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# Forest Ecology and Management

# Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities

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## ARTICLE INFO

## ABSTRACT

Tree species composition in forests can be strongly modulated by high densities of cervid herbivores ultimately leading to local extirpation of species. To establish which cervid densities are compatible with the recruitment of a browse sensitive tree species, seedlings and saplings should be surveyed under variable cervid densities rather than in their presence or absence alone. We studied the growth and survival of different demographic stages of balsam fir (*Abies balsamea*) on Anticosti island (Québec, Canada) under controlled densities of white-tailed deer (*Odocoileus virginianus*). In a seven-year experiment using deer enclosures, we followed the life stage and fate of individually tagged balsam fir seedlings/saplings under forest cover and forest logged at the start of the experiment. Almost no regeneration into the sapling stage (>30 cm) was observed under ambient deer densities after 7 years and decreased survival and growth were observed under an experimental deer density of 15 km$^{-2}$. However, mortality at ⩽15 deer km$^{-2}$ decreased over time and with age and stem height, converging towards mortality observed at 0 deer km$^{-2}$. Given the relatively high stem density of saplings at 15 deer km$^{-2}$ 7 years after the start of the treatment, our data indicate that at this density considerable balsam fir regeneration may occur, although the ultimate contribution of balsam fir to the canopy remains uncertain. The notion that small seedlings are most vulnerable to deer browsing and that balsam fir recruitment rapidly decreases after logging suggests that maintaining low deer densities is most crucial immediately after a stand-initiating disturbance (e.g. logging).

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## 1. Introduction

Large vertebrate herbivores can have strong top-down effects on the abundance of targeted plant populations. The magnitude of herbivore impacts on plant fitness depends on two types of resistance traits, either avoidance or tolerance based (sensu Belsky et al., 1993). Tolerance is the capacity of a plant to maintain fitness through growth and reproduction after sustaining herbivore damage (Rosenthal and Kotanen, 1994). Avoidance traits are traits that decrease consumption or the chance of consumption by herbivores. Resistance of plants to herbivores may change with demographic stages, since individuals may change in palatability or compensatory abilities (Boege and Marquis, 2005). In addition, the presence of palatable or unpalatable neighbouring plants influences the foraging decisions of herbivores. Such indirect avoidance is known as avoidance by association (e.g. Hjältén et al., 1993; Bee et al., 2009). The combined effects of individual resistance traits and associations are here termed inclusive resistance.

In ecosystems with long-lived plants such as forests, the inclusive resistance of different demographic stages may be of crucial importance for the survival of tree populations. Many forests worldwide nowadays have dense cervid herbivore populations scarcely regulated by predators, raising concerns about the conservation of key tree species in such ecosystems (Côté et al., 2004). In order to understand herbivore impacts on tree species composition of forests and to develop realistic management scenarios, experimental studies should assess the effects of variation in herbivore densities on the regeneration of tree species. The rare experiments dealing with multiple different deer densities have either focused on general patterns of succession (Tilghman, 1989; Horsley et al., 2003) or exclusively on the seedling stage (Tremblay et al., 2007). To obtain a more mechanistic understanding of the sensitivity of plant populations to deer, we need to study herbivore effects on different demographic stages (e.g. Knight et al., 2009). Hence, we need to test the effects of different deer densities at seedling stages as well as later stages during forest regeneration and quantify survival and transitions to later stages.

One such system in which cervid densities are exceptionally high is Anticosti Island, Québec, Canada. The island, free of large predators, exhibits unusually high densities of introduced white-tailed deer (*Odocoileus virginianus*). This circumstance allows for

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rigorous testing of the possible effects of elevated herbivore densities on boreal forest plant communities. Deer, introduced near the end of the 19th century, reached high densities in the 1930s and remained abundant ever since. From this time onward the dominant tree species on the island, balsam fir (*Abies balsamea*), decreased in abundance and has been gradually replaced by white spruce (*Picea glauca*) (Potvin et al., 2003). The demise of balsam fir may ultimately cause a setback to white-tailed deer itself, as it has become staple food for deer on Anticosti Island (Tremblay et al., 2005; Lefort et al., 2007). Because white spruce is far less palatable than balsam fir (Sauvé and Côté, 2007), eradication of balsam fir may deprive deer from a critical winter resource. In a previous paper, Tremblay et al. (2007) have shown using an enclosure experiment with controlled deer densities, that the seedling bank of balsam fir, although chronically browsed, can withstand fairly high levels of herbivory (15 deer km$^{-2}$). Here, we extend our investigation to the period of recruitment of seedlings to the sapling stage (stems taller than 15 cm) up to 7 years after a stand-initiating disturbance. We hypothesized that growth and survival of balsam fir is a function of deer density and is modulated by changes in inclusive resistance over time.

