Density-related effects of deer browsing on the regeneration dynamics of boreal forests

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Summary

1. The density of large herbivores is a major driver of forest ecosystem structure and function in conjunction with episodic disturbances, especially in forests with a regeneration strategy based on shade-tolerant seedlings capable of re-establishing canopy dominance (advance regeneration). Yet, uncertainty about the relationships between forest regeneration, herbivore density and other disturbances makes it difficult to set population goals. Using an innovative controlled browsing experiment, we investigated the relationships between the regeneration dynamics of balsam fir *Abies balsamea*, the density of white-tailed deer *Odocoileus virginianus* and timber harvesting.

2. We hypothesize that advance tree regeneration either: (i) recovers approximately linearly as deer density is reduced; (ii) recovers exponentially; or (iii) does not recover because factors other than browsing control advance regeneration. We tested these alternatives through manipulation of deer densities (0, 7·5, 15 deer km^{-2} and *in situ* local densities) and forest cover (clearcut and uncut forest).

3. Balsam fir seedling mortality decreased exponentially with decreasing deer density in clearcut and approximately linearly in uncut forest. Independently of deer density, the recruitment of seedlings in clearcut dropped from $56 \pm 5\%$ to $7 \pm 1\%$ within 3 years.

4. Seedling growth increased exponentially with decreasing deer density in clearcut whereas no height growth was observed in uncut forest.

5. Overall, the abundance of fir saplings recovered exponentially in clearcut but remained low and independent of deer density in uncut forest. The abundance of spruce *Picea* spp. saplings was unrelated to deer density and increased with time.

6. *Synthesis and applications.* Forest disturbance from selective browsing at high deer densities over an extended period of time leads to recruitment failure following a canopy disturbance such as a clearcut. Indirect competitive advantage given to species resistant to browsing can shift forest composition. Nonlinear relationships between fir regeneration and deer densities imply that the level of culling required to reach herbivore densities compatible with natural regeneration of native forest is larger than expected if tree regeneration was proportional to deer density. In the boreal forest of Anticosti Island, local densities < 15 deer km^{-2} achieved within 3 years following clearcut are compatible with the maintenance of native forest.

Key-words: boreal forest, ecosystem management, forest succession grazing, plant–herbivore interactions

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Introduction

The abundance of large herbivores is a major driver of ecosystem structure and function, with potential consequences for the conservation of numerous plant and animal species as well as for the economical and

ecological sustainability of forestry operations (Côté *et al.* 2004; Latham *et al.* 2005; Danell *et al.* 2006). The impact of selective browsing includes direct killing of seedlings of preferred species, the reduction of seedling growth and thus inhibition of the regeneration process (Risenhoover & Maass 1987; Rooney & Waller 2003), or the creation of an apparent competitive advantage for plant species that are tolerant or resistant to browsing (Horsley, Stout & deCalesta 2003; Côté *et al.* 2004). Consequently, large herbivores can force forests toward alternative successional pathways and species assemblages (Hester *et al.* 2000; Hobbs 1996; Schmitz & Sinclair 1997) depending upon climate (Price *et al.* 2001), soil fertility (Palmer & Truscott 2003), abundance and spatial distribution of preferred forage species (Palmer *et al.* 2003) and the disturbance regime (Mladenoff & Stearns 1993).

Among northern hemisphere ungulates, browsing by white-tailed deer *Odocoileus virginianus* Zimmermann has been identified as the principal cause in the conversion of eastern hemlock *Tsuga canadensis* L. dominated forest toward sugar maple *Acer saccharum* Marsh. (Alverson & Waller 1997) and mixed hardwood forest, and thence to black cherry *Prunus serotina*, Ehrh. monocultures (Horsley *et al.* 2003). Regeneration failure has also been reported in other forest–deer systems (Martin & Baltzinger 2002; Rooney, Solheim & Waller 2002; Palmer & Truscott 2003).

Regeneration dynamics describe the mechanisms occurring in late successional forest communities that do not appear to experience further successional changes (Veblen 1992). In these forests, tree species adapted to the prevailing disturbance regime tend to maintain dominance in stands of all ages in a cyclic successional pattern (Frelich & Reich 1995; Thompson, Larson & Montevecchi 2003). Seedlings of these species can establish themselves, survive and grow slowly for several years under the low light conditions under mature stands. This provides advance regeneration that give them an advantage in re-establishing canopy dominance after a windstorm or outbreak of defoliating insects (Messier *et al.* 1999). Shade-tolerance and the presence of advance regeneration are common adaptations supporting the compositional equilibrium of tree species that mature slowly and for which favourable recruitment conditions occur infrequently (Greene *et al.* 1999). However, this strategy also makes forests more susceptible to composition changes following events, such as fires or selective browsing by large herbivores, that suppress seedlings and prevent the replacement of adult trees (Noy-Meir 1981). Alteration of regeneration dynamics has wide-reaching consequences for the integrity of forest ecosystems and the sustainability of timber harvesting; both being criteria for the certification of forest operations (Forest Stewardship Council 2004).

