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Deer browsing outweighs the effects of site preparation and mechanical release on balsam fir seedlings performance: Implications to forest management

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ABSTRACT

High abundance of large herbivore has major impacts on the composition, structure, and functioning of forest ecosystems, which can result in regeneration failures. Reduction of large herbivore density, however, does not warrant the successful establishment of tree species sensitive to browsing. In such contexts, planting in combination with silvicultural treatments can be used to restore forest cover over large areas. Using an experimental plantation on Anticosti Island (Quebec, Canada), we investigated how white-tailed deer (*Odocoileus virginianus*) browsing affects the performance of planted balsam fir (*Abies balsamea* L. Mill.) seedlings following site preparation and mechanical release. After seven growing seasons, seedling height, leader length and ground-level diameter were 30% bigger in fenced plots compared to unfenced ones as a result of cumulative browsing. Seedling survival was low (62%) and unaffected by either silvicultural treatments or deer after the onset of the mechanical release treatment. Site preparation and mechanical release did not improve morphological parameters and did not increase browsing occurrence on fir, likely because they had little influence on surrounding plants that compete for resources and may hide seedlings from deer 7 years after planting. Selective browsing on neighbouring plants also acted as a release treatment for balsam fir seedlings, allowing them to reach full sunlight at a lower height (125–146 cm), compared to fir seedlings in deer exclosures (161–184 cm). We propose that managers aim at target deer densities that promote browsing positive effects. In such context, prescription for site preparation and mechanical release should be based on other considerations than promoting seedling growth, such as facilitating practical reforestation work.

1. Introduction

Very dense populations of large herbivores have major impacts on the composition, structure, and functioning of forest ecosystems (Rooney and Waller, 2003, Côté et al., 2004), yet these impacts are not always taken into account during forest planning and practices. At high density, chronic browsing can lead to the rarefaction of vulnerable tree species through selective browsing or induced changes in biotic interactions with neighbouring plants (Beguin et al., 2011, Côté et al., 2004). Therefore, a better understanding of the relationship between browsing, silviculture and tree performance is needed to maintain forest productivity or restore declining tree species, maintaining the ecological processes that favour their regeneration.

Chronic browsing directly affects palatable species by reducing their foliage biomass, with impacts on carbohydrate production through photosynthesis and survival (Gill, 1992). Damage severity usually depends on browsing intensity and the type of tissue removed (Hester et al., 2006). Selective browsing may also have indirect effects on focal plant species by modulating the cover of neighbouring plants or abiotic conditions (Gill, 2006). For example, white-tailed deer (*Odocoileus*

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virginianus) can promote the spread of species resistant to browsing (Kalisz et al., 2014, Royo and Carson, 2006), which can, in turn, negatively impact the establishment and growth of less resistant species (Waller and Maas, 2013).

Reduction of large herbivore density does not ensure the successful establishment of tree species sensitive to browsing if natural regeneration stocking is lacking (Hobbs et al., 2011, Hidding et al., 2013, Nuttle et al., 2014). In such conditions, planting and silvicultural treatments promoting seedling survival and growth (Grossnickle, 2016) can be used to restore forest cover over large areas (Stanturf and Madsen 2002, Paquette and Messier, 2010). In the boreal forest, mechanical site preparation and vegetation control are commonly used to improve seedling microsite (Wiensczyk et al., 2011). Mechanical site preparation aims at creating favourable microsites by mixing the mineral and organic layers of the soil, improving soil properties for seedling establishment (e.g. water content, temperature, and bulk density; Löf et al. (2012)). It also reduces competing vegetation cover, usually resulting in increased tree growth and survival (Prévost, 1992). Vegetation management based on mechanical or chemical methods can also be used during the early stage of seedling establishment to control unwanted species (Wiensczyk et al., 2011). It is however necessary to evaluate how silviculture interacts with herbivores to support decision making regarding regeneration scenarios (Beguin et al., 2016). For example, vegetation removal in Scots pine (*Pinus sylvestris* Linn.) and white pine (*Pinus strobus* Linn.) plantations can increase the risk of browsing by moose and deer (*Capreolus capreolus*) on remaining trees, given the lack of alternative food (Nikula et al., 2008, Ward et al., 2008).

Our main objective was to assess the interactions between (1) browsing by white-tailed deer, (2) changes in biotic and abiotic factors resulting from silviculture, and (3) planted balsam fir (*Abies balsamea* L. Mill.) performance (growth and survival) in a context of reduced large herbivores density. Given that heavy browsing usually results in a reduction in tree survival and growth (Hidding et al., 2012, Palik et al., 2015), we expected deer exclusion to directly benefit seedling height, diameter, terminal shoot length and survival. For the same reason, deer exclusion was also expected to benefit cover and height of neighbouring plants. Consequently, we predicted that site preparation and mechanical release would decrease competition in herbivore-excluded plots, thus resulting in an overall improvement of seedling performance compared to plots without silvicultural treatments. However, reduction of palatable species by deer browsing was expected to increase browsing probability on planted seedlings (Saunders and Puettmann 1999, Nikula et al., 2008).