In enclosures established in a mosaic of forest cover and clear cuts, we maintained four different deer densities: 0, 7.5, 15 deer km$^{-2}$ and ambient deer density (27–56 deer km$^{-2}$). This allowed us to quantify regeneration of balsam fir both under canopy (advance regeneration) and after a stand-initiating disturbance. We predicted that (a) browsing on balsam fir increases with deer density, (b) growth and survival of balsam fir seedlings is hence negatively affected at a higher density of white-tailed deer, and (c), that recruitment into the sapling stage and subsequent survival is less affected than seedling recruitment, given changes in inclusive resistance to herbivory. To this end, we recorded recruitment, survival, stem height and branch number of almost 6000 individually tagged balsam fir seedlings/saplings each autumn from 2002 until 2009. We also monitored browsing damage incurred by deer. Past research has shown that the regeneration of browse sensitive tree species can be severely reduced by cervid herbivory (e.g. Long et al., 2007; Olesen and Madsen, 2008; Stroh et al., 2008). Most of these studies compared herbivore presence with total absence (but see Horsley et al., 2003). Such designs are certainly helpful in establishing which species are most vulnerable and whether or not they can recover in the absence of herbivory. However, in order to understand the limits of herbivore resistance, regenerating vegetation needs to be exposed to multiple different densities of herbivores.

## 2. Methods

### 2.1. Study area

The experimental site was located on Anticosti Island (7943 km$^2$) in the Gulf of St. Lawrence, Québec, Canada (49°06′–49°95′N, 61°67′–64°52′W). The climate on Anticosti is maritime with a mean air temperature of $-13.6$ °C in January and 14.8 °C in July and a mean annual precipitation of 328 cm as snow and 610 mm as rainfall (Environment Canada, 2005). The dominant boreal forest cover is part of the eastern balsam fir – paper birch (*Betula papyrifera*) region (Saucier et al., 2009). Approximately 200 deer were introduced to Anticosti Island in 1896 and 1897. The deer population became abundant ca. 30 years after the introduction and remained at high density thereafter ($\sim$20 km$^{-2}$, Potvin and Breton, 2005). Other herbivores on the island are snowshoe hare (*Lepus americanus*) and rare moose (*Alces alces*) (Potvin et al., 2003). No natural predators are present although black bear (*Ursus americanus*), a possible predator of white-tailed deer fawns

(Mathews and Porter, 1988), has been sighted occasionally until the 1990s (Côté, 2011). However, each year in autumn at least 8000 deer are hunted on the island (Rochette and Gingras, 2007).

### 2.2. Experimental design

We conducted a controlled browsing experiment to investigate the relationships between deer density and balsam fir forest regeneration dynamics in interaction with timber harvesting. The browsing treatment included four levels of deer density (0, 7.5, 15 deer km$^{-2}$ and ambient density). Each level was applied to two types of forest cover: (1) even-aged clear cut, logged at the start of the experiment (2001), and (2) uncut forest both with >70% canopy closure by mature balsam fir forest overstorey before the beginning of the experiment. All deer densities and forest cover types were replicated within three blocks, each composed of four adjacent or close proximity experimental units. The enclosures were built of 3 m high wire game fencing and their surface area was 10 ha for the 0 deer km$^{-2}$, 40 ha for the 7.5 deer km$^{-2}$ level (3 deer per enclosure) and 20 ha for the 15 deer km$^{-2}$ treatment level (3 deer per enclosure). Effects of ambient deer density were estimated in a 40 ha area, where we estimated deer density from pellet counts at 27 deer km$^{-2}$ in blocks B and C, and 56 deer km$^{-2}$ in block A (see Tremblay et al., 2006 for details). The browsing treatment was repeated during eight consecutive years (2002–2009, y0–y7).

Wild deer were captured in the vicinity of the experimental blocks each May, relocated in the enclosures and culled in November. Both in May and in November there was generally substantial snow cover on the ground (>20 cm). Mainly yearlings (11–12 months old at the time of capture) but also adults were distributed evenly among the experimental units. We used multiple control procedures to maintain the target densities, including lethal and non-lethal drives and checking for tracks in the snow before stocking. All deer were fitted with VHF collars (Lotek Wireless Inc., Newmarket, Ont., Canada) during the course of the experiment. All animal handling protocols were approved by the Université Laval Committee of the Canadian Council on Animal Care (2008017-2).

In June of y0, before the first application of the browsing treatment, we randomly selected 20 circular plots (0.5 m$^{-2}$) for each combination of deer density and forest cover in each block ($n$ = 480 plots). We used numbered glass rods to tag all balsam fir seedlings that had passed the cotyledon stage and were less than 10 cm tall and had a single unbrowsed stem per plot ($n$ (y0) = 3300 seedlings). We removed seedlings that did not meet those criteria and woody debris to obtain homogeneous conditions. We monitored the height and status of tagged seedlings and the emergence of new seedlings during annual visits in September from y0 to y7 as: (1) alive and unbrowsed, (2) browsed, (3) browsed-to-death, (4) dead from unknown causes, (5) new seedlings past the cotyledon stage, (6) newly emerged seedlings with browsing damage or (7) lost to the experiment (e.g. due to windblown trees damaging plots). Browsing by deer leaves shredding marks that are easily discernible from the sharp cuts made by snowshoe hare. Browsing damage by snowshoe hares was only very rarely observed in our experiment. From the autumn of 2002 until autumn 2009 we obtained 29,988 observations on 5933 tagged seedlings.

