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Stock type performance in addressing top-down and bottom-up factors for the restoration of indigenous trees

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ABSTRACT

Using planted trees to restore the attributes of natural forest is especially challenging when disturbances are still effective. Chronic browsing by large herbivores can act as such a chronic disturbance curtailing natural regeneration and potentially altering successional trajectory of forest. In the context of herbivore overabundance encountered in many regions of the world, plantation strategies must thus address both the top-down pressure exerted by consumers on planted trees and the bottom-up control related to competition for resources. In this paper, we explore whether selection of competition-adapted balsam fir (*Abies balsamea* L.) seedling stock types (small, 110 cm^3 container; medium; 200 cm^3; or large, 350 cm^3) could be used together with the management of white-tailed deer (*Odocoileus virginianus*) populations in order to lower the effect of local competition as well as minimizing browsing on seedlings. When the top-down pressure from herbivores is low or absent, we hypothesize that height and diameter growth as well as survival will be proportional to the initial size and biomass of seedlings. Inversely, in plantations exposed to deer, the apparency hypothesis predicts that herbivores are most likely to feed on taller, more obvious seedlings. Overall, we predict that medium stock size seedlings will outperform small and larger ones as they offer the best size compromise to withstand competition while maintaining a minimum level of apparency in the establishment phase. After 3 growing seasons, the height and diameter of medium stock size seedlings (48.6 ± 0.7 cm and 1.06 ± 0.05 cm, respectively) were similar to large ones (51.7 ± 1.1 cm, $p = 0.12$ and, 1.22 ± 0.05 cm, $p = 0.07$) that had been almost twice their biomass at the onset of plantation. The overall browsing occurrence was under 10% for all stock types exposed to browsing, yet the relative risk of being browsed increased by almost 20% for seedlings 30 cm vs. 60 cm at the end of the previous growing season. Mortality rate was unrelated to the browsing regime ($p = 0.14$) but overall, medium stock seedlings performed slightly better (2.9 ± 0.3%) than both small (7.0 ± 0.2%, $p = 0.10$) and large ones (10.5 ± 0.4%, $p = 0.03$). Based on the prominent effect of bottom-up control over top-down control in our experimental plantation, we conclude that choosing a size-adapted stock can optimize the cost of the restoration scheme following herbivore population reduction.

1. Introduction

Forest plantations are a form of artificial succession mainly used to fulfill the demand for wood fiber (Forest Stewardship Council, 2002; Park and Wilson, 2007; Fao, 2010). It can also be used to achieve ecological goals (Forest Stewardship Council, 2002; Paquette and Messier, 2010), such as reestablishing indigenous species following intense or repeated disturbances (see Parrotta et al., 1997 for a review; Thiffault et al., 2013). However, restoration efforts can be compromised if planted trees are exposed to the disturbances that initially interfered with natural regeneration. For example, selective browsing by large herbivores can act as a chronic disturbance, curtailing natural regeneration and potentially altering successional trajectory of forests (Coomes et al., 2003; Stroh et al., 2008; Gosse et al., 2011), with cascading impacts on other plants and animals (Allombert et al., 2005; Cardinal et al., 2012; Brousseau et al., 2013; Chollet and Martin, 2013). Moreover, competitive pressure by fast-growing, opportunistic species that are characterized by browsing-tolerant traits can impair the regeneration success of late successional species (Balandier et al., 2006; Diaz et al., 2007).