2. Materials and methods

2.1. Study area

We conducted this study on Anticosti Island (7943 km^2; Québec, Canada, 49°44′01″N, 63°44′22″W), located within the eastern balsam fir–paper birch (*Betula papyrifera* Marsh.) bioclimatic domain described by Saucier et al. (2009). The maritime climate of the island is characterized by an average annual precipitation of 930 mm (Environnement Canada, 2016). Mean temperature in January and July is −10.7 °C and 16.4 °C, respectively (Environnement Canada, 2016). Pre-industrial forests were dominated by mature stands composed mainly of balsam fir, white spruce (*Picea glauca* (Moench.) Voss) and paper birch (Potvin et al., 2003). The site was within the Vaureal geological formation, characterized by calcarenite with calcareous mudstone interbeds (Long and Copper, 1987). Surface deposits are sandy-loams with a 20 cm-thick organic layer.

Approximately 200 white-tailed deer were introduced on Anticosti Island in 1896–97 (Newsom, 1937). Without natural predators, the population increased rapidly and reached > 20 deer/km^2 in the last decades (Potvin and Breton, 2005, Rochette and Gingras, 2007), in spite of marked environmental stochasticity (Simard et al., 2010). As a comparison, mainland density in the same bioclimatic domain is estimated between 0.4 and 1.7 deer/km^2 (Huot and Lebel, 2012). Balsam fir became white-tailed deer key winter forage, representing 70% of his diet (Lefort et al., 2007, Sauvé and Côté, 2007). Despite the relatively short browsing history, deer on Anticosti Island have transformed plant communities, converting the balsam fir forests into white spruce dominated forests (Potvin et al., 2003, Tremblay et al., 2006, Barrette et al., 2014).

2.2. Experimental design

The study was conducted within a large management enclosure (11.3 km^2) erected after clearcutting in 2005, as part of an integrated forest management plan to promote the natural regeneration of balsam fir (Beaupré et al., 2005). Inside the enclosure, built with fences 3 m high, sport hunting and culling were used to reduce local deer densities to a target density of < 15 deer/km^2 (Tremblay et al., 2007). We planted nursery-grown balsam fir seedlings in June 2009 in a replicated design testing factorial combinations of mechanical release, mechanical site preparation, and deer presence-absence. The experimental layout consisted of a split-split-plot design with 3 randomized blocks (Fig. 1). Each ~1 ha block was composed of 2 main plots (~150 m × 40 m each) to which we randomly assigned a mechanical release treatment (with or without; Fig. 1). We performed mechanical release at the tree level with motor-manual brush saws in August 2013, over a variable radius equivalent to 1.5 times the length of the longest branch of the target seedling. Within each main plot, subplots consisted of three 50 m wide adjacent sections in which the soil was either mechanically prepared with a passive disk trencher in June 2008 (1-year delay between plantation and site preparation), in June 2009 (no delay between plantation and site preparation), or left untreated (control; Fig. 1). Following site preparation in June 2009, we excluded deer from half of the sub-subplots by creating experimental exclosures using 2.4 m-high wire fences (Fig. 1). We then planted 8 seedlings (110 cm^3 containers; average height = 24 ± 1 cm) in each exclosure (6 m × 8 m) and 16 in the unfenced part (20 m × 20 m), for a total of 432 observational units corresponding to a density of ~2500 trees/ha. Each seedling was identified with a permanent individual tag for long-term measurements and monitoring (Fig. 1). Seedlings were grown over 2 years from a continental seed source in a governmental nursery (Saint-Modeste, Quebec; 48°26′N; 65°35′W).

2.3. Data collection

2.3.1. Seedling responses

We monitored seedling survival, height (cm), ground level diameter (cm) and the occurrence of browsing on terminal shoots in October 2009 (end of the 1st growing season), 2010 (2nd growing season), 2013 (5th growing season), and 2015 (7th growing season) and calculated the height:diameter ratio (h:d ratio). We also monitored the occurrence of browsing on lateral shoots, except in 2013. In 2015, we also measured terminal shoot length (cm) and estimated the percent of browsed shoots for browsed seedlings using 10% classes.