### 2.3. Deer density and seedling growth

To estimate growth of seedlings under the different herbivore pressures, we compared the length of stems over time since the seedlings were tagged across the different cover types and deer densities. Because no transformation of individual stem heights

would meet normality and homoscedasticity assumptions, we calculated mean seedling height for each combination of block, deer density (0, 7.5, 15 deer km$^{-2}$ and ambient density), cover and time since tagging (from 0 to 7 years), yielding 192 data points. We consider this approach justified as the unit of replication in the experiment was at the level of blocks. A linear mixed model was constructed using the lme4 package (Bates and Maechler, 2010) in R with inverse stem height as the response variable. Inverse stem height was chosen after performing a Box–Cox procedure to find the data transformation that meets the assumption of normally distributed residuals. Fixed predictor variables were deer density, cover, and seedling age (time since tagging). A random intercept for block was included as well as a random intercept for the interaction between block, deer density and cover. A random slope for age was nested in this interaction accounting for repeated measurement correlations. A Levene's test was applied to the model residuals to check whether variances were indeed homogeneously distributed ($F_{63,128} = 0.709$, $p = 0.936$). We checked whether the residuals were normally distributed by visual inspection. To test the significance of the model factors and interactions we performed deviance tests (likelihood ratio tests) comparing the maximum likelihood (ML) estimated from models including the fixed variable of interest and models without them. The same procedure was applied to assess significance of random variables, albeit in this case restricted maximum likelihood estimates were compared (Zuur et al., 2009). Post-hoc contrasts to determine which deer densities had distinct effects on seedling growth for a given cover type were performed according to Crawley (2007). For each individual comparison, the two levels of interest of the factor deer density within cover type were pooled and compared with the original model (ML-estimates). As the simplified model is nested within the original model we estimated significance of the individual comparison using deviance statistics ($\alpha = 0.05$).

### 2.4. Deer density and browsing damage

The same procedure as for seedling growth was applied in the analysis of the proportion of seedlings with browsing damage, either dead or alive. Here, proportions calculated per block, deer density and forest cover combination were arcsine – square-root transformed, resulting again in 192 data points. The tested models had a design identical to those on seedling growth, with the exception of the factor seedling age which was replaced by sampling year. Normality and variance homogeneity were checked visually. In addition, a Levene's test was applied to assure variance homogeneity ($F_{63,128=}0.615$, $p = 0.984$).

### 2.5. Deer density and stem survival

Since the growth model ignores mortality due to herbivore browsing, a Cox proportional hazard survival analysis with mixed effects terms was performed using all seedlings alive in the autumn of 2002, using the coxme package in R (Therneau, 2009). A Cox proportional hazard model evaluates the hazard function $h(t)$, which indicates the instantaneous risk of mortality at time $t$, given survival to time $t$. Hence, time is implicit to the response variable and is thus not included as a predictor in the analysis (Crawley, 2007). Individual stems alive at the end of the experiment or individuals in plots that were destroyed (e.g. by fallen trees during the experiment) were considered censored, meaning that their survival was included in model fitting but not their status afterwards (Crawley, 2007). We constructed a model with cover and deer density and the interaction term as fixed effects. Block, site (the combination of the density and cover treatments inside a block) and plot were included as random factors, where plot was nested in

site and site was nested in block. Site was included instead of the interaction between block, density and cover since the R-package coxme does not allow crossed random effects. The significance of random and fixed terms was evaluated using deviance statistics (likelihood ratio tests) on a model including the variable of interest and one lacking this factor. To assess which deer densities caused significant changes in the hazard function, post hoc tests were applied in the same manner as in the growth model, that is by merging factor level combinations followed by deviance statistics. For plotting purposes, the mean effect from a full Cox model was fitted including only the fixed effect terms.

### 2.6. Matrix projection under different deer densities

To determine which early life stages were most vulnerable to herbivory and how vulnerability translated into sapling recruitment, we constructed stage-structured matrix models using the popbio package in R (Stubben and Milligan, 2007). We constructed a life table with four stages for each combination of deer density and forest cover level: seedlings (<15 cm) with one primary branch (s1), seedlings (<15 cm) with more than one branch (s2), small saplings (15–30 cm [e1]), i.e. established saplings according to Frank (1990), and larger saplings >30 cm (e2), representing established juveniles (following Chouinard and Filion, 2001; Potvin et al., 2003). Transition probabilities were the proportional observed state transitions in the experiment for each deer density and forest cover type. The matrix models were incomplete as we do not have data on complete life cycles of balsam fir for the different treatments, i.e. the saplings in our study were too young to reproduce. Hence, because in such models calculation of the intrinsic growth rate ($\lambda$) is meaningless, the matrix models are limited to the calculation of balsam fir recruitment into the sapling stage. We included recruitment of seedlings through time from the forest cut until 2009 for cut areas and for forest stands separately.

