

Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities

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Abstract The early responses of the field layer to changes in biotic and abiotic conditions are key determinants of the future composition and structure of forests where sustained heavy browsing pressure has depauperated the shrub understory. We investigated the relationships between white-tailed deer density and field layer plant community dynamics in boreal forests managed for wildlife and timber production. We hypothesized that the growth and reproduction of field layer plants are either: (H₁) directly proportional to deer density, or (H₂) related to deer density through nonlinear relationships or (H₃) through nonlinear relationships with thresholds. We tested these hypotheses using data from a controlled browsing experiment involving a gradient of deer densities

(0, 7.5, 15, 27 and 56 deer km⁻²) in interaction with timber harvesting conducted on Anticosti Island, Canada. In recent clearcuts, the dominant responses of the field layer plants were exponential recovery in growth and reproduction with decreasing deer densities. The abundance of browse-tolerant species such as grasses was positively related to deer density, suggesting an apparent competitive gain. These results support the prediction from our second hypothesis, although the presence of ecological thresholds should not be ruled out. Rapid changes in the early successional stages have potentially long-term consequences on successional patterns through processes such as the modulation of germination and early establishment success of seedlings from later successional species. Quantitative data as those presented here are essential for the development of ecosystem management prescriptions. On Anticosti Island, reduction of local deer densities to levels <15–7.5 deer km⁻² in the first 3 years following timber harvesting appears to be compatible with the regeneration dynamics of this system although lower levels of deer densities may be required for the conservation of browse-sensitive plant species.

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1 Introduction

In their native range, northern cervids are key components of forest ecosystems (Humphrey et al. 1998; Danell et al. 2006). At intermediate density levels, disturbances induced by direct and indirect cervid impacts (Rooney and Waller 2003) can result in higher

species diversity (intermediate disturbance hypothesis; Connell and Slatyer 1977) and contribute to landscape heterogeneity (Humphrey et al. 1998; Kirby 2004). Yet, following release from limiting factors the density of cervids has increased in many regions of the northern hemisphere during the last decades and has influenced the integrity of forest ecosystems (see Côté et al. 2004 for a review). That is, cervids have changed the distribution of native species, the composition of plant communities as well as the successional patterns and ecological processes deemed characteristic of some natural region (De Leo and Levin 1997; Parks Canada Agency 2000).

At high cervid densities, selective browsing induces a decline in the abundance and distribution of preferred species and promotes the dominance of resistant or browse-tolerant ones (Augustine and Frelich 1998; Horsley et al. 2003; Rooney et al. 2004). Forest structure is altered as heavy browsing pressure removes the shrub layer (Pimlott 1963; Horsley and Marquis 1983) or contributes to turn closed forest into park forest (Healy et al. 1997). Ultimately, compositional and structural changes affect ecosystem properties and dynamics (De Leo and Levin 1997; Côté et al. 2004) such as nutrient cycles (Pastor et al. 1993; Seagle 2003). Depending on the level of disturbance imposed by cervids, forests may thus lose resilience (*sensu* Walker et al. 2004). The early successional stage following a canopy disturbance is critical because community assembly and successional pathways have been shown to be contingent on the initial composition of species (Fukami et al. 2005). In a forest where heavy browsing pressure has depauperated the shrub layer, the early responses of the field layer community may have long-term consequences on compositional and functional integrity of forest ecosystems through the modulation of processes such as germination and early establishment success of trees (Zasada et al. 1992; Rooney et al. 2000; Horsley et al. 2003).

The relative abundance of cervids versus forage availability may be a driver of ecological change (Hobbs et al. 1996; deCalesta and Stout 1997; Schmitz and Sinclair 1997). The impacts of browsing are generally assumed to be directly proportional to cervid density (Westoby et al. 1989). However, nonlinear relationships may emerge from indirect effects of selective browsing, such as modifications of competitive interactions between plants (Rooney and Waller 2003), or functional relationships between cervids and their food resources (Schmitz and Sinclair 1997; Palmer and Truscott 2003). Experiments that directly manipulate cervid densities are the most direct approach to yield insights on the nature of the relationships be-

tween forest regeneration dynamics and cervid numbers (Hobbs 1996; Hester et al. 2000; Bergström and Edenius 2003; Côté et al. 2004). However, since Hobbs' (1996) recommendation for the establishment of controlled browsing experiments, little development has occurred in this field (but see Horsley et al. 2003; Persson et al. 2005). In addition, interactions between browsing and other disturbances, such as forest harvesting, also need to be controlled as they may modulate deer-forest relationships (Tilghman 1989; Horsley et al. 2003; Wisdom et al. 2006).