2.3.2. Treatment effects on seedling environment

In July 2015, to characterize immediate competition, we visually estimated the percent vegetation cover and measure modal height (cm) for 6 functional groups of silvicultural interest (conifers, deciduous species, tall herbaceous species, small herbaceous species, graminoids, and raspberries (*Rubus idaeus* Linn.); adapted from Balandier et al. (2006)) using 10% cover classes. Measures were taken in sampling plots centred on the planted seedlings. Plot radius was equal to twice the tree crown's length, with a minimum plot radius of 1.13 m. We assessed light interception by measuring the percent of photosynthetic active radiation (PAR) using an AccuPAR ceptometer (Decagon Devices Inc.,

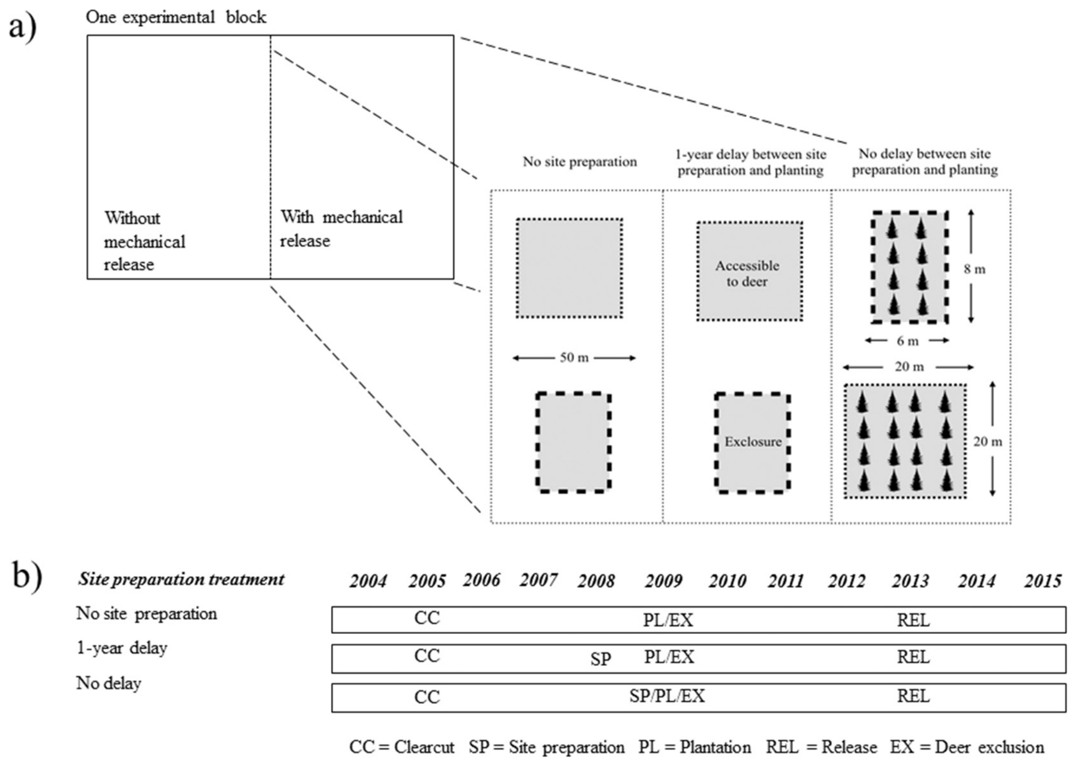

Fig. 1. Example of one experimental block, with details of one main plot that received a mechanical release treatment in July 2013 (a), with a detailed timeline of treatment application (b). Release was performed at the tree level over a radius equivalent to 1.5 times the length of the longest branch of the target seedling. Subplots were submitted to a mechanical site preparation treatment. Sub-subplots correspond to a deer exclusion treatment, for which 8 seedlings were planted in exclosures (no browsing – solid lines) and 16 seedlings in an adjacent area accessible to deer (at management enclosure density – dotted lines). A total of 432 balsam fir seedlings were planted in 2009.

Pullman, WA, USA) on cloudless days between 10:00 and 14:30 (Jobidon, 1992). We measured PAR at (1) mid-height, (2) the tip of the terminal shoot, and (3) above the vegetation (full sunlight) using two orthogonal measurements each time. We expressed average readings as percent of the full sunlight level. Within each sub-subplot, we counted the number of saplings with diameter ≥1 cm and < 9 cm at 1.3 m aboveground by height class (1.3–2 m, 2–3 m, > 3 m) to calculate stem density for conifers (black spruce (*Picea mariana* Mill. BSP), white spruce, and balsam fir) and deciduous species (paper birch, balsam poplar (*Populus balsamifera* Linn.), trembling aspen *(Populus tremuloides* Michx.), pin cherry (*Prunus pensylvanica* Linn. f.), willow (*Salix* sp.) and American mountain ash (*Sorbus americana* Marsh.)).