The abundance of deer relative to resource availability is a major influence on the regeneration dynamics of forest systems (Tilghman 1989; Rooney *et al.* 2000; Martin & Baltzinger 2002; Horsley *et al.* 2003). On

Anticosti Island, Canada, chronic browsing on balsam fir *Abies balsamea* (L.) P. Mill. seedlings at high white-tailed deer densities has led to recruitment failure and the conversion of balsam fir dominated forest communities toward white spruce stands *Picea glauca* (Moench) Voss (Potvin, Beaupré & Laprise 2003). Moose *Alces alces* L. have also been reported to alter the regeneration dynamics of balsam fir to the benefit of white spruce on Isle Royale, USA (McInnes *et al.* 1992) and in Newfoundland, Canada (Thompson & Curran 1993). Balsam fir is a shade-tolerant, late-successional species that thrives in the absence of fire (Frank 1990; Greene *et al.* 1999; Thompson *et al.* 2003). Seedlings germinate under the shaded understorey and survive for more than 30 years with their growth suppressed and form an advance regeneration bank (Frank 1990). Following a major disturbance that removes most or all of the mature trees (a stand-replacing disturbance), the advance regeneration resumes its growth and thus supports a cyclic succession where reproduction by seeds occurring after disturbance is only a minor contribution (Baskerville 1975). In the eastern part of its distribution range in North America, the regeneration dynamics of balsam fir are usually driven by large-scale outbreaks of spruce budworm *Choristoneura fumiferana* Clemens and hemlock looper *Lambdina fiscellaria* Guenee.

In this study, we investigate the relationships between deer density and the dynamics of advance regeneration in boreal forests managed for wildlife and timber production. We seek to identify the range of white-tailed deer density compatible with the natural regeneration dynamics of balsam fir dominated forests. We examined three alternative hypotheses relating the state of the advance regeneration to deer density. First, demographic and numeric status of the advance regeneration could change as an approximately constant proportion of deer density in the range of densities encountered in nature (Horsley *et al.* 2003). According to this hypothesis, a reduction in deer density should lead to a linear recovery in the state of the advance regeneration through progressively reduced mortality, better growth and increased recruitment in the upper height classes. Alternatively, relatively small changes in deer density could lead to rapid changes in the state of the advance regeneration if the relationship is nonlinear (Schmitz & Sinclair 1997; Suding, Gross & Houseman 2004). For example, we could expect a fast recovery of the advance regeneration as deer density is reduced from high to intermediate levels followed by a gradual phasing out of the recovery at lower densities (Schmitz & Sinclair 1997; Augustine, Frelich & Jordan 1998; Nugent, Fraser & Sweetapple 2001; Persson, Danell & Bergström 2005). Inversely, we could expect a slow recovery when deer density is reduced from high to intermediate levels followed by an exponential increase at lower densities (Nugent *et al.* 2001; Schmitz & Sinclair 1997). For both hypotheses, we expect steeper responses in open areas where advance regeneration has been released from shade suppression. Finally, there could be no recovery

following a reduction in deer density if factors other than browsing are controlling advance regeneration (Schmitz & Sinclair 1997; Augustine *et al.* 1998). We tested these hypotheses by conducting a controlled browsing experiment that involved manipulating both the white-tailed deer density and forest cover.

Materials and methods

STUDY AREA

The experiment was conducted 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 forests belong to the eastern balsam fir–paper birch *Betula papyrifera* March region (Saucier *et al.* 2003). Approximately 220 deer were introduced to the predator-free island in 1896–97. The deer population reached its first peak *c*. 30 years after its establishment and remained abundant thereafter (~20 deer km^{-2}; Potvin & Breton 2005). Presently, the island's forests are managed primarily for deer and timber production.

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 (*in situ* natural densities, 15, 7·5 and 0 deer km^{-2}). Each level was applied to two types of forest cover: (1) even-aged CLEARCUT, 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 CLEARCUT forest type simulates a stand-replacing disturbance that releases the advance regeneration by removing growth suppression from shade. The mosaic of CLEARCUT and uncut FOREST was created simultaneously in all blocks in the summer of 2001 (Y_0) by clear felling all trees > 9 cm at breast height in ~70% of the area of each of the experimental units. The browsing treatment was repeated during three consecutive years (2002, 2003 and 2004 hereafter referred to as Y_1, Y_2 and Y_3) by stocking three deer per enclosure. The enclosures were built of 3 m high wire game fencing and their surface area was 20 ha for the 15 deer km^{-2} treatment level and 40 ha for the 7·5 deer km^{-2} level. For the 0 deer km^{-2} level, we excluded deer from 10 ha enclosures. We monitored *in situ* deer densities in unfenced control units using annual pellet group surveys by distance sampling (Buckland *et al.* 2001; see Tremblay, Huot & Potvin 2006 for details on pellet

group survey protocol). We scaled up from pellet groups to deer density using a multiplier obtained from the slope of the linear regression between known deer densities and the corresponding pellet group density estimates, assuming density-independent rates of defecation and pellet groups decay (Tremblay *et al.* 2006). Estimated *in situ* deer density levels in blocks A and C were similar among blocks and years (median = 56 deer km^{-2}) while density in block B was lower but constant in all three years (median = 27 deer km^{-2}).

The effects of deer density could have been confounded by differences in enclosure size. Our experimental approach, however, allowed us to maintain at least three deer per enclosure in order to reduce the potential effects of individual variability in deer behaviour. In Y_1, the browsing treatment was applied to all experimental units, except for the 20 and 40 ha enclosures in two blocks where we did not succeed in removing all deer previously present. We did manage to reduce the densities to levels that we assumed approached the desired density levels. Accordingly, we used 15 and 7·5 deer km^{-2} in our analysis in Y_1, while acknowledging that this could limit our ability to detect the effect of the browsing treatment. The targeted density levels were reached in all blocks in Y_2 and Y_3.

We captured deer in the vicinity of the experimental blocks, relocated them in enclosures each spring and removed them by culling in the late autumn. Fawns (11–12 months old at the time of capture) and adults were distributed among the experimental units. We used multiple control procedures to maintain the target densities, including lethal and non-lethal drives, checking for tracks in the snow before stocking, and monitoring the status of VHF-equipped deer (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 (UL 2003–014).