Our objectives were to investigate the relationships between the density of white-tailed deer and the dynamics of the field layer plant community in boreal forests managed for wildlife and timber production. We examined three alternative hypotheses in relation to the dynamics of the field layer plant community following a canopy disturbance, such as timber harvesting. We hypothesized that the growth and reproduction of field layer plants are either: (H₁) directly proportional to deer density as suggested by the classical theory of succession (see Westoby et al. 1989), or (H₂) related to deer density through smooth nonlinear relationships or (H₃) through nonlinear relationships with thresholds (May 1977; Schmitz and Sinclair 1997; Augustine et al. 1998; Weisberg et al. 2005; Fig. 1). From the former hypothesis, we predict inverse linear relationships between indicators of the field layer plant reproduction or growth and deer density (Horsley et al. 2003). The outcome of the second and third hypotheses should be exponential functions (Sweetapple and Nugent 2004) or sigmoid functions where a relatively small increase in deer densities result in a rapid changes in field layer plants growth or reproduction (Augustine et al. 1998; Hester et al. 2000; Nugent et al. 2001). We tested these hypotheses using a multifactor controlled browsing experiment, which manipulates both white-tailed deer densities and forest cover, and monitored the early responses of the field layer plant community in terms of reproduction and species-specific productivity.

2 Materials and methods

2.1 Study area

The experiment was conducted on Anticosti Island (7943 km²) in the Gulf of St. Lawrence, Quebec, Canada (49.06–49.95°N, 61.67–64.52°W). Anticosti is located 70 km north of the north-eastern natural limit of the white-tailed deer distribution range. Approximately 220 deer were introduced on the predator-free

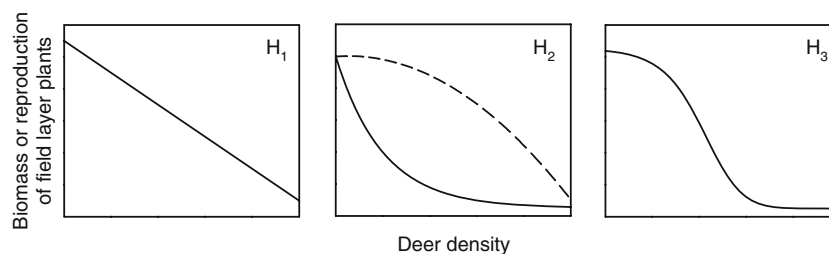


Fig. 1 Alternative hypothetical relationships between deer density and the recovery of field layer plant communities in forests. H_1 the recovery is directly proportional to deer density, leading to a linear relationship; H_2 the recovery follows a smooth

nonlinear relationship; H_3 the relationship is nonlinear with a response threshold. For H_2 lines with different patterns represent alternative forms of the predicted relationships

island in 1896–1897. No other large ungulates occurred on the island prior to the introduction. The population erupted and reached a first peak approximately 30 years after its establishment and has remained abundant thereafter (approx. 20 deer km^{-2} ; Potvin and Breton 2005). The climate is maritime and characterized by cool summers and long but relatively mild winters. Mean annual snow precipitation is 406 cm, while rainfall averages 63 cm. Mean air temperature is -13.6°C in January and 14.8°C in July, with an average of 1005 degree-days above 5°C (Environment Canada 2005). The forests of Anticosti Island belong to the boreal zone and are part of the eastern balsam fir-white birch bioclimatic region (Saucier et al. 2003). The climatic conditions of Anticosti Island favour a long return rate for fire, and thus the cyclic succession of balsam fir stands on mesic and xeric sites (Thompson et al. 2003). The forest dynamics are usually driven by spruce budworm (*Choristoneura fumiferana*) and hemlock looper (*Lamdina fiscellaria*) outbreaks and windthrows. The white-tailed deer population has been exerting dramatic impacts on native plant communities, leading to the eradication of palatable shrubs (Potvin et al. 2003; Tremblay et al. 2005) and to the conversion of balsam fir-dominated forest stands to white spruce (*Picea glauca*) stands and park forest (Potvin et al. 2003).

2.2 Experimental design

We used a controlled browsing experiment to investigate the relationships between deer density and the reproduction and growth of field layer plants in interaction with timber harvesting. The design consisted of three replicated blocks (A, B and C), each including all treatments levels. Each block was composed of four adjacent or close by experimental units receiving one level of the browsing treatment (0, 7.5, 15 deer km^{-2} and in situ density). We applied the

browsing treatment in each block by removing all deer from a 10-ha enclosure (0 deer km^{-2}), stocking three deer inside a 40-ha enclosure (7.5 deer km^{-2}) and a 20-ha enclosures (15 deer km^{-2}) and monitoring in situ deer densities in an unenclosed 40-ha area. Enclosures were built of 3-m-high wire game fencing. Each experimental unit was divided into two forest cover categories (even-aged CUTOVER and uncut $>70\%$ canopy closure of mature balsam fir FOREST). The CUTOVER treatment was applied simultaneously in all blocks in the summer of 2001 (Y_0) by harvesting all trees >9 cm at breast height in approximately 70% of the area of each experimental unit. The browsing treatment was repeated during three consecutive years (2002, 2003 and 2004; hereafter referred to as Y_1 , Y_2 and Y_3 , respectively).