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As overabundant populations of large herbivores are a growing concern in many regions of the world (see Côté et al., 2004 for a review; Danell et al., 2006), it is imperative to develop restoration approaches to maintain forest composition within its natural range of variation (Lindenmayer et al., 2008). In this context, plantation strategies must address both the top-down pressure exerted by herbivores on the planted trees and the bottom-up control related to resource availability, as controlled by plant–plant competition. Predator reintroduction programs, although they can promote the regeneration of sensitive tree species (Ripple and Beschta, 2006), are difficult to implement (Fritts and Carbyn, 1995). Reduction of herbivore abundance through sport hunting and culling is often advocated (e.g. Kamler et al., 2010), but continuous commitment to reduction programs is difficult to secure (Fryxell et al., 2010). Moreover, sport hunting cannot completely replace the top-down control exert by natural predators (Kuijper, 2011). At the seedling level, individual physical protection from herbivores can be used to favor high survival and rapid growth, but it is hardly compatible with large-scale forestry operations (Tuley, 1985; Devine et al., 2007). On the other hand, seedling size at planting can also influence their establishment success (Thiffault, 2004). Due to their increased competitive ability, large seedling stock exhibit higher survival and growth than smaller seedlings (Newton et al., 1993; South and Mitchell, 1999). However, according to the "apparency" theory, herbivores are most likely to feed on plants that are easier to find (Feeny et al., 1976). Seedlings that are either taller or grow faster than the average would then be more susceptible to be found and browsed (Miller et al., 2006), thus reducing their initial size advantage over smaller stock.

Here, we explore whether selection of competition-adapted seedling stock types could be used together with management of large herbivore populations to reduce the effect of local competition on planted trees, while minimizing browsing impacts on their establishment success. When the top-down pressure from herbivores is low or absent, we predict that seedling performances (evaluated in terms of survival, dimensions and growth) will be proportional to the initial seedling height and biomass. In conditions where planted trees are exposed to browsers, we predict that browsing risk will be proportional to their initial dimensions. As a result, we predict that medium stock size seedlings will outperform smaller and larger ones, as they offer the best size compromise to withstand competition, while maintaining a minimum level of apparency.

2. Material and methods

2.1. Study area

We established an experimental plantation of balsam fir (*Abies balsamea* L.) on Anticosti Island, Québec, Canada (49°44′01″N, 63°44′22″W). Anticosti (7943 km^2) is part of the balsam fir – white birch (*Betula papyrifera* Marsh.) bioclimatic domain described by Saucier et al. (2009). Historical reconstructions have shown that the landscape was naturally dominated by a balsam fir forest matrix (Barrette et al., 2010). However, forests are being converted to white spruce (*Picea glauca* (Moench) Voss) stands due to chronic browsing pressure (Potvin et al., 2003; Casabon and Pothier, 2007) from a deer (*Odocoileus virginianus*) population introduced in 1896 and now reaching >20 deer km^{-2} (Potvin and Breton, 2005; Rochette and Gingras, 2007). As a part of an integrated forest management plan (Beaupré et al., 2004), containerized balsam fir seedlings are planted in large management enclosures (up to ~10 km^2) around recent clearcuts, within which local deer densities are reduced through sport hunting and culling.

The regional climate is sub-humid continental with total annual precipitation of 937 mm, with 327 mm falling as snow (Environment Canada, 1982). The mean monthly temperature is −11.0 °C in Jan. and 16.1 °C in July (Environment Canada, 2006). Prior to harvest (see below), the study site was a mature stand composed mainly of balsam fir, white spruce and paper birch. The soil is sandy loam textured (40% sand, 34% silt and 25% clay; based on the Bouyoucos method; McKeague, 1978) with an average pH of the surface mineral soil (0–0.15 m) of 4.9.

2.2. Experimental design

We conducted our experiment in a 11.3 km^2 management enclosure that was clearcut in 2004 and fenced (3 m high) in 2005. At the time of fencing, deer density was estimated at 24 deer km^{-2} and over the study period (2008–2010; see below), it ranged from 10 to 15 deer km^{-2} (G. Laprise, pers. comm.). Sport hunting was conducted in the management enclosure during fall from 2005 to 2010. The site was mechanically prepared with a passive disk trencher in late fall 2007.