2.4. Statistical analyses

We analyzed the fixed effects of mechanical release, site preparation, deer exclusion and their interactions on survival (binomial variable) using generalized linear mixed models (GLMM) fitted with the GLIMMIX procedure in SAS (v. 9.4, SAS Institute, Cary, NC, USA) using a logit link function. We parametrized GLMMs separately for the 2009–2010 and 2013–2015 periods to take into account the onset of the mechanical release treatment in 2013. In both cases, we considered blocks and interactions involving blocks as random effects. We analyzed morphological measurements of seedlings (height, diameter, terminal shoot length, h:d), % cover of competing vegetation and modal height of each functional group, % PAR and sapling density using linear mixed models (LMM) with the *lmer* function of the *lme4* package v. 1.1–10 (Bates et al., 2015) in R v. 3.2.2 (R Core Team, 2015). Tree height was included as an explanatory variable when analyzing treatment effect on % PAR. We used the *glmer* function from *lme4* to analyze the effect of treatments on browsing occurrence and proportion of browsed shoots. We constrained our analyses to observations from 2015 when evaluating the effect of mechanical release on these variables. To evaluate browsing probability as a function of seedlings height, we used a logistic regression with data from 2009 to 2015 outside experimental exclosures and considered individual trees as a random effect. For LMM, we verified normality and homoscedasticity of residuals assumptions using standard graphical approaches and performed transformations prior to analyses when necessary but we present results on their original (unstranformed) scale. We used $\alpha = 0.05$ to identify significance for all analyses. Treatments for which a significant effect was detected were compared using *a posteriori* least square mean tests.

3. Results

3.1. Seedlings survival

Overall, 62% (n = 266) of the planted seedlings survived until 2015, irrespective of treatments. Before the onset of the mechanical release treatment, survival was influenced by the interaction between deer exclusion and time ($F_{1,1248} = 3.19$, $p = 0.04$), however, yearly differences in survival between fenced an unfenced seedlings were not statistically significant (Table A1). After the onset of the mechanical release treatment (post 2013), none of the treatments significantly influenced survival, although it tended to be lower when deer were excluded (56.0 ± 5.4%; mean ± standard error) compared to control conditions (65.7 ± 4.1%) ($F_{1,12} = 3.51$, $p = 0.09$; Fig. 2). We observed a trend for higher seedling survival in non-scarified plots compared to scarified plots ($F_{2,8} = 3.48$, $p = 0.08$; Fig. 2).

3.2. Seedling morphology

Seven years after planting, seedling height, leader length and ground-level diameter in fenced plots were 130 ± 7 cm, 24 ± 2 cm and 2.6 ± 0.2 cm, respectively. These values were significantly higher than those measured in unfenced plots (97 ± 3 cm, 17 ± 1 cm and

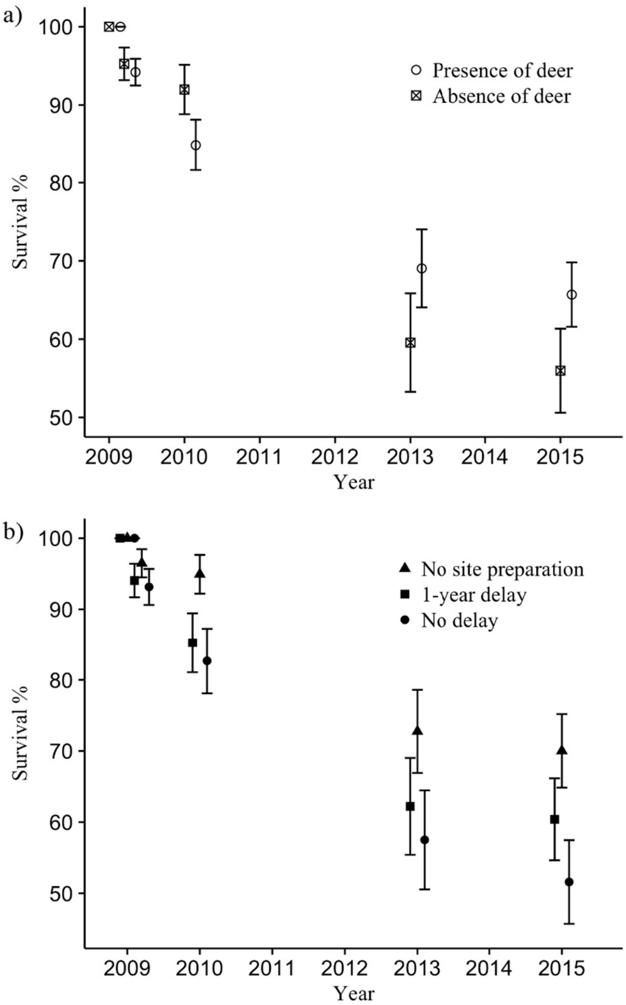

Fig. 2. Balsam fir survival (mean ± standard error) (a) in the presence or absence of white-tailed deer and (b) as a function of site preparation (no site preparation, 1-year delay between plantation and site preparation; spring 2008 or no delay between plantation and site preparation; June 2009). Survival was monitored in October 2009 (end of the 1st growing season), 2010 (2nd growing season), 2013 (5th growing season), and 2015 (7th growing season).