DEMOGRAPHIC RESPONSES OF BALSAM FIR SEEDLINGS

In June of Y_1, 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 (*n* = 480 plots). We used numbered glass rods to tag up to 10 balsam fir seedlings < 10 cm tall ($\bar{X}_{CLEARCUT} = 4·7 \pm 0·1$ cm and $\bar{X}_{FOREST} = 4·4 \pm 0·1$ cm) with a single unbrowsed stem per plot (*n* = 3300 seedlings) and removed seedlings that did not meet those criteria and also woody debris. We monitored the height and status of tagged seedlings during annual visits in September from Y_1 to Y_3 as: (1) alive and unbrowsed, (2) browsed, (3) browsed-to-death, (4) dead from non-browsing causes, or (5) lost. Browsing from snowshoe hares *Lepus americanus* Erxleben can be discerned from that of white-tailed deer by the nature of the browsing scar (cut vs. chewed) but no sign of hare browsing was found. Snowshoe hare abundance was

low based on pellet counts ($\bar{X}_{Y2+Y3} \pm SE$ in CLEARCUT $= 0\cdot3 \pm 0\cdot1$ pellets m^{-2}, $n = 145$ and in FOREST $= 1\cdot3 \pm 0\cdot4$ pellets m^{-2}, $n = 146$). The only other species of forest small mammal present on the island is the deer mouse *Peromyscus maniculatus* Wagner whose diet is mainly composed of seeds, berries and invertebrates. Moose are also present on Anticosti Island but at very low density (Rochette, Gingras & Potvin 2003). At each annual visit, we tagged newly established seedlings that survived the cotyledon stage. We estimated the seedling recruitment rates from the percentage of plots with at least one recruit. In June of Y_2 and Y_3, we monitored seedling mortality in one-third of the plots in CLEARCUT ($n = 84$ plots) to estimate winter mortality due to frost, snow damage, fungi or other sources.

NUMERIC RESPONSES OF ADVANCE REGENERATION

We counted balsam fir and spruce spp. seedlings (> 1–10 cm tall), small saplings (> 10 cm–30 cm) and tall saplings (> 30–300 cm) in 20 randomly selected clusters of three subplots (4 m^2 at 5-m intervals) for each combination of deer density and forest cover ($n = 480$ clusters; single-stage cluster sampling, Cochran 1977). We carried out a first survey before applying the browsing treatment in the spring of Y_1. We repeated the survey in the spring of Y_2 and Y_3, before or soon after the stocking of deer, to measure the density of advance regeneration after Y_1 and Y_2. In Y_3, the surveys were conducted in late September so we limited the measurements to saplings because the visibility of seedlings was reduced by ground vegetation.

STATISTICAL ANALYSIS

We investigated the relationships between mortality or recruitment of balsam fir seedlings and deer density using Generalized Linear Mixed Models (GLMM) with a binomial distribution and logit link function (GLIMMIX procedure; SAS Institute Inc. 2003). Deer density and year since the beginning of the controlled browsing treatment were computed as fixed factors in an incomplete strip-block design with block as a random factor. We conducted distinct analyses for CLEARCUT and FOREST cover. The ratio of dead or browsed seedlings to the total number of tagged seedlings inside each monitoring plot at each visit was used as the response variable. The year and density–year interactions were tested with block × density × year included in the error term to avoid pseudoreplication. The incomplete nature of the design is due to the difference between *in situ* densities among blocks. The structure of correlation between repeated observations was assumed to be exchangeable (Quinn & Keough 2002). We ran models on the response variables in order to examine: (1) the overall mortality rate, (2) the mortality rate unrelated to browsing, i.e. excluding lost seedlings and those that were browsed during the pre-

ceding visit and died afterwards, and (3) the mortality rate related to deer browsing, i.e. including seedlings that were browsed and found dead during the following visit. We assumed that seedlings that disappeared were uprooted by deer and grouped them together with the browsed-to-death seedlings.

We examined the effects of deer density and forest cover on height of balsam fir seedlings and abundance of advance regeneration with mixed model ANOVA or ANCOVA (SAS Institute Inc. 2003) for an incomplete split-strip-block design with block as a random factor. Since the advance regeneration surveys were repeated on the same plots each year, we included this factor in a repeated measures design and considered the potential for temporal correlation in all models (SAS Institute Inc. 2003). The height of seedlings when first tagged (June of Y_1) and the density of seedlings/saplings in the same height class and in the same regeneration plot prior to the application of the browsing treatment were used as covariates in analysis of growth and advance regeneration abundance. Competing models with or without a covariate were compared using Akaike's information criterion.

We investigated the structure of the relationships between the response variables and the deer density factor using polynomial contrasts for linear ($_{lin}$) and quadratic ($_{quad}$) trends in the observations. We verified the normality of residuals and homogeneity of the variance assumptions for the parametric statistics and applied transformations when needed (SAS Institute Inc. 2003). For presentation purposes, we back-transformed the predicted means and corrected for potential biases associated with the skewed distribution of raw data (Duan 1983). Back to the original scale, first and second degree polynomials on the logit scale correspond to a logistic and Gaussian function, respectively. However, when the inflexion point of the logistic function is outside the range of experimental deer density level, the relationships can be approximated by an exponential function or by a linear function for relatively small values of the slope parameter on the logit scale. Linear and quadratic polynomial trends on the logarithmic scale correspond to exponential decay or sigmoid functions on the original scale. For ANCOVA, we visually checked the linearity assumption and tested for the homogeneity of slopes between the covariate and dependent variable by building preliminary models that included only deer density or the forest cover category and the interaction terms with the covariate (Quinn & Keough 2002). The significance threshold was set to $\alpha = 0\cdot05$ for all analyses.