Our experimental design consists of 6 randomized complete blocks established in June 2008 (Fig. 1). Each block was formed of 2 adjacent main plots (15 m× 45 m) separated by 35–50 m buffers. We randomly assigned one level of a fencing treatment to each main plot (Fenced: browsing exclusion using a 2.4 m-high wire fence; and Unfenced: management enclosure deer density). We split main plots into 3 subplots, to which we randomly assigned one of 3 balsam fir seedling stock types (small, medium or large stock seedlings). Seedlings were produced in containers of various sizes (small seedlings: 110 cm^3; medium seedlings: 200 cm^3; large seedlings: 350 cm^3) over 2 years, from a continental seed source (48°26′N; 65°35′W). Within every subplot, we planted balsam fir seedlings according to a 2× 2 m grid (2500 stem ha^{-1}) and individually tagged 16 seedlings per subplot for long-term measurement (a total of 576 observation units). At the time of planting (June 2008), we randomly collected 50 seedlings from each stock type to assess their height, basal diameter and dry biomass (following drying at 68 °C for 48 h; Table 1).

2.3. Seedling morphology and nutrition

We measured seedling height, leader's length, ground-level diameter, mortality and occurrence of browsing on at least one

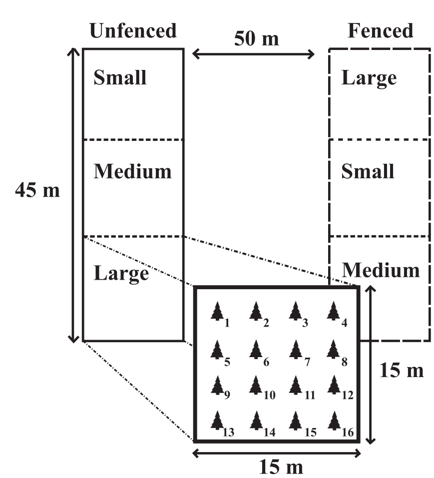

Fig. 1. Design of one block out of 6 from a split-plot experiment testing the performance of planted balsam fir (*Abies balsamea*) seedlings with different initial stock sizes subject to herbivory by white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, QC, Canada. Within each fenced or unfenced main plot, 16 seedlings of 3 stock types (small, medium, large) were planted in randomly allocated subplots (n = 36, n_{obs} = 576). Browsing, mortality and growth were measured annually for 3 years.

Table 1
Initial dimensions and biomass (mean (±SD)) of small, medium, and large balsam fir (*Abies balsamea*) seedlings prior to plantation on Anticosti Island, QC, Canada.

	Stock type					
	Small		Medium		Large	
Foliar biomass (g)	1.8	(0.4)	2.9	(0.6)	5.1	(1.5)
Woody biomass (g)	1.6	(0.3)	3.1	(0.8)	4.7	(1.2)
Root biomass (g)	1.9	(0.8)	2.8	(1.06)	5.0	(2.1)
Height (cm)	18.7	(2.2)	24.8	(2.9)	26.4	(3.5)
Ground-level diameter (mm)	3.8	(0.6)	5.1	(0.7)	6.4	(0.9)
n	50		50		50	

branch in September 2008, 2009 and 2010, and calculated height:diameter ratio (h:d ratio). At the end of the third growing season (August 2010), we harvested 2 untagged seedlings from each subplot for biomass assessment and evaluation of foliar nutrient concentration. We measured the biomass of needles and woody parts separately. Foliar samples were analyzed for N, P, K, Ca and Mg concentrations following standard protocols (Walinga et al., 1995) and controlling for growing stage (current year needles on leader, current year needles or previous year needles). Tissues were dissolved in sulfuric acid combined with selenium and peroxide, and heated to 370 °C for 60 min. Samples were analyzed by ICP emission spectrometry (iCAP 61e, Thermo Scientific, Waltham, MA). We determined Nitrogen concentration by Flow Injection Analysis (FIA) colorimetry (Quickchem 8000, Lachat Instruments, Loveland, CO).

