower growth also means a likely decrease in dominance within the stand and slower cedar production, which can in turn contribute to a decline in deer overwintering areas.

The effect of partial harvests on regeneration of cedar on upland sites has been documented, but silviculture on lowland sites has generally focused on favouring advance regeneration of cedar (Verme and Johnston, 1986; Bergeron, 2000). However, we found partial harvests to have a positive effect on cedar regeneration regardless of drainage. This suggests that partial harvests could also be used in lowland sites where post-harvest seedling establishment is desired. Although this strategy would increase the risk of regeneration failure compared with release of advance regeneration, it could be used where regeneration is not properly established prior to harvesting or could help compensate for the losses brought by harvesting operations.

Given the negative relationship between browsing indices and cedar abundance observed in this study, managers might consider retaining overstory seed-bearing cedar beyond the regeneration period in partially harvested stands. Deferring overstory removal (if planned) until cedar regeneration has recruited to a height that is safe from browsing (3 m) may be prudent to prevent regeneration failure (Boulfroy *et al.*, 2012; Villemaire-Côté *et al.*, 2017). Furthermore, the absence of cedar saplings in the present study, the low abundances of cedar saplings observed elsewhere (Larouche *et al.*, 2010; Reuling *et al.*, 2019; Fraver *et al.*, 2020) and the fact that cedar sapling mortality can increase following partial harvesting (Bose *et al.*, 2023) suggest that protecting as much advance regeneration as possible is important. Care should also be given to control companion species which could outcompete slower-growing cedar seedlings, as competition can reduce the positive effect of partial harvests on cedar vertical gain (Saucier *et al.*, 2018). Our findings suggest that while partial harvests can increase cedar regeneration, they may not maintain cedar dominance in the regenerating stratum of mixed stands. Post-harvest inventories are advisable to identify regeneration problems and adjust management accordingly.

Conclusion

In this study, we demonstrate that partial harvests can positively affect the abundance and vertical gain of cedar seedlings. We also show a negative effect of past deer and hare browsing on the abundance of cedar seedlings, but no detectable effect on their current vertical gain. However, it can be difficult to properly assess browsing pressure in a natural setting. Seedlings disappear with time and it is impossible to determine the cause of disappearance without constant monitoring. These disappearances also show that the delay between harvest and inventories can greatly influence the perception of regeneration; this may be important for species with challenging regeneration such as cedar. To remedy this situation, it is necessary to conduct follow-up studies initiated before forest disturbance. Such studies would also benefit from using occupancy modelling to account for detection errors. Collectively, these efforts could contribute to better monitor and promote slower-growing, browse-sensitive or later successional species, which are seeing widespread regeneration challenges.

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Supplementary data

Supplementary data are available at *Forestry* online.

Author contributions

Olivier Villemaire-Côté (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Jean-Pierre Tremblay (Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, Writing—review & editing), Laura Kenefic (Investigation, Methodology, Validation, Writing—review & editing) and Jean-Claude Ruel (Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing—review & editing).

Conflict of interest statement

None declared.

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Data availability

The datasets generated during and/or analysed during the current study are available on the Figshare repository, https://figshare.com/s/cd4e8d3d24e5f9dcf14a.

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