Results

DEMOGRAPHIC RESPONSES OF BALSAM FIR SEEDLINGS

We monitored 5080 balsam fir seedlings in the course of the study (2010 in CLEARCUT and 3070 in FOREST) for

Table 1. Demographic responses and recruitment of balsam fir seedlings in a controlled browsing experiment with four white-tailed deer density levels (*in situ* local density, 15, 7·5 and 0 deer km^{-2}) and two forest cover categories (CLEARCUT and FOREST understorey). The browsing treatments were replicated in three blocks over 3 years (Y$_1$ to Y$_3$). We reported significant polynomial contrasts related to the most parsimonious interactions of GLMMs with a binomial distribution and logit link function

| | | F | | | |
| | | Annual mortality rate | | | |
Sources of variation	d.f.	Total	Other than browsing	Browsing	Recruitment
CLEARCUT					
Deer density	4/5	16·6**	0·8	9·7**	1·9
Year	2/14	20·3***	22·7***	12·9***	39·3***
Year$_{lin}$	1/14		7·7**	18·7***	67·2***
Year$_{quad}$	1/14		41·6***	9·0*	
Deer density × year	8/14	2·8*	0·6	1·9	0·2
Density$_{lin}$ × Y$_1$	1/14	5·2*			
Density$_{lin}$ × Y$_2$	1/14	18·0***		16·6**	
Density$_{lin}$ × Y$_3$	1/14	53·5***		40·4**	
Density$_{lin}$ × Y$_1$ vs. Y$_3$	1/14	14·4**			
Density$_{lin}$ × Y$_1$ vs. Y$_3$	1/14	7·3*			
FOREST					
Deer density	4/5	4·6	2·0	2·6	0·6
Year	2/14	25·1***	7·5**	21·4***	39·4***
Year$_{lin}$					78·7***
Deer density × year	8/14	1·1	0·5	1·4	0·9
Density$_{lin}$ × Y$_2$	1/14	24·8*			
Density$_{lin}$ × Y$_3$	1/14	14·5*		19·3*	

*$P < \alpha = 0.05$; **$P < \alpha = 0.01$; ***$P < \alpha = 0.001$.

a total of 13 822 observations over 3 years. The total annual mortality rate of balsam fir seedlings in CLEAR-CUT decreased as deer density was reduced. The decrease began in Y$_1$ (on the logit scale $\beta_0 = -2.65 \pm 0.3$, $\beta_1 = 0.016 \pm 0.007$; Table 1, Fig. 1a) but became more important in Y$_2$ ($\beta_0 = -1.7 \pm 0.3$, $\beta_1 = 0.030 \pm 0.007$), and approximately exponential in Y$_3$ ($\beta_0 = -2.9 \pm 0.3$, $\beta_1 = 0.053 \pm 0.007$). The total mortality rate was lower in FOREST but also tended to decrease approximately linearly at Y$_2$ and Y$_3$ (Y$_2$: $\beta_0 = -3.3 \pm 0.2$, $\beta_1 = 0.022 \pm 0.005$; Y$_3$: $\beta_0 = -3.1 \pm 0.2$, $\beta_1 = 0.026 \pm 0.005$; Table 1, Fig. 1a). In CLEARCUT, mortality unrelated to browsing was higher in Y$_2$ than in either Y$_1$ or Y$_3$ (Table 1, Fig. 1b) probably due to the greater light exposure and water stress experienced by small seedlings in the summer following clear felling as the cover of mosses dries out. The annual variation in mortality from sources other than browsing in FOREST was < 3% in all years and thus not biologically significant (Table 1, Fig. 1b). Deer browsing was the main source of mortality for balsam fir seedlings in CLEARCUT (Fig. 1c) reaching 41 ± 12% at high deer densities and decreasing exponentially to under 7% at densities ≤ 15 deer km^{-2} (parameters for the year-specific relationships in Y$_2$ and y$_3$ were not different on the logit scale; $\beta_0 = -3.3 \pm 0.3$, $F_{1,28} = 2.72$, $P = 0.11$; $\beta_1 = 0.052 \pm 0.008$, $F_{1,663} = 3.23$, $P = 0.07$; Table 1). Under FOREST cover, mortality from browsing was low and decreased slightly with decreasing deer density at Y$_3$ ($\beta_0 = -3.8 \pm 0.3$, $\beta_1 = 0.031 \pm 0.006$; Table 1, Fig. 1c). The cumulative total mortality rate in CLEARCUT and FOREST reached a maximum of

74 ± 8% and 26 ± 5% at 56 deer km^{-2}, of which 64 ± 11% and 14 ± 4% was due to browsing. We may have over-estimated mortality of seedlings due to browsing by assuming that disappeared individuals were uprooted by deer. However, mortality so attributed to browsing in exclosures (0 deer km^{-2}) suggests that it is a minor concern (CLEARCUT = 2·0 ± 0·7%, FOREST = 0·9 ± 0·3%, Fig. 1c).

We considered that most seedlings/saplings mortalities occurred during the snow-free period. From the 598 and 525 seedlings alive and unbrowsed in September of Y$_1$ and Y$_2$ in a subsample of 84 plots in CLEARCUT, only 51 and 7 were dead in June of Y$_2$ and Y$_3$, respectively. The winter mortality rate was unrelated to the experimental units in June of Y$_2$ ($F_{4,5} = 0.87$, $P = 0.54$) while the number of mortality events recorded in June of Y$_3$ was too low to allow for a valid statistical inference.

The recruitment of new seedlings decreased with time from 56 ± 5% at Y$_1$, 20 ± 4% at Y$_2$ and 7 ± 2% at Y$_3$ in CLEARCUT and from 68 ± 5% at Y$_1$, 48 ± 6% at Y$_2$ and 20 ± 4% at Y$_3$ in FOREST but was unrelated to deer density in both forest cover types (Table 1).