2.4. Seedling competitive environment

In 2010, we randomly selected 8 trees in every subplot ($n = 288$ trees) to estimate percent cover (in 10% classes) of neighboring vegetation (by species) in a 0.8 m radius around the seedling. A competition index around any given seedling was computed a posteriori by summing the product of height and percent cover of each competing species. We also measured the percent of photosynthetically active radiation (%PAR) reaching the upper half of the planted seedling following Jobidon (1992) to assess the quantity of light intercepted by the competing vegetation. Measurements were conducted between 10:00 and 14:00 during cloudless days of July and August 2010, using an AccuPAR ceptometer (Decagon Devices Inc., Pullman, WA). Two orthogonal measurements were taken at mid-height of all seedlings, at the tip of their leader, at 1 m above ground and above the vegetation canopy (full sunlight). Average readings were expressed as a percentage of the full sunlight level.

2.5. Data analyses

We performed analyses of variance for repeated measurements (ANOVAR) using mixed linear models (MIXED procedure of the SAS system, v.9.2; Littell et al., 2002) to evaluate the main and interacting effects of fencing, stock type and number of growing seasons on seedlings' height, leader length, ground-level diameter, and h:d ratio. Block and interaction terms involving block were considered as random factors. Biomass, %PAR and foliar nutrient concentrations at the end of the study were analyzed using similar mixed linear models with seedlings parts as repeated measurements. The structure of the variance-covariance structure was selected among competing model using the Akaike Information Criteria (AIC). Normality and homocedasticity were verified using standard graphical approaches; no transformations were deemed necessary.

Using the ratio of dead to living tagged seedlings as the response variable, we analyzed treatment effects (fencing and stock type) on annual mortality using generalized linear mixed models (GLMM) with a binomial distribution and a *logit* link function (GLIMMIX procedure of the SAS system, v.9.2; SAS Institute Inc., 2009). Due to the low mortality, we had to parameterize a simpler model with simple effects only. Receiver Operator Characteristic (ROC) curves were used to assess the sensitivity of the model. In all analyses, differences were deemed significant at $\alpha = 0.05$. When significant differences were found, treatment means were compared using least square mean tests with the SIMULATE adjustment for multiple comparisons in SAS. Unless otherwise mentioned, means are reported with their standard error (SE).

Using the LOGISTIC procedure (SAS Institute Inc., 2009), we regressed the ratio of cumulative browsing occurrence to the total number of seedlings (alive) in non-fenced plot against seedling height during the previous season. We used the *c* statistic of the ROC curve to quantify the capacity of the estimated browsing probability to discriminate between seedlings of different height (Hosmer and Lemeshow, 2000).

Finally, competing plant species were grouped based on their functional traits following Balandier et al. (2006; see Appendix A). We performed principal component analyses (PCA) and k-means clustering to detect natural grouping in vegetation organization and relate them to the fencing treatments (FACTOR and CLUSTER procedures; Khattree and Naik, 2000; SAS Institute Inc., 2009).

3. Results

3.1. Seedling morphology

The initial difference in seedling height (Table 1) was maintained through the study with small stock seedlings being on average 20–25% shorter than both medium (39.6 ± 1.1 cm vs. 48.5 ± 1.1 cm, $t_{20} = 5.81$, $p < 0.0001$; Table 2, Fig. 2A) and large stock seedlings (51.7 ± 1.1 cm, $t_{20} = 7.86$, $p < 0.0001$). Although our analysis suggested an interaction between the fencing treatment and year (Table 2), adjusted comparisons for multiple pairwise comparisons did not reveal significant differences between seedling's height inside and outside fences from September 2008 ($t_{60} = -0.17$, $p = 1$) to September 2010 ($t_{60} = -1.77$, $p = 0.44$).