To estimate recruitment, we took into account that balsam fir seeds are rarely viable for longer than a year after reaching the ground (Frank and Safford, 1970). Indeed, in cutovers we observed a sharp drop-off in seedling recruitment in the three years after forest cut. We estimated a recruitment decay function by fitting a regression line to log-transformed recruitment per site per year. The intercept provides the recruitment rate in the first year and the negative slope the log-transformed rate of decrease in recruitment. Although stands of balsam fir are known to exhibit masting years, we assumed a constant recruitment rate in forest for the sake of simplicity.

We calculated bootstrap confidence intervals by randomly resampling with replacement all seedlings in a given stage for a given combination of browsing and logging treatments, resulting in bootstrapped transition probabilities. Size of the bootstrap samples equalled the original sample size. To calculate bias-corrected 95% percentile confidence intervals we sorted 10,000 bootstrap estimates per matrix entry and designated the 250th and 9750th sample of each matrix element as lower and upper bounds of the confidence interval (Caswell, 2001) as measures of parameter estimation precision. However, they cannot be interpreted as the bounds of a matrix projection as the condition that transition probabilities add up to 1 would not be met (Caswell, 2001). Therefore we sorted bootstrap replicates per stage column, in the order of their direct *and* indirect contribution to the transitions to e2 (>30 cm). To this end, we weighed bootstrap fate columns by approximating the survival probabilities to e2 of all stage column elements as follows:

$$W(b) = b_4 + \sum_{k=1}^{3} b_k \prod_{i=k+1}^{4} a_{(i,j=i-1)}$$

where $W(b)$ is the weight of the bootstrapped stage column (b) relative to other bootstrap samples for the same stage column. All elements represent different fates and so b4 denotes the probability that a stem reaches e2 *directly*, $b_k$ is the $k$th element of the bootstrapped stage column, $a_{(i,j=i-1)}$ gives the observed transition probability (those in the original matrices) to the next stage. The bootstrapped transition probability to stage $k$ is thus multiplied by the observed probability that it will reach stage e2 at time $t = 4 - k$ years, where the "4" denotes the fourth and final stage within a stage column (e2). $W(b)$ hence does not include probabilities that stems will reach e2 at a later time than $4 - k$ years. This is justified since these probabilities are negligibly small. We hence sorted bootstrap replicates according to weight and extracted from these sorted replicates 95% confidence limits. To correct for the difference between the bootstrap means and the original means, bootstrap replicates were bias-adjusted following Caswell (2001, p. 317). We used the generated confidence limit matrices for matrix projection with confidence limits for stage e2. To establish how much variation in seedling demography was attributable to deer density, a $r^2$ value was calculated from a comparison of the full set of models (8 matrices) with a model set containing only cover type (2 matrices).

## 3. Results

### 3.1. Deer density and seedling growth

In the analysis of balsam fir seedling growth the best fit was obtained for a model including the three-way interaction between deer density, cover and age: higher deer densities negatively influenced growth of balsam fir seedlings and this effect was modulated by cover type, with faster growth in cutover than in forest (Fig. 1). The random part of the best model fit included a random slope for time since tagging of seedling (random slope vs. random intercept only: $G^2 = 208.28$, df = 35, $p < 0.001$). Also the random interaction block × deer density × cover ($G^2 = 133.74$, df = 1, $p < 0.001$) and block ($G^2 = 4.31$, df = 1, $p = 0.008$) were significant. The post hoc analysis revealed that growth at 7.5 deer km$^{-2}$ was not significantly different from growth at 0 deer km$^{-2}$ both in forest and in cutover. In forest, we observed no significant difference in growth between seedlings under ambient densities and 15 deer km$^{-2}$.

### 3.2. Deer density and browsing damage

Observed browsing damage on stems depended on deer density, forest cover and varied over years ($G^2 = 36.85$, df = 21, $p = 0.018$; Fig. 2). Damage was low at 0 deer km$^{-2}$ but was not zero. This can be the result of punctual accidental introduction of deer or browsing by snowshoe hares falsely identified as deer browsing. A random slope for year in the random block × density × cover interaction was significant (random slope vs. random intercept only: $G^2 = 143.25$, df = 35, $p < 0.001$). Post-hoc analysis revealed that increments in deer density led to significant increments in the observed browsing damage. In the forest, this effect was smaller; not every increment in deer density resulted in a significantly higher proportion of browsed stems (Fig. 2).