1.9 ± 0.1 cm, respectively; Table 1). The delay between site preparation and planting did not influence any of the response variables (Table 1). Mechanical release had no significant effect on seedling height, but balsam fir seedlings submitted to mechanical release tended to have a larger diameter (2.4 ± 0.1 cm vs. 1.6 ± 0.1 cm) and a smaller h:d ratio (50 ± 1 vs. 59 ± 1) than seedlings that had not been released (Table 1).

3.3. Browsing probability

In 2015, out of the 186 seedlings still alive, 46% experienced browsing (9 experienced lateral and terminal browsing, 75 lateral browsing only and 2 terminal shoot browsing only). Neither site preparation nor mechanical release influenced terminal or lateral browsing occurrence on fir seedlings in 2015 (Table 1). Site preparation ($F_{2,8} = 2.08$, $p = 0.19$) and mechanical release ($F_{1,2} = 6.48$, $p = 0.13$) did not impact the proportion of browsed shoots for seedlings that had experienced browsing in 2015. Cumulative browsing on terminal shoot (ranging from 0 to 4 browsing events) had a negative effect on height ($F_{1,162} = 3.8$, $p = 0.05$) and diameter ($F_{1,163} = 5.3$, $p = 0.02$). At each browsing event, seedling height and diameter were 5.4 ± 2.7 cm and 0.13 ± 0.05 cm smaller compared to seedlings that did not experience browsing. Over the 2009–2015 period, browsing probability on terminal shoots decreased ($F_{1,864} = 60.49$, $p < 0.001$) while browsing probability of lateral shoots increased ($F_{1,676} = 20.01$, $p < 0.001$) as a function of seedling height (Fig. 3).

3.4. Competitive environment

The cover and modal height of large herbaceous species decreased from 35 ± 2% and 94.7 ± 3.0 cm in fenced plots to 18 ± 1% and 62.6 ± 1.4 cm in unfenced plots ($F_{1,12} = 21.0$; $p < 0.01$ and $F_{1,12} = 43.8$, $p < 0.01$, respectively). The effects of mechanical release on the height of large herbaceous species was dependent on the delay in site preparation ($F_{2,8} = 5.33$; $p = 0.03$); 1-year delay between site preparation and planting led to a 16.1 ± 6.8 cm increase in modal height of tall herbaceous species in released plots ($t_{9.1} = -2.0$; $p = 0.08$); while it decreased from 80.0 ± 5.8 cm to 67.4 ± 3.0 cm in unprepared, released plots ($t_{8.1} = 2.2$; $p = 0.06$). Other combinations of site preparation and mechanical release were not significant ($|t| < 1.96$, $p > 0.1$).

In fenced plots, the cover of graminoids tended to increase in prepared plots (1-year delay = 56.4 ± 4.0% and no delay = 53.5 ± 5.1%), compared to unprepared plots (34.5 ± 3.3%; site preparation × deer exclusion: $F_{2,12} = 3.39$, $p = 0.07$, *a posteriori* mean comparisons respectively $t_{25.3} = 2.3$; $p = 0.03$ and $t_{25.4} = 2.0$; $p = 0.06$). We did not find any difference between site preparation levels in unfenced plots (unprepared: 61.8 ± 3.8% vs 1-year delay: 62.3 ± 2.8% ($t_{14.9} < 0.1$; $p = 0.99$), unprepared vs no delay: 51.5 ± 3.8% ($t_{15.7} = -1.6$; $p = 0.13$) and 1-year delay vs no delay ($t_{16.0} = 1.6$; $p = 0.13$)).

Deer exclusion increased the cover of deciduous species in unprepared plots (site preparation × deer exclusion: $F_{2,12} = 3.75$, $p = 0.05$; no deer: 18.6 ± 4.5%; with deer: 9.3 ± 2.2%, $t_{8.7} = -3.3$; $p = 0.01$), whereas it had no effect in prepared plots (1-year delay: $t_{11.8} = 0.7$; $p = 0.50$; no delay: $t_{13.1} = -0.9$; $p = 0.40$). We noticed a trend towards a possible interaction between mechanical release and deer exclusion ($F_{1,12} = 4.04$; $p = 0.07$), suggesting a higher cover of

Table 1
ANOVA summary for mechanical release, mechanical site preparation and deer exclusion effects on morphological parameters and terminal/lateral browsing probability of planted balsam fir seedlings on Anticosti Island (Canada) after seven growing seasons (2015 measurements). Browsing occurrence (terminal and lateral) was only measured in unfenced plots. df = numerator, denominator degrees of freedom; h:d ratio = height/diameter ratio. Statistically significant effects ($p \leq 0.05$) are indicated in bold and statistical trends ($p \leq 0.1$) are indicated in italic.