At the end of the first growing season (September 2008), the leader's length of small stock seedlings was 24% shorter than that of medium and large stock seedlings ($t_{60} = 3.87$, $p = 0.008$ and $t_{60} = 4.53$, $p = 0.0009$ respectively; Table 2, Fig. 2B). By the end of the second growing season (September 2009), we observed a general decrease in apical growth, such that all stock types had a similar leader elongation ($0.49 < t < 1.12$, $0.97 < p < 1$). After the third growing season, the leader of small stock seedlings were smaller than large stock ones ($t_{60} = 3.20$, $p = 0.05$) (September 2010; $0.80 < t < 1.64$, $0.70 < p < 0.99$). Seedling ground-level diameter increased by 0.32–0.42 cm year^{-1} (Table 2, Fig. 2C). As for height, the basal diameter of medium and large stock seedlings were similar ($t_{60} = 2.30$, $p = 0.08$) with small stock seedlings remaining thinner ($4.40 < t_{60} < 6.60$, $p < 0.007$; Table 2, Fig. 2C). The h:d ratio did decline over time at a different rate depending on stock type (Table 2, Fig. 2D). Whereas medium stock seedlings had an initial h:d ratio similar to small stock ones ($t_{60} = -2.08$, $p = 0.50$), their increased radial growth relative to vertical growth during the second growing season led to a 32% reduction of the ratio. From that point thereon, their h:d ratio was similar to large stock seedlings (2nd season: $t_{60} = 0.35$, $p = 1.00$, 3rd season: $t_{60} = -0.75$, $p = 1.00$) while the ratio of small stock seedlings remained higher to those of both medium (2nd season: $t_{60} = -3.77$, $p = 0.009$; 3rd season: $t_{60} = -3.54$, $p = 0.02$) and large stock seedlings (2nd season: $t_{60} = 4.12$, $p = 0.003$; 3rd season: $t_{60} = -4.28$, $p < 0.001$).

Table 2
Contribution of browsing exposure (fenced or unfenced) and stock type (small, medium or large) to variation in the morphological parameters of balsam fir (*Abies balsamea*) seedlings in an experimental plantation located on Anticosti Island, Québec, Canada. The effects of the experimental treatments were modeled using mixed linear models with block ($n = 6$) as a random factor. d.f. = numerator/denominator degrees of freedom, h:d ratio = height:diameter ratio. Square brackets indicate nested factors.

Factors	d.f.	Seedling height		Leader's lenght		Ground-level diameter		h:d ratio	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Fencing (F)	1/2	4.85	0.08	1.14	0.33	0.18	0.69	1.90	0.22
Stock Type (T)	2/20	33.24	<0.0001	14.19	0.0001	23.19	<0.0001	28.88	<0.0001
F(T)	2/20	0.63	0.54	0.48	0.62	0.10	0.90	2.01	0.16
Year (Y)	2/60	60.75	<0.0001	213.09	<0.0001	95.29	<0.0001	253.85	<0.0001
F[Y]	2/60	4.16	0.02	1.36	0.26	0.18	0.84	0.29	0.75
T[Y]	4/60	1.11	0.36	2.65	0.04	2.10	0.09	4.83	0.001
F∗T[Y]	4/60	0.32	0.86	0.35	0.84	0.13	0.97	0.23	0.92