BALSAM FIR SEEDLING GROWTH

Balsam fir seedlings in CLEARCUT resumed their net growth at deer density < 27 deer km^{-2} leading to a linear trend in seedling height with reduced deer density at Y$_2$ ($\beta_0 = 1.95 \pm 0.05$, $\beta_1 = -0.005 \pm 0.002$; $P < 0.1$, Table 2, Fig. 2a) that turned into an exponential recovery at Y$_3$ ($\beta_0 = 2.57 \pm 0.06$, $\beta_1 = -0.030 \pm 0.007$, $\beta_2 = 0.0003 \pm 0.0001$;

CLEARCUT   ····o···· Y_1 — o — Y_2 — ● — Y_3 —·—·— $Y_2 + Y_3$
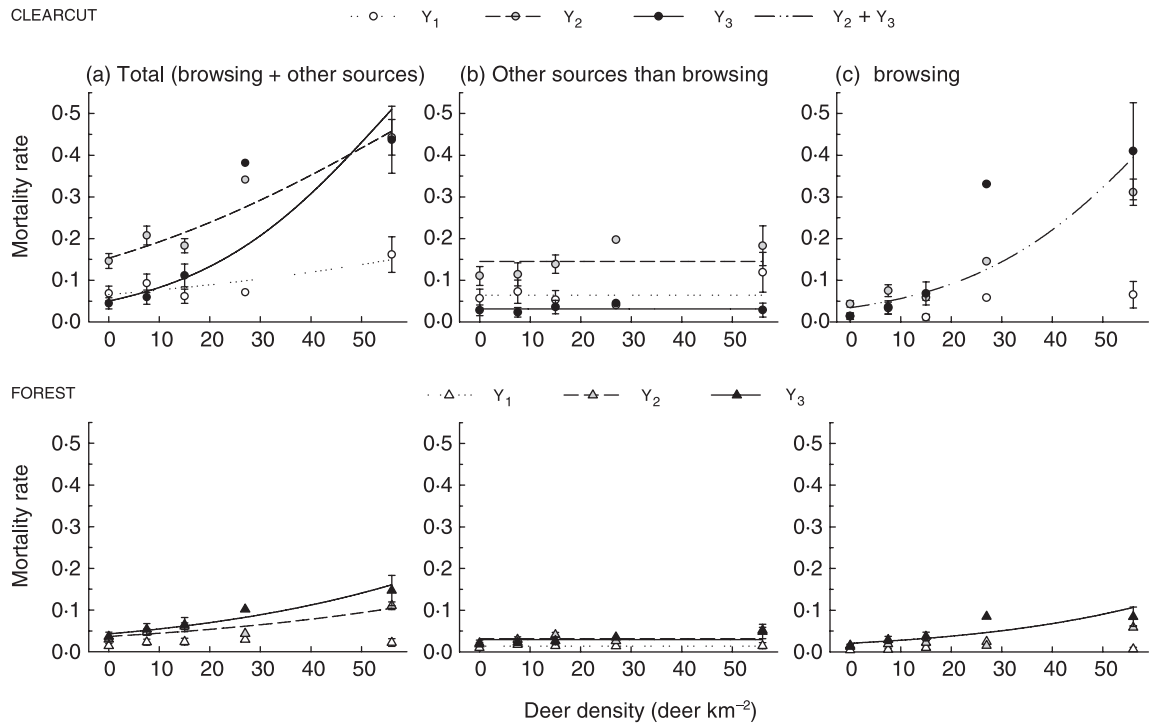

Fig. 1. Relationships between white-tailed deer density and the annual mortality rate of balsam fir seedlings in CLEARCUT and FOREST understorey for 3 years following timber harvest. Relationships shown in (a) include all mortality sources (browsing, mechanical damage and desiccation) and lost seedlings; (b) only mortality events not related to browsing are shown, excluding seedlings that were lost or browsed during the preceding visit and died afterwards; (c) the mortality rate directly influenced by deer browsing, including seedlings that were browsed and found dead at the following visit as well as lost seedlings that were assumed to be uprooted by deer. Data are LSmeans ± 1 SE for each deer density level replicated over three blocks (except for *in situ* treatment levels of 27 deer km^{-2} which is unreplicated and 56 deer km^{-2} which has two replicates).

Table 2. Height growth and density of balsam fir advance regeneration in a controlled browsing experiment with four white-tailed deer density levels (*in situ* local density, 15, 7·5 and 0 deer km^{-2}) and two forest cover categories (CLEARCUT and FOREST understorey). The browsing treatments were replicated in three blocks over three years (Y_1 to Y_3; monitored over Y_1 and Y_2 only for seedlings). We reported significant polynomial contrasts related to the most parsimonious interactions of a repeated measures, mixed model ANOVA/ANCOVA[a]

	Growth stage							
	ln[b] height growth		ln seedlings		ln small saplings		large saplings$^{0·5}$	
Sources of variation	d.f.	F	d.f.	F	d.f.	F	d.f.	F
Deer density	4/5	2·8	4/5	0·5	4/5	3·0	4/5	1·9
Cover	1/7	89·3***	1/6	11·8*	1/7	4·0	1/6	2·2
Deer density × cover	4/7	3·0	4/6	0·2	4/7	1·6	4/6	0·8
Density$_{lin}$ × CLEARCUT					1/7	13·0**		
year	2/28	214·6***	1/14	42·4***	2/28	23·5***	2/28	4·4*
Deer density × year	8/28	5·7**	4/14	5·6**	8/28	2·5*	8/28	1·9
Density$_{lin}$ × Y_2			1/14	3·4	1/28	6·2*		
Density$_{lin}$ × Y_3					1/28	9·5**	1/28	7·3**
Cover × year	2/28	41·2***	1/14	23·5**	2/28	3·0	2/28	3·5*
CLEARCUT × year$_{lin}$							1/28	11·9**
Deer density × cover × year	8/28	2·8*	4/14	2·1	8/28	0·5	8/28	0·5
Density$_{lin}$ × CLEARCUT × Y_2	1/28	10·2*			1/28	11·3**		
Density$_{lin}$ × CLEARCUT × Y_3	1/28	42·9***			1/28	15·7**		
Density$_{quad}$ × CLEARCUT × Y_3	1/28	10·9*						

*$P < \alpha = 0.05$; **$P < \alpha = 0.01$; ***$P < \alpha = 0.001$.