Source of variation (fixed effects)	df	Seedling height		Leader length		Ground-level diameter		h:d ratio		Terminal browsing		Lateral browsing	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Mechanical release (MR)	1,2	5.57	0.14	7.28	0.11	*12.92*	*0.07*	*9.39*	*0.10*	0.40	0.59	3.79	0.19
Site preparation (SP)	2,8	0.96	0.42	1.10	0.38	1.15	0.37	2.56	0.14	0.23	0.80	2.16	0.18
MR × SP	2,8	1.50	0.28	2.87	0.12	1.17	0.36	0.78	0.49	0.14	0.87	0.35	0.71
Exclusion (EX)	1,12	**13.77**	**0.00**	**5.73**	**0.03**	**5.85**	**0.03**	0.91	0.36	–	–	–	–
MR × EX	1,12	2.45	0.14	1.25	0.29	1.24	0.29	0.45	0.52	–	–	–	–
SP × EX	2,12	1.25	0.32	0.01	0.99	0.83	0.46	0.98	0.40	–	–	–	–
MR × EX × SP	2,12	0.43	0.66	0.21	0.81	0.48	0.63	1.23	0.33	–	–	–	–

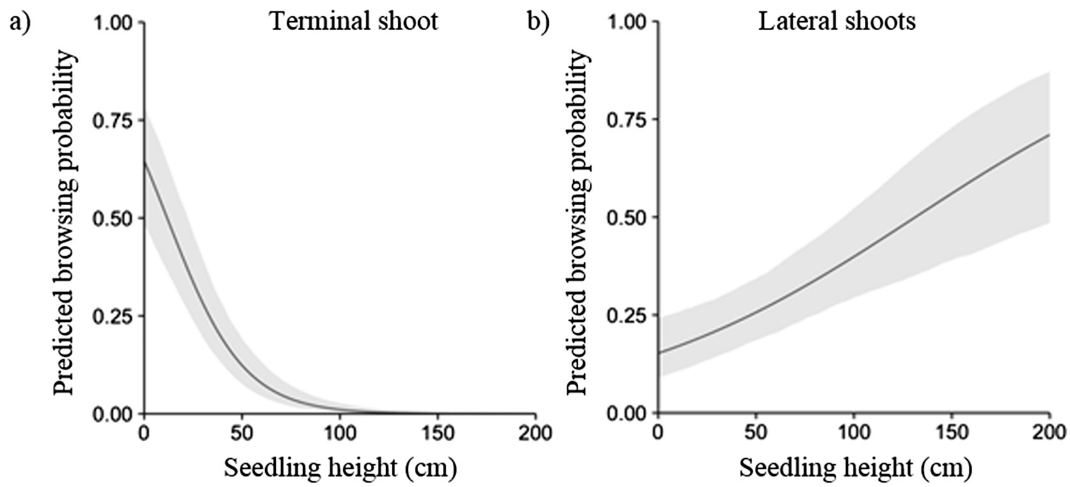

Fig. 3. Predicted probabilities of white-tailed deer browsing on terminal shoot (a) and lateral shoots (b) as a function of planted balsam fir seedling height (cm). Seedlings were planted in June 2009 on Anticosti Island (Canada). Browsing occurrence on terminal shoot was measured after the 1st, 2nd, 5th and 7th growing season (n = 965 seedlings * years). We also monitored lateral browsing, except during the 5th growing season (n = 769 seedlings * years). Gray areas present 95% confidence intervals.

deciduous in fenced than unfenced plots without mechanical release (respectively 22.6 ± 4.6% and 13.5 ± 2.2%; $t_{14} = -2.6$; $p = 0.02$) while there was no difference when mechanical release was carried out (respectively 7.0 ± 1.6% and 8.2 ± 1.3%; $t_9 = 0.1$; $p = 0.92$). Finally, the delay in site preparation influenced the cover of raspberry ($F_{2,8} = 4.81$; $p = 0.04$); a 1-year delay between site preparation and planting increased raspberry cover from 22.5 ± 2.6% (no delay) to 38.9 ± 2.4% ($t_{20.1} = 3.1$; $p = 0.01$), but we did not detect any difference between 1-year delay and unprepared plots (28.6 ± 2.3%; $t_{18.4} = 1.57$; $p = 0.13$). We did not detect any effects of treatments on cover or height of conifers and small herbaceous (Table A2).