### 3.3. Deer density and stem survival

Increasing deer density had a strong negative effect on survival of seedlings, but the effect was different for the different cover types (Density × cover, $G^2 = 13.77$, df = 3, $p = 0.003$), with initial mortality higher in cutover but an overall mortality higher in forest (Fig. 3). Also, the random variables explained a large amount of variation in the data (plot, $G^2 = 238.91$, df = 1, $p < 0.001$, site, $G^2 = 62.04$, df = 1, $p < 0.001$ and block, $G^2 = 46.41$, df = 1, $p < 0.001$), suggesting that unmeasured variables associated with this random variation may have been important. Post-hoc analysis revealed highest stem mortality at ambient deer densities. At 15 deer km$^{-2}$ stem mortality was higher than at 0 deer km$^{-2}$, but lower than at ambient density. This was observed both in forest and in cutover (Fig. 3).

### 3.4. Matrix projection under different deer densities

In the cutover treatment, we observed a sequence of stage dominances beginning with the smallest seedling stage (s1) towards codominance of sapling stages e1 and e2 after seven years at deer density 0 and 7.5 km$^{-2}$ (Fig. 4). At a deer density of 15 km$^{-2}$, a mix of stages s2, e1 and e2 were dominant. At all deer densities in cutover, we observed a rapid decrease of stage s1, indicating that recruitment of seedlings stopped after logging and that surviving seedlings started growing. At ambient deer density all stages of balsam fir became rare. In forest, on the other hand, con-
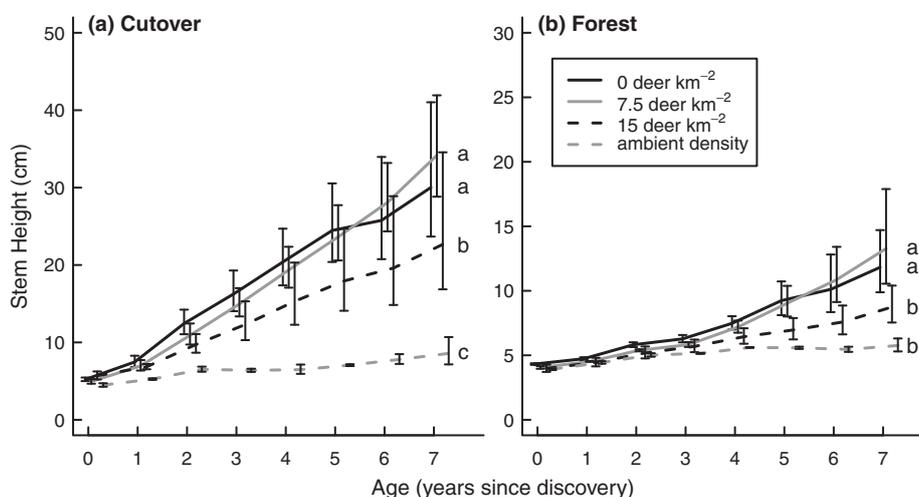


**Fig. 1.** Mean height of balsam fir seedlings in relation to their age since tagging per forest cover at each deer density (seedlings at the cotyledon stage were not tagged). Error bars denote standard errors of mean stem heights with blocks ($n = 3$) as replicate units. Different letters to the right of the curves denote significant differences between the treatment levels over the whole study period based on post hoc tests. Note different scales on the y-axes.
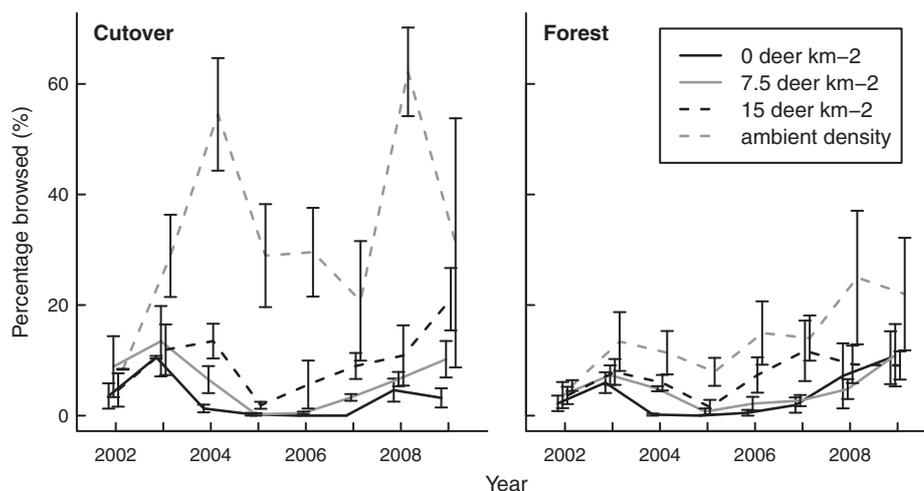
**Fig. 2.** Proportion of stems with browsing damage at each density of deer and forest cover treatment. Both death and live stems were included, but cases in which balsam fir seedlings were missing were excluded, even if they were likely eaten. Error bars denote standard errors with blocks as replicate units. Different letters to the right of the curves denote significant differences between the treatment levels over the whole study period based on post hoc tests. Letter codes ordered from lowest to highest deer densities.
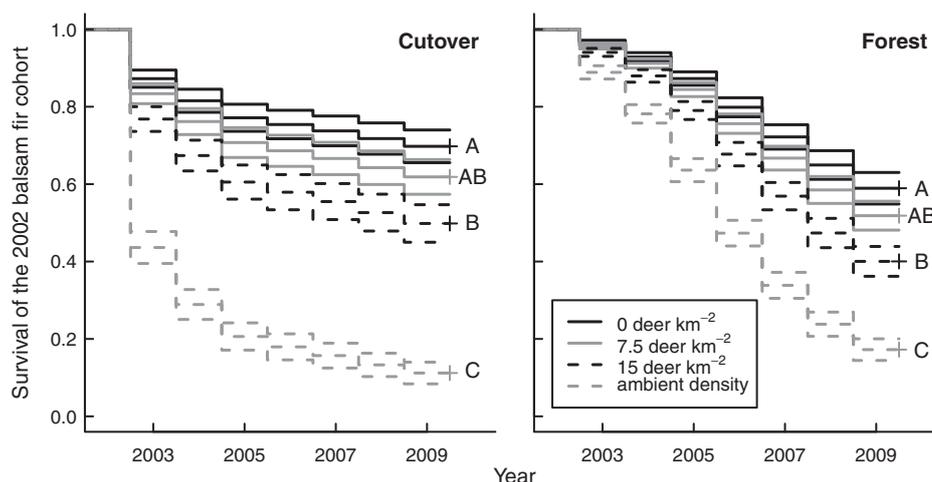