The effect of deer densities could have been confounded by differences in enclosure size and, consequently, factors such as habitat heterogeneity. Our strategy, however, allowed us to maintain at least three deer per enclosure to reduce potential effects of individual variability in deer behaviour. Moreover, the large size of our experimental units most likely encompassed all major mesic habitats of the balsam fir forest, while the blocking of adjacent experimental units reduced within block habitat variability. In Y_1 , the browsing treatment was applied in most experimental units apart from the 20- and 40-ha enclosures in two blocks where we did not succeed at removing all deer previously present. We did, however, manage to lower densities, so we were able to assume partial control. Accordingly, we used the 15 and 7.5 deer km^{-2} density levels in our analysis in Y_1 , while acknowledging that this could limit our ability to detect the effect of the browsing treatment (i.e. may increase type II error rate). Targeted density levels were reached in all blocks in Y_2 and Y_3 .

We captured deer on Anticosti Island, relocated them in the experimental enclosures each spring and

euthanized them in late fall. Capture methods included Stephenson box traps, drop nets, cannon nets, net guns (Coda Enterprises, Mesa, Ariz.) from a helicopter, and remote chemical immobilization (Pneu-dart, Williamsport, Pa.). Fawns (11–12 months old at the time of capture) and adults were distributed among experimental units (Y_1 : five fawns and one adult male; Y_2 : nine fawns, two adult males and seven adult females; Y_3 : 12 fawns, five adult males and one adult female). We equipped deer with VHF radio transmitters with mortality and activity sensors (Lotek Wireless, Newmarket, Ont.). We used multiple control procedures to maintain the target density levels, including lethal and nonlethal drives, checking for tracks in the snow before stocking and monitoring the status of VHF-equipped deer during the course of the experiment. All animal handling protocols were approved by the Université Laval Animal Care Committee of the Canadian Council on Animal Care (UL 2003-014).

In experimental units which received the in situ density treatment level, we estimated deer density from annual line transect surveys of summer fecal pellet groups using a distance sampling protocol (Buckland et al. 2001). Details about the sampling protocol can be found in Tremblay (2005). We estimated deer density from pellet counts using DISTANCE 5.0 software (Thomas et al. 2002). To scale up from pellet groups to deer densities, we used a scaling-up factor (740 ± 70 pellet groups per deer over a 100-day study period) obtained from the slope of the linear regression between known deer densities and the corresponding pellet group density estimates in Y_2 (44 ± 8 and 116 ± 23 pellet groups ha^{-1} at 7.5 and 15 deer km^{-2} , respectively). This factor assumes constant rates of defecation and pellet groups decay. We confirmed the validity of the latter assumption through an experimental decay rate comparison at low and high deer densities (Appendix S1 in Supplementary material). We estimated that in situ deer density levels in blocks

A and C were similar for Y_2 and Y_3 (median = 56 deer km^{-2}), based on their 90% confidence intervals (Table 1). In situ deer density level in block B was significantly lower than that in block A and C in both years (median = 27 deer km^{-2} ; Table 1). Data from Y_1 were used as a pilot survey only, so we assumed the same block-specific in situ density levels in Y_1 .

Snowshoe hare (*Lepus americana*) abundance was low based on pellet counts in seven randomly located 4-m² plots per forest cover category ($\bar{X}_{Y_2+Y_3} \pm SE$: CUTOVER = 0.3 ± 0.1 pellets m^{-2} , $n=145$; FOREST = 1.3 ± 0.4 pellets m^{-2} , $n=146$).

2.3 Early responses of the field layer plant community

In both forest cover categories of each experimental unit, we randomly selected twenty 10×10-m² quadrates ($n=20$ quadrates × two forest cover categories × four deer density levels × three blocks = 480) and randomly selected two 1×1-m² subquadrates for the floristic survey (two-stage cluster sampling; Cochran 1977). We counted the number of individual plants bearing reproductive structures (flower shoots or fruits) in Y_2 and Y_3 as an indicator of reproductive performance for common broadleaved herbs and shrubs regularly browsed by deer (*Anaphalis margaritacea*, *Aster* spp., *Clintonia borealis*, *Conioselinum chinense*, *Epilobium angustifolium*, *Hieracium* spp., *Maianthemum canadense*, *Prenanthes* spp., *Ranunculus acris*, *Senecio* spp., *Streptopus roseus*, *Rubus idaeus*, *Rubus* spp., *Trientalis borealis*, *Vaccinium* spp.). We used aboveground biomass of focal species (*Abies balsamea* and *Betula papyrifera* <30 cm height, *E. angustifolium*, *Rubus* spp., *Cornus canadensis* and gramineae) as an indicator of the compositional responses of the field layer plant community. Focal species were chosen based on their ubiquitous presence or their expected ecological significance in our study system (see Appendix S3 in Supplementary material for a list of observed species). We predicted the aboveground dry biomass from visual estimation of horizontal cover (<1, 1–5, 10 class up to 95, 95–99 and 100%) and median height for woody shrubs, grass and tall-growing forbs using double sampling with regression estimator (Cochran 1977). The aboveground portion of focal plants was harvested in subplots each year ($\bar{n} = 97$) to develop allometric regression with cover and height. The same two observers did the cover estimations within a single year. Harvested plants were sorted and dried at 45°C until they reached a constant mass (± 0.1 g).