[a]The density of seedlings in Y_1 improved the fit of the model for seedlings (AIC$_{+cov}$ = 41·5 vs. AIC$_{-cov}$ = 44·4) and large saplings (AIC$_{+cov}$ = 312 vs. AIC$_{-cov}$ = 316), but not for small saplings (AIC$_{+cov}$ = 108 vs. AIC$_{-cov}$ = 107) and height growth (AIC$_{+cov}$ = −55 vs. AIC$_{-cov}$ = −54).
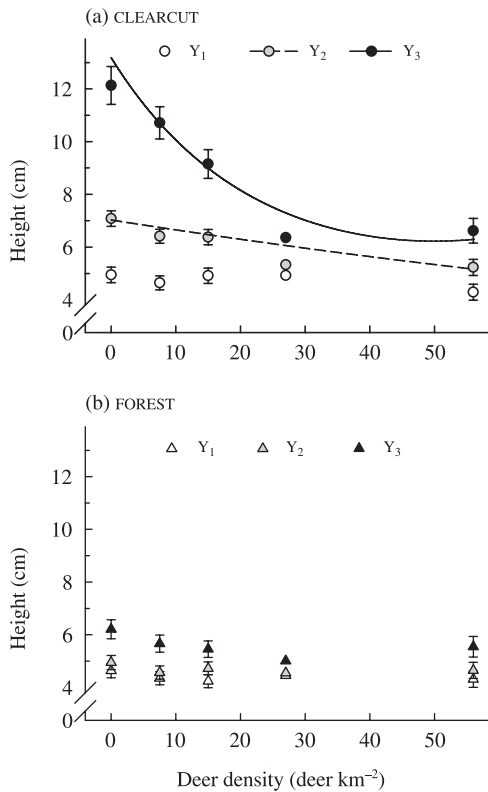
[b]Logarithmic transformation.

Fig. 2. Relationships between white-tailed deer density and height growth of balsam fir seedlings in (a) CLEARCUT and (b) FOREST understorey for 3 years following timber harvest. Data are LS means ± 1 SE for each deer density level replicated over three blocks (except for *in situ* treatment levels of 27 deer km^{-2} which is unreplicated and 56 deer km^{-2} which has two replicates).

The abundance of balsam fir seedlings tended to increase as deer densities were reduced, independently of the forest cover category at Y_2 ($P = 0\cdot09$, $\beta_0 = 3\cdot9 \pm 1\cdot4$, $\beta_1 = -0\cdot010 \pm 0\cdot007$, $\beta_{cov} = 0\cdot7 \pm 0\cdot1$; Table 2; Fig. 3a). There were no data available for balsam fir seedlings in Y_3. The abundance of seedlings decreased in CLEARCUT from 19 000 ± 3000 seedlings ha^{-1} in Y_1 to 11 000 ± 2000 seedlings ha^{-1} in Y_2 ($F_{1,14} = 64\cdot51$, $P < 0\cdot0001$; Table 2; Fig. 3a). Small saplings were maintained at very low density levels at deer densities > 15 deer km^{-2} in CLEARCUT but recovered exponentially at lower deer densities in Y_2 and Y_3 (Y_2: $\beta_0 = 11\cdot0 \pm 0\cdot4$, $\beta_1 = -0\cdot04 \pm 0\cdot01$; Y_3: $\beta_0 = 11\cdot6 \pm 0\cdot4$, $\beta_1 = -0\cdot05 \pm 0\cdot01$; Table 2, Fig. 3b). The abundance of small saplings under FOREST canopy remained low and independent of deer density (Table 2, Fig. 3b). The abundance of large balsam fir saplings was very low in all of the experimental units thus reducing the statistical power; however, they tended to increase in Y_3 at lower deer densities (density × year: $P = 0\cdot10$; $\beta_0 = 16 \pm 2$, $\beta_1 = -0\cdot22 \pm 0\cdot08$; Table 2, Fig. 3c). Large saplings increased with time in CLEARCUT from 90 ± 30 and 110 ± 30 saplings ha^{-1} in Y_1 and Y_2, respectively, to 340 ± 80 saplings ha^{-1} in Y_3 (Table 2) but this is largely due to the recovery at low deer densities in Y_3.