**Fig. 3.** Survival of the 2002 balsam fir seedling cohort. Curves represent Cox proportional hazard model fitted for each combination of forest cover and deer density. Random effects are not included in this model. Different letters to the right of the curves denote significant differences over the whole study period based on post hoc tests. Linear confidence intervals are plotted as the lower and upper bounds of the curve using the same format as the mean curve, which is denoted by a plus sign.

tinued seedling recruitment occurred for s1 and an increase of later stages at low deer densities, albeit at a much lower pace than in cutover, was observed. At ambient deer densities no recruitment of saplings occurred.

In the analysis of model matrices our main focus was on the transition probabilities of stems to sequential stages (e.g. s1 -> s2 or s2 -> e1) and on the quantification of differences among these transitions and mortality rates at different deer densities. The model matrices showed that the confidence interval of the transition probability to sequential stages overlapped between 0 and 7.5 deer km$^{-2}$ in cutover (Table 1, Appendix A in Supplementary Material). On the other hand, sequential stage transition probabilities of the 15 deer km$^{-2}$ had non-overlapping confidence intervals for s1 and s2. Yet, transition probabilities from stage e1 to e2 had strongly overlapping CIs among deer densities 0, 7.5 and 15 km$^{-2}$, indicating that once stems have reached the sapling stage in our experiment, they may be less vulnerable to high densities of white tailed deer. All transition probabilities to sequential stages were significantly lower at ambient density (Table 1, Appendix A in Supplementary Material). In forest, a similar pattern was observed with overlapping confidence intervals between the

sequential transitions of 0 and 7.5 deer km$^{-2}$. At 15 deer km$^{-2}$ the transition s1 → s2 was significantly less probable than at 0 deer km$^{-2}$. Although a trend towards a lower transition probability was observed, s2 → e1 was not significantly different at 15 deer km$^{-2}$ than at 0 and 7.5 km$^{-2}$. The e1 → e2 transition probability at 15 deer km$^{-2}$ was significantly lower than at 7.5 or 0 deer km$^{-2}$ (Table 1, Appendix A in Supplementary Material). Observed densities of balsam fir stems in stage e2 fell within the ranges of the projection of the matrix model confidence intervals (Appendix B in the Supplementary Material). Goodness of fit of the matrix model was calculated in comparison with a reduced model that had only cover type as an explanatory variable: $r^2 = 0.336$ (square-root transformed variables).