Table 1 Estimation of in situ white-tailed deer density levels from fecal pellet groups surveys. The coefficients of variation of the surveys varied from 10 to 19%

Block	Predicted in situ deer density level			
	Year Y_2^a		Year Y_3^a	
	Deer km^{-2}	CI 90%	Deer km^{-2}	CI 90%
A	55 (6)	41–67	57 (6)	48–69
B	26 (4)	20–34	28 (5)	21–37
C	48 (7)	37–63	61 (7)	50–73

^aThe standard error (SE) is given in parenthesis

2.4 Statistical analyses

We built species- and year-specific allometric equations to predict aboveground dry biomass from horizontal cover and height estimation (Appendix S4 in Supplementary material). We tested the reliability of estimations between observers within a year using intra-class correlations (ICC, Shrout and Fleiss 1979). ICC ranged from 0.60 to 0.99 for cover and from 0.64 to 0.99 for height, thus we pooled data and selected the most parsimonious regression model using a backwards-stepwise procedure. The fit of the models was satisfying for all focal species based on cross-validated regression coefficients (R^2 ranging from 0.40 to 0.96; Appendix S4).

We examined the effects of deer density and forest cover on the early responses of field layer plants using mixed model ANOVAs (Littell et al. 2002) in SAS (SAS Institute 2003) for an incomplete split-strip-block design with block as a random factor and year as a repeated measure. The incomplete structure of the design is due to the presence of a different in situ density level in block B (Table 1). We considered the potential for temporal correlation in all models (repeated measures design; Littell et al. 2002). We investigated the structure of the relationship between response variables (density of stems with reproductive structure and aboveground biomass of focal species), deer density and year through polynomial contrasts for linear ($_{lin}$), quadratic ($_{quad}$) and cubic ($_{cub}$) trends in the observations. For all tests, we checked the normality of residuals and homogeneity of variance assumptions and applied logarithmic or power transformations when needed. For the sake of presentation, we inverted the predicted parameters from the transformed scale back to the original scale and corrected for potential bias associated to the skewed distribution of raw data (Duan 1983). Once back to the original scale, logarithmic polynomial trends correspond to exponential decay functions or sigmoid functions of the form:

$$y = I_0 e^{(\beta_1 \times \text{density} + \beta_2 \times \text{density}^2 + \beta_3 \times \text{density}^3)},$$

where $I_0 = e^{\beta_0}$ is the value of the response variable when deer density is zero. Power transformations produce complex polynomial trends on the original scale.

Since we were interested in identifying polynomial trends, we fixed the significance threshold (α) at 0.1 and applied a sequential Bonferroni adjustment to this level for tests based on the polynomial decomposition of nonsignificant main effects (Quinn and Keough 2002). All results are presented as least-square means \pm 1 standard error.

3 Results

3.1 Reproductive response

At in situ deer densities, sexual reproduction was very rare in both widespread herbs and shrubs generally browsed on by deer in both forest cover categories, and it remained low in the FOREST understory independently of deer density (Fig. 2). In CUTOVER, there was a slight increase in sexual reproduction after Y_2 mainly due to a recovery at densities ≤ 7.5 deer km^{-2} ($\beta_0=0.6\pm 0.2$, $\beta_1=-0.014\pm 0.007$; Table 2, Fig. 2). The recovery increased sharply in Y_3 for densities < 15 deer km^{-2} , leading to an exponential increase in reproduction with decreasing deer density ($\beta_0=2.1\pm 0.2$, $\beta_1=-0.14\pm 0.02$, $\beta_2=0.0018\pm 0.0003$; Table 2, Fig. 2).