The abundance of spruce seedlings and saplings was not related to deer density in any height class (Table 3). Seedlings decreased from 4000 ± 700 seedlings ha^{-1} in CLEARCUT in Y_1 to 2270 ± 500 seedlings ha^{-1} in Y_2 but remained the same in FOREST with 5700 ± 1000 seedling ha^{-1} (Table 3). Independently of the forest cover, small spruce saplings increased from 3200 ± 300 saplings ha^{-1} in Y_1 to 4000 ± 300 in Y_2, and levelled off in Y_3 with 3900 ± 300 saplings ha^{-1} (Table 3). Large sapling abundance also increased log-linearly with time from 4900 ±

Table 1, Fig. 2a). The growth of balsam fir seedlings in the shade of FOREST overstorey remained suppressed at all deer density levels and did not change significantly during the study period (Table 1, Fig. 2b).
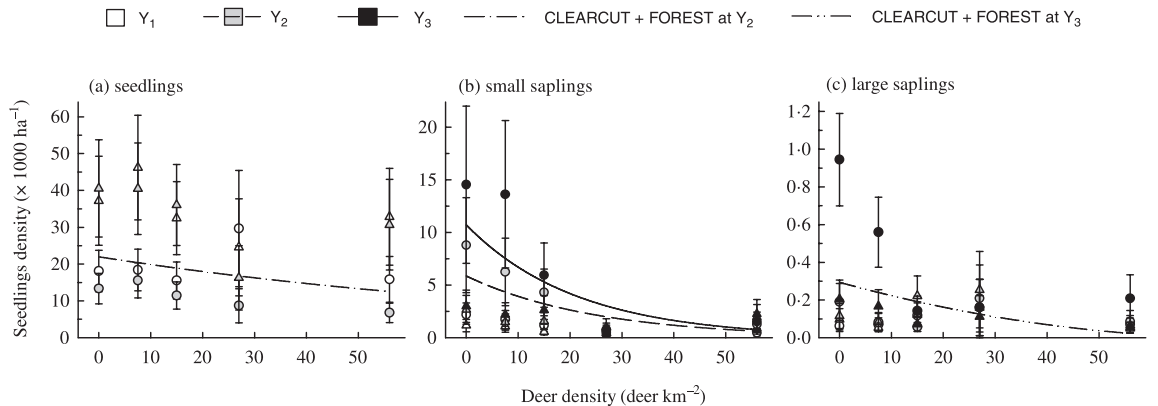

Fig. 3. Relationships between white-tailed deer density and the abundance of balsam fir as: (a) seedlings (> 1–10 cm); (b) small saplings (> 10–30 cm); and (c) large saplings (> 30–300 cm), in CLEARCUT (circles) and FOREST understorey (triangles) for 3 years following timber harvest. Data are LS means ± 1 SE for each deer density level replicated over three blocks (except for *in situ* treatment levels of 27 deer km^{-2} which is unreplicated and 56 deer km^{-2} which has two replicates). Significant relationships are shown as: CLEARCUT in Y_2 → dashed line, CLEARCUT in Y_3 → solid line, CLEARCUT + FOREST in Y_2 → dash-dot line, and CLEARCUT + FOREST in Y_3 → dash-double dot line. In panel b, the relationship is adjusted to the mean value of the covariate corresponding to $\bar{x} = 7 \pm 10$ seedlings$^{0\cdot5}$ ha^{-1} before the first application of the browsing treatment.

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Table 3. Numeric responses of the advance regeneration of spruce spp. in a controlled browsing experiment with four white-tailed deer density levels (*in situ* local density, 15, 7·5 and 0 deer km^{-2}) and two forest cover categories (CLEARCUT and FOREST understorey). The browsing treatments were replicated in three blocks over three years (Y$_1$ to Y$_3$; monitored over Y$_1$ and Y$_2$ only for seedlings). We reported significant polynomial contrasts related to the most parsimonious interactions of repeated measures, mixed model ANOVA/ANCOVA[a]

	Growth stage					
	ln[b] seedlings		small saplings		ln large saplings	
Sources of variation	d.f.	F	d.f.	F	d.f.	F
Deer density	4/5	0·7	4/5	0·6	4/5	2·0
Cover	1/6	19·4**	1/6	0·1	1/7	0·2
Deer density × cover	4/6	1·5	4/6	1·6	4/7	0·9
Year	1/14	8·5*	2/28	8·3**	2/28	35·1***
Year$_{lin}$			1/28	10·6**	1/28	67·4***
Year$_{quad}$			1/28	5·9*		
Deer density × year	4/14	1·1	8/28	1·3	8/28	0·5
Cover × year	1/14	13·1**	2/28	2·0	2/28	5·4*
CLEARCUT × year$_{lin}$					1/28	64·8***
FOREST × year$_{lin}$					1/28	12·7**
Deer density × cover × year	4/14	0·4	8/28	0·8	8/28	1·3

*P < α = 0·05; **P < α = 0·01; ***P < α = 0·001.
[a]The density of seedlings in Y$_1$ improved the fit of the model for seedlings (AIC$_{+cov}$ = 37 vs. AIC$_{-cov}$ = 41), but not for small saplings (AIC$_{+cov}$ = 727 vs. AIC$_{-cov}$ = 727) and saplings > 30 cm tall. (AIC$_{+cov}$ = 46 vs. AIC$_{-cov}$ = 44).
[b]Logarithmic transformation.

2500 to 6200 ± 3200 saplings ha^{-1} in FOREST and from 3900 ± 2000 to 6900 ± 3600 saplings ha^{-1} in CLEARCUT (Table 3).

Discussion

Our controlled browsing experiment provides evidence for nonlinear relationships between herbivore density and the regeneration dynamics of forest in interaction with timber harvesting. In the balsam fir forest–white-tailed deer system of Anticosti Island, selective browsing at high deer density is the main source of mortality of advance regeneration. As balsam fir seedlings resume their growth following a stand-replacing disturbance, their height and survival increase exponentially with decreasing deer densities. Although growth suppression in shaded understorey prevents seedling growth and thus reduces their apparency (Palmer & Truscott 2003), the mortality of seedlings is also related to deer density in forest. The demographic responses are mirrored by an exponential increase in the abundance of balsam fir saplings with decreasing deer density. We conclude that selective browsing at high deer densities over an extended period of time sets the conditions for recruitment failure of preferred species following a stand-replacing disturbance.