We observed no difference in the density of conifer stems, including fir, among treatments (374 ± 57 stem/ha). The density of deciduous stem decreased from 575 ± 96 stem/ha in fenced plots to 244 ± 96 stem/ha in unfenced plots ($F_{1,2} = 13.63$, $p < 0.003$, Fig. A3).

The difference in % PAR between fenced and unfenced plots increased as a function of seedling height, until unfenced seedlings reach full sunlight around 146 cm tall compared to 184 cm for seedlings in the absence of deer ($F_{1,259} = 8.33$, $p = 0.004$; Fig. 4).

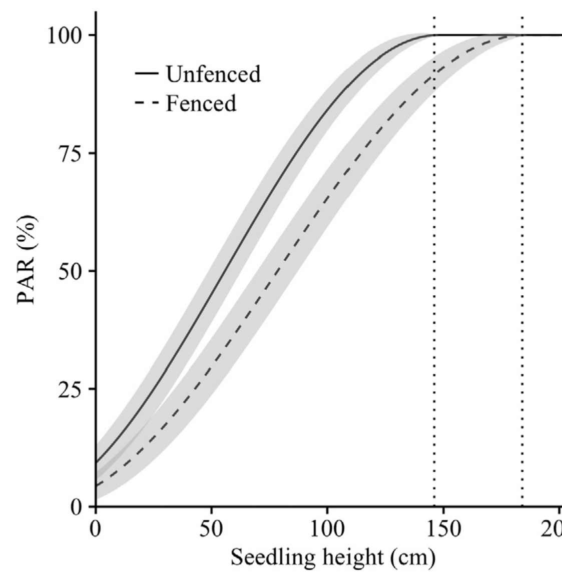

Fig. 4. Photosynthetic active radiation reaching the seedlings relative to full sunlight (% PAR), seven years after planting as a function of balsam fir seedling height. Solid line represents seedlings in the presence of deer; dashed line represents seedlings planted in the absence of deer. Vertical lines define the seedling height where full sunlight is reached. Gray areas correspond to the standard error of the mean.

4. Discussion

4.1. Effect of browsing on balsam fir seedlings

Using a controlled field experiment, we showed that white-tailed deer browsing is simultaneously inducing a negative direct effect on balsam fir seedlings and a positive effect through release from competition by surrounding vegetation. Deer browsing on surrounding species modifies vegetation structure and composition towards more open environments, improving light conditions for the planted seedlings. The magnitude of the negative effects on seedling height, however, far outweighs the potential benefits associated with vegetation control by the herbivore.

Contrary to our prediction, deer exclusion did not improve seedling survival. It suggests that, at deer densities under 15 deer/km^2 (the approximate density of our unfenced plots), browsing pressure allows growth and survival of balsam fir (Tremblay et al., 2007) and plays a role in reducing competition from palatable species. During the 2010–2013 period, we noticed a shift in survival between fenced and unfenced plots, which could indicate an increase in competition for resources by palatable species following harvesting, and their recovery following deer exclusion. Although balsam fir is very shade tolerant, competition for other resources than light may drive its survival at the late seedling stage. The trend for higher survival in the presence of deer may also indicate that browse induced mortality acts on longer time scale than what we measured in the present study (Bergerud and Manuel, 1968).

We observed that planted seedling height, diameter and terminal shoot length were smaller in the presence of white-tailed deer as a consequence of cumulative browsing effects. When browsed, most conifers need to allocate resources to damaged tissues, and then have fewer resources to invest in growth (Wallgren et al., 2014). This is expected for diameter growth specifically, as it is not a priority in conifer resource allocation (Lanner, 1985, Morris et al., 1990). White-tailed deer browsing negatively influenced height and diameter with similar effect sizes, which could explain the lack of statistical significance for treatment effect on the h:d ratio.

We found that browsing probability decreased for terminal shoot and simultaneously increased for lateral shoots as seedlings gained height. As terminal shoots become unavailable, deer appear to switch to lateral shoots that are readily available and become more abundant and visible as seedlings grow (Nikula et al., 2008, Faure-Lacroix et al., 2013). A similar shift from terminal to lateral shoots was observed for white-tailed browsing on white pine: a shift occurs at 140 cm for white pine, a limit probably set by the height of adult deer (Saunders 1988). Comparable result was also found in a red oak (*Quercus rubra* L.) plantation, where seedlings greater than 148 cm initial planting height did not experience terminal browsing (Oswalt et al., 2006).