3.2 Growth responses

The biomass of *A. balsamea* seedlings < 30 cm tall was maintained at < 1 g m^{-2} at in situ deer densities even when seedlings were released from growth suppression by timber harvesting (Fig. 3). The biomass remained low and independent of deer density in FOREST understory after 3 years of controlled browsing (Table 3,

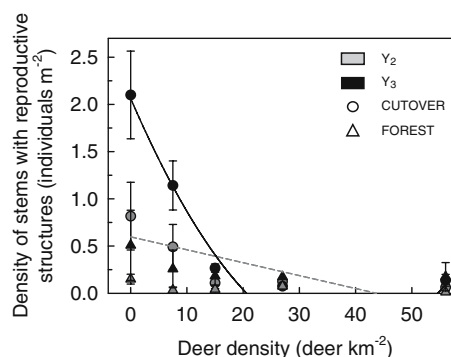


Fig. 2 Relationships between the density of white-tailed deer and sexual reproduction of plants from the field layer of balsam fir forest in CUTOVER and FOREST understory after two (Y_2) and three consecutive years (Y_3) of controlled browsing on Anticosti Island, Canada. The number of flowers shoots or fruits of an integrated group of species commonly grazed by deer (*Anaphalis margaritacea*, *Aster* spp., *Cerastium vulgare*, *Clintonia borealis*, *Conioselinum chinense*, *Epilobium angustifolium*, *Geum macrophyllum*, *Gnaphalium uliginosum*, *Hieracium* spp., *Maianthemum canadensis*, *Petasites* spp., *Prenanthes* spp., *Ranunculus acris*, *Senecio* spp., *Streptopus roseus*, *Rubus idaeus*, *Rubus* spp., *Taraxacum officinale*, *Trientalis borealis*, *Vaccinium*) was used as an indicator of sexual reproduction potential. Data points are LSmeans \pm 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: dashed line CUTOVER \times Y_2 , solid line CUTOVER \times Y_3

Table 2 Reproductive response (density of stems with reproductive structure) of focal forbs species in a controlled browsing experiment involving four white-tailed deer density levels (in situ density, 15, 7.5 and 0 deer km⁻²), two balsam fir forest cover categories (CUTOVER and FOREST understory) and 3 years (Y₁–Y₃; Y₁ not included in this analysis) replicated within three blocks. We reported significant polynomial contrasts related to the most parsimonious interactions

Sources of variation	df	F
Density	4/5	5.74**
Cover	1/7	5.50*
Density × cover	4/7	3.34*
Year	1/14	24.83****
Density × year	4/14	5.86***
Cover × year	1/14	3.67*
Density × cover × year	4/14	3.23**
Density _{in} × CUTOVER × Y ₂	1/14	5.49**
Density _{in} × CUTOVER × Y ₃	1/14	30.41*****
Density _{quad} × CUTOVER × Y ₃	1/14	15.18***

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.001$; ***** $P < 0.0001$

Fig. 3). The reduction of deer densities combined with the opening of the canopy in CUTOVER allowed a progressive recovery of fir beginning in Y₁ and Y₂ (although it did not exceed 2 g m⁻² at any deer density; Y₁: $\beta_0=2.2\pm 0.2$, $\beta_1=-0.017\pm 0.025$; Y₂: $\beta_0=2.9\pm 0.2$, $\beta_1=-0.029\pm 0.025$; Table 3, Fig. 3). In Y₃, we observed an exponential recovery in balsam fir biomass with decreasing deer density ($\beta_0=4.0\pm 0.2$, $\beta_1=-0.103\pm 0.026$; Table 3, Fig. 3). The biomass of *B. papyrifera* followed a similar pattern (Fig. 3), with values <1 g m⁻² in the FOREST independent of deer density as well as at in situ densities in the CUTOVER. There was a slight linear recovery in Y₁ and Y₂ ($\beta_0=0.72\pm 0.05$, $\beta_1=-0.0025\pm 0.0020$; Y₂: $\beta_0=0.85\pm 0.05$, $\beta_1=-0.029\pm 0.0020$; Table 3, Fig. 3) that became exponential in Y₃ as the biomass of birch increased rapidly at densities ≤ 15 deer km⁻² ($\beta_0=1.56\pm 0.07$, $\beta_1=-0.0367\pm 0.0075$; Table 3, Fig. 3).

Two years after the beginning of the experiment, pioneer species such as *E. angustifolium* and *Rubus* spp. became more abundant in CUTOVER areas at reduced deer densities (Fig. 3). *E. angustifolium* remained absent in the FOREST and was not recorded before Y₂ in CUTOVER at densities ≤ 7.5 deer km⁻² ($\beta_0=1.3\pm 0.2$, $\beta_1=-0.017\pm 0.007$; Table 3, Fig. 3). In Y₃, *E. angustifolium* was still controlled by selective browsing at densities ≥ 15 deer km⁻², while it recovered rapidly at lower densities, leading to an exponential decay function with deer density ($\beta_0=2.2\pm 0.2$, $\beta_1=-0.10\pm 0.02$; $\beta_2=0.0013\pm 0.0004$; Table 3, Fig. 3). *Rubus* spp. biomass was maintained <4 g m⁻² by heavy browsing pressure at in situ deer densities in both forest cover categories, but recovered rapidly at den-

sities <27 deer km⁻² after 3 years (Y₃) of controlled browsing in CUTOVER ($\beta_0=3.8\pm 0.2$, $\beta_1=-0.048\pm 0.008$; Table 3, Fig. 3). The biomass of *C. canadensis* was more variable than that of other species, especially in FOREST understory. In CUTOVER, we observed a recovery at densities <27 deer km⁻² in Y₃ ($\beta_0=5.1\pm 0.2$, $\beta_1=-0.025\pm 0.007$; Table 3, Fig. 3).