During the first 3 years of a controlled browsing experiment conducted in Pennsylvania, the densities of saplings from dominant tree species in clearcut areas did not show any significant trend (Horsley *et al.* 2003). By 10 years, there were positive and negative linear relationships between deer density and the density of *Prunus serotina* and *Acer pensylvanicum* L., respectively, and nonlinear relationships with the density of *P.*

pensylvanica L. (exponential decay) and *A. rubrum* L. (quadratic relationship). Interpretation of the data reported by Persson *et al.* (2005) on the changes in the biomass of birch (*B. pendula* Roth and *B. pubescens* Ehrh.) under simulated moose browsing also suggests an exponential relationship.

In the context of forest characterized by cyclic successional pathways supported by advance regeneration, nonlinear relationships may have long-term consequences on the successional pattern and composition of the forest as well as on management strategies aiming at maintaining native forests. Under low to intermediate browsing pressure, cyclic succession should lead to a long-term compositional equilibrium in balsam fir dominated stands (Baskerville 1975; Thompson *et al.* 2003). Although heavy browsing pressure over an extended period of time precludes the expression of the demographic momentum characteristic of size-structured populations (Rooney *et al.* 2002), abundant small and unapparent seedlings in the understorey of mature balsam fir (see Fig. 3) support the resilience of these stands. This suggests that they have not yet reached an alternate state (Schmitz & Sinclair 1997; Augustine *et al.* 1998; Scheffer *et al.* 2001). However, our experiment shows that high deer densities maintained for only a few years after a stand-replacing disturbance (f. ex. clearcut, insect outbreak or windthrows) could shift the successional pathways of balsam fir stands (see also Tremblay *et al.* 2006). Based on Greene *et al.* (1999), we estimated that a postharvest density of 10 000 balsam fir seedlings ha^{-1} is required to achieve a fully stocked mature stand with 2500 stems ha^{-1}. By combining seedling and sapling density estimates (Fig. 3), we determined that this target would be reached for local densities between 15 and

27 deer km^{-2}. However, very few seedlings are recruited into taller height classes at local densities > 15 deer km^{-2} (Figs 2 and 3b,c). We also observed a reduction in recruitment of new seedlings with time that is partly explained by good seed crop during the previous year but also, in the case of CLEARCUT, by the low effective seed dispersal distance of balsam fir (25–60 m; Frank 1990). The exponential increase in seedling mortality at local deer density ~ > 15 deer km^{-2}, the parallel exponential decline in seedling abundance, the lack of seedling recruitment and the failure of already established seedlings to get recruited into the sapling stage will probably result in regeneration failure following a stand-replacing disturbance.

On the other hand, we observed an increase in the advance regeneration of browse-resistant black and white spruces with time as established seedlings and saplings were recruited into taller height classes. Thus, both spruce species indirectly gain an apparent competitive advantage from deer browsing (Rooney & Waller 2003). A shift from native balsam fir forest toward spruce (mainly white spruce) at high deer densities is observed on Anticosti Island (Potvin *et al.* 2003) as well as on Isle Royale (McInnes *et al.* 1992), Newfoundland (Thompson & Curran 1993). In the absence of advance spruce regeneration, other browse-resistant or tolerant species such as grasses could eventually dominate (Tremblay *et al.* 2006) leading to a park forest ecosystem (Healy 1997). In a companion paper, Tremblay *et al.* (2006) reported rapid changes in the field layer plant communities induced by variation in browsing intensity, for example invasion by grasses at high deer densities, that could exacerbate modification in successional pathways through processes such as modulation of germination and early establishment success of tree seedlings.

The nature of the relationships between forest regeneration, herbivore density and timber harvesting that were revealed by our controlled browsing experiment has strong implication for the establishment of herbivore population management goals. This information is essential for the development of ecosystem-based strategy (Hester *et al.* 2000; Côté *et al.* 2004; Wisdom *et al.* 2006) and for the certification of forestry operations (Forest Stewardship Council 2004). Nonlinear relationships imply that the level of culling required to reach population levels compatible with natural forest regeneration is larger than if we assume linear relationships. The range of deer densities compatible with the natural regeneration of balsam fir dominated forest that we measured is slightly higher than the prescribed target for the regeneration of hardwood forest in Pennsylvania (7–9 deer km^{-2}; Horsley *et al.* 2003). Deer densities were maintained throughout the year in the Pennsylvanian experiment so that during winter, even at lower density levels, taller forbs and shrubs may have suffered a higher browsing pressure. At the southward edge of its distribution range, balsam fir is gradually replaced by red spruce *Picea rubens* Sarg. at relative deer densities

of 14–39 deer km^{-2} (Michael 1992); a result similar to ours. The target density range that we propose should be scaled down to account for negative bias in population estimates of wild ranging deer (Tilghman 1989; Potvin & Breton 2005; Tremblay *et al.* 2006). The insular context of our experiment is most probably representative of many deer–forest systems where forest fragmentation supports high deer densities and intensifies declines in preferred plants.

A challenge that needs to be addressed is the assessment of the risk of compositional shifts due to deer browsing and timber harvesting and the appraisal of their reversibility (Augustine *et al.* 1998; Hobbs 1996; Scheffer *et al.* 2001). The density level of a large herbivore population is especially critical for advance regeneration in the period following a stand-replacing disturbance. Recruitment and growth parameters will need to be assessed as the forest enters into a new phase in which competitive exclusion will be an important factor modulated by deer density. Our ability to predict forest regeneration and succession patterns in order to provide sound management prescriptions requires the pursuit of long-term experimental studies that control for multiple sources of variation (Hester *et al.* 2000; Côté *et al.* 2004; Wisdom *et al.* 2006).

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