Browsing by white-tailed deer acted as a release treatment for balsam fir seedlings by diminishing the cover of deciduous and large herbaceous species, creating favourable growing conditions. Consistent results have been found for deer and moose browsing, suggesting that large browsers can indeed provide a release effect from competition for less preferred trees (Posner and Jordan, 2002, McLaren et al., 2009, Dalgleish et al., 2015). Graminoids then tend to increase following palatable species decline, which further prevent the establishment of other species by actively competing for resources and creating low quality germination sites (Rooney, 2001, Beguin et al., 2011, Gosse et al., 2011).

4.2. Effects of silvicultural treatments on fir seedlings and their environment

Site preparation is used in plantation establishment mainly to improve seedling microclimate conditions by manipulating soil properties and reducing competition for resources; which can result in increased seedlings growth and survival (Wiensczyk et al., 2011). However, we did not find any effect of site preparation on balsam fir seedling performance or survival, either in fenced or in unfenced plots. Thiffault et al. (2003) also observed that site preparation did not affect 3rd year height nor diameter of black spruce (a shade-tolerant species) planted in the boreal mixed woods of southeastern Québec. Although not statistically significant, seedlings in the no delay treatment tended to have lower survival compared to control seedlings planted without site preparation. Lower survival can be a result of the negative effect of site preparation on soil properties, as it modifies the hydraulic regime by simultaneously increasing evapotranspiration and water retention (Örlander et al., 1990). Water stress may have negatively influenced survival for the recently planted seedlings characterized by a superficial root system (Örlander et al. 1990). The objective of site preparation on the study site was to decrease competition from surrounding vegetation however, graminoids positively responded to the soil disturbance, probably as a result of the dispersing and fragmenting of rhizomes (Beaudet et al., 2013). White-tailed deer strengthen this positive effect of site preparation on graminoids by browsing on palatable species that were competing with them (Rooney, 2008, Beguin et al., 2011). Thus, site preparation should be used with care on these sites as it can lead to multiple interactions with soil physical and chemical properties that affect plant performance and can be a poor tool for vegetation management (Löf et al., 2012). The marginal effect of ground preparation on performance of planted balsam fir seedlings also led Charron and Hermanutz (2017) recommending avoiding this silvicultural treatment for forest restoration following regeneration failure due to overabundant moose in Newfoundland (Canada).

Contrary to our predictions, mechanical release did not stimulate seedling height, terminal shoot length or survival. Although not statistically significant, the size effect of mechanical release on diameter suggests that released trees may have benefited from an increase in resources availability. This effect, however, probably only occurred during a short period of time as we did not observe major impacts of the treatment on competing vegetation cover or modal height two years following treatment application. The rapid regrowth of the surrounding plants, which could be due to their tolerance to browsing (Coughenour, 1985, Safford et al., 1990, Baleshta et al., 2015), or the establishment of other competing species in released plots can explain this low difference between treatment levels (Hart and Comeau, 1992, Wiensczyk et al., 2011). We have not found support for the use of mechanical release in those conditions, although this treatment can have positive effects on seedling performance and survival when planting other conifer species (Wagner et al., 2006, Cyr and Thiffault, 2009).

5. Management implications and recommendations

When large herbivores are present at high densities, the objectives of common silvicultural treatments may not be met due to the direct damage caused by selective browsing and their interactive impacts on vegetation composition and structure. Our findings emphasize the need to reduce the direct effect of browsing on terminal shoots of seedlings under 150 cm, as they are most vulnerable to white-tailed deer at this stage. To promote fir seedling growth and survival, managers should adopt a target deer density that reduce negative effects (see Tremblay et al., 2006, 2007 for early establishment targets) while promoting positive effects by reducing vegetation competition for light without damaging fir. If the focus species was a more preferred food item than fir, more efforts should invest in reducing deer density, as the probability of heavy browsing would be higher for a same density. Site preparation and mechanical release treatments must take into account vegetation composition, as the treatments could be ineffective or even negatively affect planted seedlings by promoting unwanted species such as graminoids, which can further inhibit natural regeneration (Balandier et al., 2006). When large herbivores are abundant, prescriptions for site preparation should therefore be based on other considerations than promoting seedling growth, such as facilitating practical reforestation work if required (see Thiffault et al., 2003). Finally, mechanical release at the tree level is not required when deer density reach a level where competition by shrubs and small trees is controlled by selective browsing. Overall, our results highlight that rationales supporting the application of site preparation and mechanical release are context-dependent and may only be valid in ecological systems where top-down controls by large herbivores is low or moderate. When browsing pressure by large herbivores is high, however, applying the same rationales with no consideration to herbivores may lead to suboptimal outcomes with low regeneration success and unnecessary costs.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.024.

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