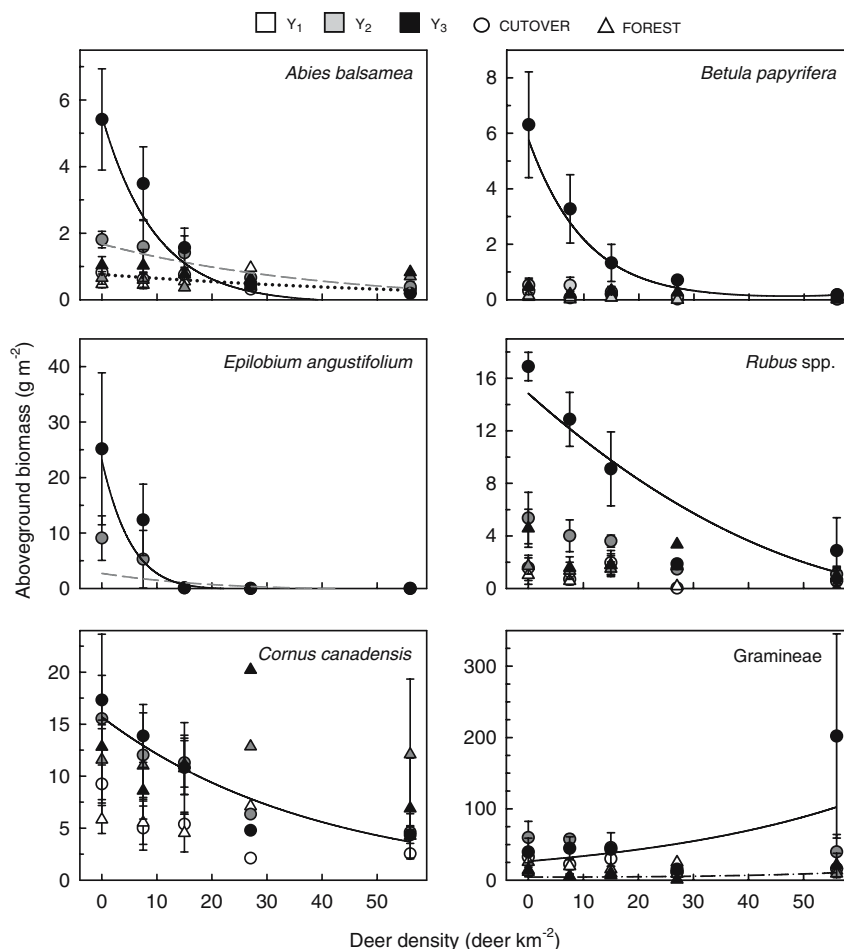
Contrasting with forbs and shrubs, we observed an increase in the biomass of the gramineae with deer density in Y₃ in CUTOVER ($\beta_0=5.6\pm 0.3$, $\beta_1=0.02\pm 0.01$) and in FOREST ($\beta_0=3.8\pm 0.3$, $\beta_2=0.0003\pm 0.0002$; Table 3, Fig. 3), mostly due to their greater biomass at 56 deer km⁻².

4 Discussion

The short-term (3 years) results from a controlled browsing experiment conducted on the balsam fir forest-white-tailed deer system of Anticosti Island highlight divergent relationships between deer densities and the field layer plant community. The dominant relationships are exponential increase in most of the field layer plant reproductive and productivity indicators with decreasing deer density, especially in CUTOVER. These relationships are characterized by fast recovery at local deer densities lower than 7.5–15 deer km⁻² and the suppression of growth or reproduction at higher density levels. The steepness of the recovery generally increased with subsequent years. On the other hand, the abundance of browse-tolerant grasses increased with increasing deer density. This supports the prediction from the hypothesis of non-linear relationships between deer density and the field layer plant community dynamics (Fig. 1, H₂).