## 4. Discussion

Our enclosure study, exposing tagged balsam fir seedlings to four different densities of white-tailed deer for 7 years, showed an unequivocally strong inhibition of balsam fir under ambient deer densities exceeding 20 deer km$^{-2}$. Growth and survival of
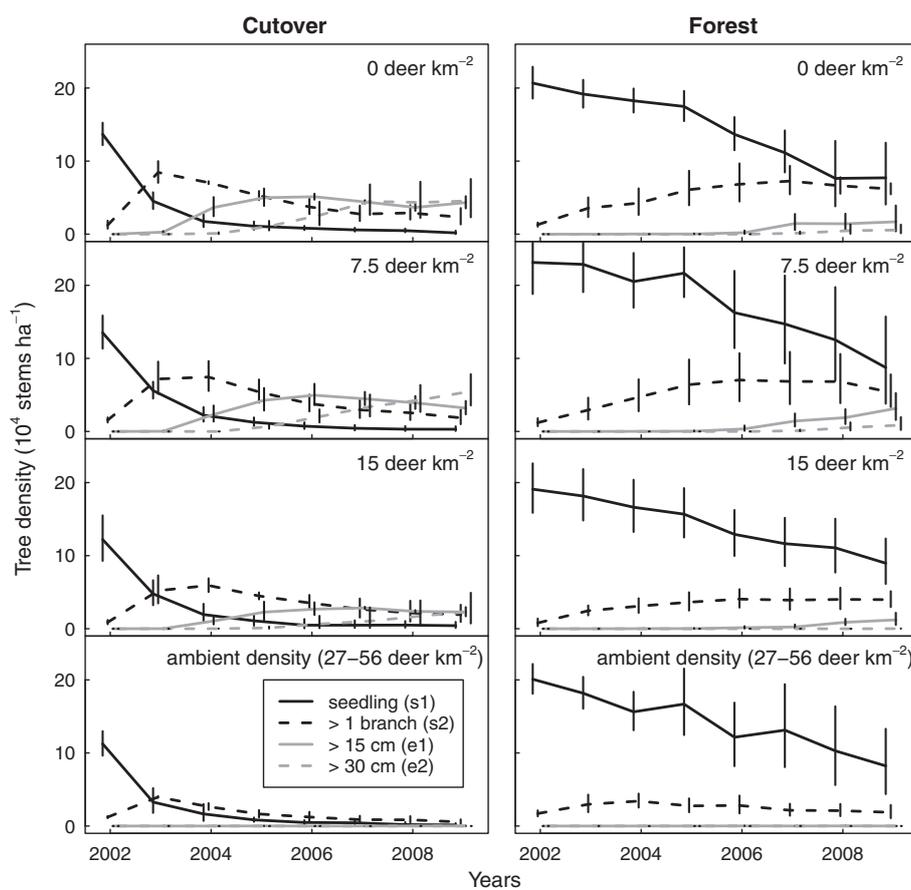
**Fig. 4.** Observed mean densities of seedling/sapling classes of balsam fir for each combination of deer density and forest cover treatment over time. Data were back-transformed from square-root transformed stem densities. Error bars indicate standard errors with blocks as the replicate units ($n = 3$). Curves are juxtaposed around the sampling points to illustrate standard errors.

**Table 1**

Transitions probabilities to consecutive stages in a matrix model of balsam fir seedlings and saplings under the different deer densities and forest cover types. The 95% percentile corrected bootstrap confidence intervals based on 10,000 bootstrap replicates are shown between brackets. Transition confidence intervals that do not overlap with those at 0 deer km$^{-2}$ for a given stage, and hence differ significantly, are indicated in bold.

| Cover | | Deer density km$^{-2}$ | | | |
|---|---|---|---|---|---|
| | | 0 | 7.5 | 15 | Ambient |
| Cutover | Transition | | | | |
| | s1 → s2 | 0.456 (0.419–0.493) | 0.427 (0.390–0.461) | **0.346 (0.312–0.381)** | **0.275 (0.241–0.313)** |
| | s2 → e1 | 0.306 (0.277–0.335) | 0.290 (0.263–0.320) | **0.209 (0.182–0.240)** | **0.008 (0.000–0.016)** |
| | e1 → e2 | 0.261 (0.227–0.294) | 0.283 (0.247–0.318) | 0.263 (0.222–0.313) | **0.000 (0.000–0.000)** |
| Forest | Transition | | | | |
| | s1 → s2 | 0.111 (0.100–0.123) | 0.103 (0.093–0.113) | **0.082 (0.073–0.092)** | **0.081 (0.071–0.091)** |
| | s2 → e1 | 0.084 (0.064–0.102) | 0.092 (0.073–0.109) | 0.067 (0.048–0.085) | **0.004 (0.000–0.008)** |
| | e1 → e2 | 0.321 (0.214–0.464) | 0.247 (0.172–0.355) | **0.023 (0.000–0.114)** | **0.000 (0.000–0.000)** |

stems at high browsing pressure were heavily reduced, with few remaining stems alive in cutover 7 years after logging (7 stems × 10$^3$ ha$^{-1}$ ± 4 × 10$^3$ SE), and no seedlings reaching the larger sapling stage (>30 cm height). Both significant growth suppression and reduced survival were also observed at 15 deer km$^{-2}$ relative to complete deer exclusion. Nonetheless, at 15 deer km$^{-2}$, recruitment of saplings (>30 cm height) was frequently observed under sufficient light (e.g. in cutover), whereas it was rare under forest canopy. In contrast, despite higher browsing damage at 7.5 deer km$^{-2}$ than without deer, no negative effects on growth, survival and transition probabilities were observed. At such relatively low deer density, balsam fir may be tolerant to browsing in terms of growth, survival and transition to sapling stages.

Matrix models enabled us to elucidate which stage transitions were least resistant to herbivory at the different deer densities.

We hence found that transition probabilities from seedling stages to consecutive stages were significantly lower at 15 deer km$^{-2}$ than at lower deer density, but that once the first sapling stage was reached (15–30 cm), this effect was no longer observed. Small saplings were as likely to reach the large sapling stage (>30 cm) at 0, 7.5 or 15 deer km$^{-2}$. Hence, also at higher deer densities, survival chances increased with time for taller stems, converging to the survival rates observed in the absence of deer. Hence, matrix models can be a useful tool to identify critical stage transitions in relation to different deer densities.