In a similar experiment carried out in a temperate hardwood forest-white-tailed deer system of western Pennsylvania, USA (Tilghman 1989; Horsley et al. 2003), the ground cover of the dominant forb, *Rubus* spp., had not yet responded to the deer density treatment after 3 years. In fact, it took 5 years for *Rubus* spp. to recover at deer densities lower than 15 deer km⁻². Horsley et al. (2003) concluded that most trends between deer densities and plant densities, height, composition and diversity were linear after 10 years. This contrasts with the exponential decay structure that we observed for *Rubus* spp., *C. canadensis*, *E. angustifolium* as well as for *A. balsamea* and *B. papyrifera* after only 3 years of controlled browsing. This may be due to the higher productivity of hardwood forests, the smaller range of deer densities, the different interval between treatment levels and the length of the experiment. In addition, deer densities

Fig. 3 Relationships between the density of white-tailed deer and the dry aboveground biomass of focal species of woody seedlings and small saplings, forbs and grass in the field layer of balsam fir forest in CUTOVER and FOREST understory for the first 3 years (Y_1 – Y_3) of a controlled browsing experiment on Anticosti Island. Data points are LSmeans \pm 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: dotted line CUTOVER \times Y_1 , dashed line CUTOVER \times Y_2 , solid line CUTOVER \times Y_3 , dashed-dotted line FOREST \times Y_3



were maintained year long in the Pennsylvania experiment so that during winter, even at lower density levels, taller forbs and shrubs may have suffered a higher browsing pressure than in our system. This may have delayed responses compared to Anticosti Island where snow accumulation protects forbs and shrubs from deer browsing in winter. As in our experiment, there was usually no short-term response in the forest understory in Pennsylvania. One of the few other known controlled browsing experiments which involved cervids was conducted in the Sagebrush steppe-elk (*Cervus elaphus canadensis*) system (Hobbs et al. 1996). Although the attributes of this system are quite different, it is interesting to note that it revealed the presence of negative linear relationships between elk density levels (0, 9, 15 and 31 elk km^{-2}) and the standing herbaceous biomass as well as quadratic relationships with the canopy cover of the dominant shrub, *Artemisia tridentata*, and grasses. Rangeland systems have a longer evolutionary history of browsing; this may favour less pronounced and more predictable interactions between grazers and vegetation (Cingolani et al. 2005).

Nonlinear relationships between deer and the vegetation may involve the presence of thresholds effects related to deer densities (Schmitz and Sinclair 1997; Augustine et al. 1998; Hester et al. 2000). We did not observe any threshold response at low densities, but we did note a suppression of reproduction and growth after 3 years at approximately >15 deer km^{-2} for most relationships. In a simulated moose (*Alces alces*) browsing experiment in a Scandinavian boreal forest, Persson et al. (2005) found threshold responses for the browse biomass produced by large Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *B. pendula*) at low to moderate clipping intensities corresponding to 8–15 moose 10 km^{-2} . We conclude that at an early successional stage following timber harvesting, the negative impact of deer on the field layer plant communities is present, even at the low browsing pressure in our system. The short co-evolutionary history between plants and white-tailed deer (Cingolani et al. 2005), the small size of deer which allow them to maintain their foraging efficiency even at low plant biomass and their high rate of resource use in the absence of predators (Crête et al. 2001) explain our results.

Table 3 Variation in the biomass of woody species seedlings and small saplings (<30 cm), focal forbs species and gramineae in a controlled browsing experiment involving four white-tailed deer density levels (in situ density, 15, 7.5 and 0 deer km⁻²), two

balsam fir forest cover categories (CUTOVER and FOREST understory) and 3 years (Y₁–Y₃) replicated within three blocks. We reported significant polynomial contrasts related to the most parsimonious interactions

Sources of variation	Response variables ^a							
		ln <i>Abies balsamea</i>	<i>Betula papyrifera</i> ^{0.25}	<i>Epilobium angustifolium</i> ^{0.25}	<i>Rubus</i> spp. ^{0.5}	ln <i>Cornus canadensis</i>	ln gramineae	
	df	F	F	df ^b	F	F	F	F
Deer density	4/5	2.64	3.17	4/5	7.87**	2.26	1.74	0.48
Cover	1/7	5.49*	13.56***			12.69***	0.81	15.93***
Deer density × cover	4/7	4.83**	1.13			2.29	1.16	0.37
Year	2/28	21.58*****	64.07*****	1/7	9.28**	40.03*****	64.74*****	2.14
Deer density × year	8/28	3.96***	4.94****	4/7	4.71**	3.25***	1.44	4.19***
Density _{lin} × Y ₂				1/7	8.93**			
Density _{lin} × Y ₃				1/7	23.12***			
Density _{quad} × Y ₃				1/7	6.98**			
Cover × year	1/28	3.42**	20.36*****			11.03****	0.15	22.82*****
CUTOVER × year _{lin}	1/28					13.67***		
Deer density × cover × year	8/28	4.05***	2.50**			1.15	1.63	2.13*
Density _{lin} × CUTOVER × Y ₁	1/28	4.28**						
Density _{lin} × CUTOVER × Y ₂	1/28	12.15***						
Density _{lin} × CUTOVER × Y ₃	1/28	52.47*****	24.33*****			29.69*****	10.71*****	2.87*
Density _{quad} × FOREST × Y ₃	1/28							5.50**