At present, we do not know whether the increased inclusive resistance of balsam fir to deer in later stages is due to ontogenetic changes (Boege and Marquis, 2005), to selection of resistant individuals (Vourc'h et al., 2002) or to changes in avoidance by association (Hjältén et al., 1993). Given the significant increase of

browsing damage with deer density without a concomitant impact on transitions to the largest sapling stage, changes in direct resistance may play an important role. However, selection based on palatability may have played a role as well. Vourc'h and co-workers (2002) found that *Thuja plicata* heavily browsed by deer may contain less chemical defences than those with little browsing damage. Balsam fir juveniles are also likely to vary in palatability. Bergerud and Manuel (1968) noted that moose (*Alces alces*) preferred dark green balsam fir branches over lighter and sclerotic ones, possibly due to green branches being richer in nitrogen (cf. Mengel et al., 2001). Selective pressure exerted by herbivores may certainly be important and may shift the genotypic composition of the population towards individuals with greater chemical defences. Additionally, the environment matters. Unpalatable neighbours may decrease the chance of seedlings being browsed (Smit et al., 2006), but the contrary may also be true, as deer may choose the best food relative to the patch in which they forage (Bergvall et al., 2005). In our study, at lower than ambient deer densities there may have been an increase in overall community palatability, diverting browsing pressure from balsam fir. Raspberry (*Rubus idaeus*), white birch (*Betula papyrifera*) and fireweed (*Chamerion angustifolium*) became common at lower deer densities (Tremblay et al. 2006). Even so, browsing damage was an increasing function of deer density throughout the study period, also at densities below ambient.

Although it may seem obvious that larger individuals become more browse resistant through ontogenetic changes and selection, browsing on saplings may strongly suppress regeneration. In the Polish Bialowezsa forest, smaller stems were less damaged as they were too low for most herbivores to browse (Kuijper et al., 2010). Rooney et al. (2000) showed in a broad geographic study in the US upper midwest that juvenile *Tsuga canadensis* were most affected by white-tailed deer browsing in the sapling stage. Also, smaller individuals, especially those without side branches, may temporarily escape herbivory as they are less conspicuous. Such was possibly the case under forest cover in our experiment. Here, mortality was lower in the smallest stage than for the second smallest stage under ambient deer density. Naturally, such inconspicuousness offers no selective advantage to balsam fir as it will most certainly face detection in later stages.

On Anticosti Island, elevated browsing damage to balsam fir seedling stages was observed at a deer density as low as 7.5 km$^{-2}$. This suggests that, even if more palatable plant species are readily available (Tremblay et al. 2006), white-tailed deer do browse balsam fir. It also hints that on the island, balsam fir may have moved from being solely used as starvation food as was suggested by Ullrey et al. (1968), to staple forage. White-tailed deer are thought to be highly physiologically plastic and to have suffered a decrease in diet quality over the last decades on Anticosti Island (Simard et al., 2008; Tremblay et al., 2005). However, despite elevated browsing damage to balsam fir at 7.5 deer km$^{-2}$, no negative effects on survival and growth were observed under this density. Hence, browsing at low deer density may be offset by benefits such as preferential feeding on competing fast growing broadleaved species (see e.g. McLaren et al., 2009). Alternatively, balsam fir may simply compensate for light browsing pressure through growth at low deer density. Thresholds in effects of deer on tree regeneration were also found, among others, for white birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L. f.) in a controlled deer density experiment in Pennsylvania (Horsley et al., 2003).

A 90-year-old balsam fir forest, which no longer exhibits self-thinning, typically has a stem density around 2 to $3 \times 10^3$ ha$^{-1}$ (McCarthy and Weetman, 2007). Even under 15 deer km$^{-2}$, densities of saplings (>30 cm) after 7 years are much higher than this in our study. Given that the mortality of saplings at 15 deer km$^{-2}$

is not significantly different than mortality at 0 deer km$^{-2}$, we expect regeneration of balsam fir to be possible at such density. However, given that deer may modulate competitive interactions between balsam fir and less palatable competitors, climax tree species composition might deviate from a climax under deer-free conditions. On Anticosti Island, this may for instance be expressed in a higher contribution of white spruce and black spruce (*Picea mariana*) to the canopy. In addition, our controlled browsing experiment was conducted in summer. Small balsam fir seedlings and saplings may be relatively protected from herbivores in winter given a usually thick snow cover on Anticosti Island (1–2 m), but taller saplings up to deer maximum browsing height are likely under threat. Future research should therefore explicitly focus on the relationship between sapling height and deer herbivory in winter. Such studies should be aimed at testing whether the demonstrated higher herbivore resistance of saplings shown here is sufficient to outgrow starved white-tailed deer in winter.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.03.023.

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