P* < 0.1; *P* < 0.05; ****P* < 0.01; *****P* < 0.001; ******P* < 0.0001; ******P* < $\alpha_{adjusted}=0.006$

^aLogarithmic (ln) or power transformation (numerical superscript) of response variables is indicated before or after each variable name

^b*Epilobium angustifolium* was absent from the FOREST cover category and did not occur in CUTOVER before Y₂

The relationships between deer density and the field layer plant community also reveals processes through which deer induce change in the early successional stage with potentially long-term consequences on the successional pathways (Hobbs 1996). These relationships integrate basic direct and indirect impacts of deer (Rooney and Waller 2003; Côté et al. 2004) on the mechanisms that influence plant populations (e.g. survival, sexual and vegetative reproduction, photosynthetic capacity, plant-plant competitive interactions, etc.) and plant consumption (e.g. tradeoffs between growth and constitutive defences, herbivore physiology and feeding behaviour). Assuming that any future forest composition is contingent on the state of the plant community in the early successional stages (Fukami et al. 2005), the rapid and divergent changes induced by deer following a stand-replacing disturbance could force forest stands over ecological thresholds and towards alternate successional pathways (see Côté et al. 2004 for a review). This is based on the assumption that selective deer browsing acts as a chronic disturbance before timber harvesting or another stand-replacing disturbance. Although deer populations are dynamically linked to the vegetation, spatial or temporal uncoupling may allow a prolonged

period of high deer density (Mayer and Rietkerk 2004; Tremblay et al. 2005).

Seminal work by Pastor et al. (1993) revealed that selective foraging by moose on hardwoods and the avoidance of more resistant conifers alter forest community composition and structure, which in turn can affect nutrient cycles and productivity. These authors suggest that the effects of cervids on ecosystems may be amplified by positive feedbacks between plant litter and soil nutrient availability. Such a retroaction between biotic factors and the physical environment may reduce our capacity to restore the system simply by reducing deer densities (Schmitz and Sinclair 1997; Augustine et al. 1998; Scheffer et al. 2001; Suding et al. 2004). Dominance by browse-resistant or -tolerant species, such as grasses, can lead to positive feedback loops as those species gain an apparent competitive advantage under heavy browsing pressure (Augustine and McNaughton 1998; Cooke and Farrell 2001; Horsley et al. 2003; Rooney and Waller 2003). Grasses have the potential to build up a thick layer of litter which insulates the soil surface and then reduces soil temperature, delays soil warming in spring and reduces root growth, light availability, water and nutrient uptake of other species (see review by Lieffers and Macdonald 1993).

4.1 Management implications

From an ecosystem management perspective (*sensu* Yaffee 1999), knowledge of the relationships between deer density and plant community is essential for setting population goals (Hester et al. 2000). Following a stand-replacing disturbance such as timber harvesting, our results indicate that deer densities between 7.5 and 15 deer km⁻² are compatible with the maintenance of the field layer plant community considered to be characteristic of the early successional stage of balsam fir boreal forests. Exponential relationships between field layer plant community dynamics and deer density imply that the level of deer population reduction to reach this goal is more important than predicted by a linear relationships. Population goals should, however, be scaled from a local to a regional level based on the accuracy of the survey data. Even though the local deer density levels used in our experiment reflect the use of an area, they may be higher than larger scale estimates based on aerial surveys, which are usually negatively biased (Potvin and Breton 2005). Tilghman (1989) proposed a population objective for white-tailed deer in a deciduous harvested forest of 15–25 deer km⁻², which corresponds, after adjustment, to a management objective of <8 deer km⁻². Using a conceptual framework based on deer density relative to the carrying capacity of the habitat, deCalesta and Stout (1997) reached a similar conclusion for sustained timber yield and a lower objective (4 deer km⁻²) if the management objective is to maintain biodiversity. These are consistent with the results obtained on Anticosti Island.

This study provides us with quantitative measurements of deer densities compatible with the maintenance of balsam fir-white birch forest regeneration dynamics in the early successional stage following forest harvesting. We also gained insights into the changes to the field layer plant communities that could force subsequent successional stages into alternative pathways, as observed on Anticosti Island (Potvin et al. 2003). The long-term monitoring of this experiment and the initiation of other studies in different deer-forest systems are needed to confirm the likely endpoint of successional pathways and to evaluate the occurrence and strength of positive feedbacks caused by the dominance of tolerant or resistant field layer plants in the early successional stages (Côté et al. 2004; Wisdom et al. 2006). The failure to account for non-linear relationships may lead to nonoptimal management strategies or, worse, to alternative regimes that may be difficult to reverse (Scheffer et al. 2001; Suding et al. 2004).

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