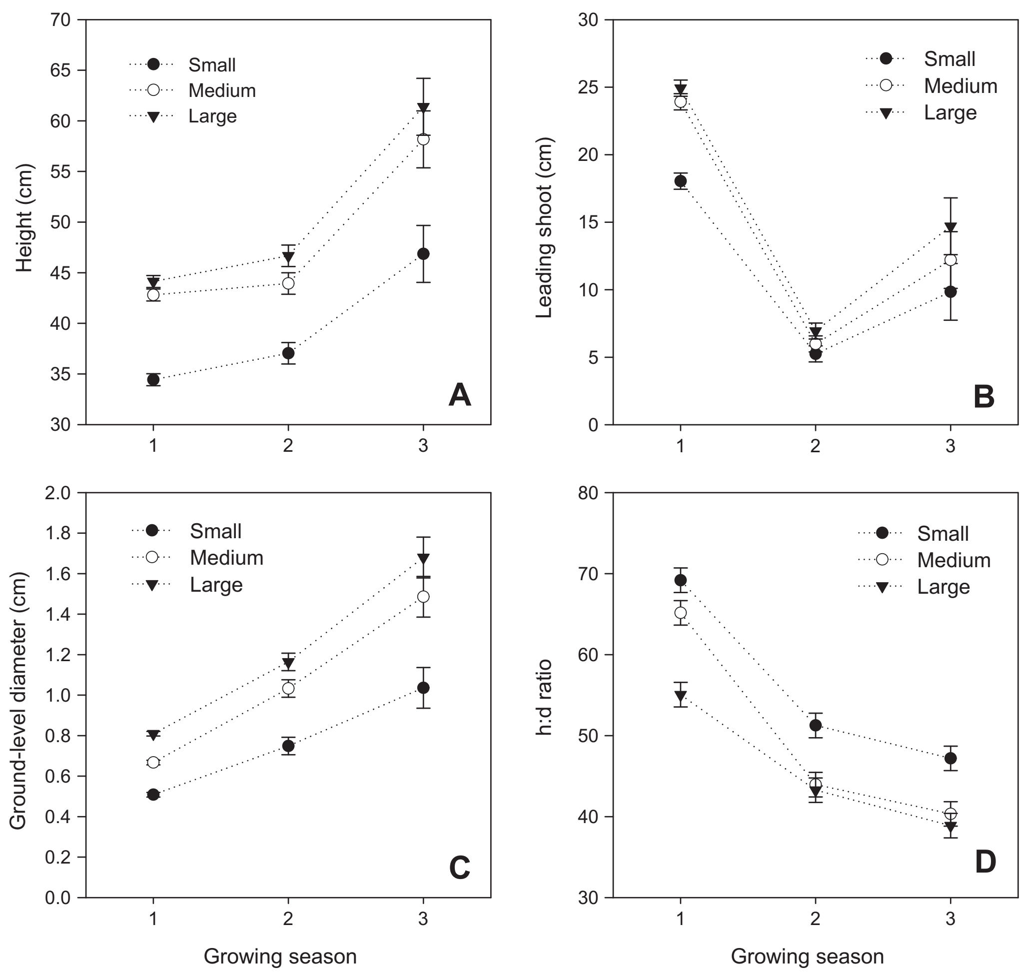

Fig. 2. Development of morphological parameters of planted balsam fir (*Abies blasamea*) seedlings of 3 initial stock sizes over 3 consecutive years following plantation on Anticosti Island, QC, Canada. Parameters are height (A), the length of the leading shoot (B), diameter at ground-level (C), and the height to diameter ratio (D). Data are reported as mean ± SE.

3.2. Seedling mortality

Seedling mortality increased over time ($F_{2,1367} = 24.81$, $p < 0.01$), from 1.6% ± 0.2 at the end of the first growing season (September 2008) to 7.4% ± 0.3 in September 2009 ($t_{1641} = 5.79$, $p < 0.01$) and 10.5% ± 0.4 in September 2010 (2nd vs. 3rd season: $t_{1159} = -2.42$, $p < 0.02$). The stock type effect was marginal ($F_{2,10} = 3.12$, $p = 0.09$), suggesting a lower mortality for medium stock seedlings (2.9% ± 0.3) than small (7.0 ± 0.2%; $t = -1.81$, $p = 0.10$) and large ones (10.5% ± 0.4; t = 2.47, $p = 0.03$). Mortality was similar across fencing treatments ($F_{2,5} = 2.91$, $p = 0.14$). Model convergence required the exclusion of the interaction terms, but the resulting model provided a fairly accurate capacity to classify dead and living seedlings across treatments (ROC curve value: 0.78).

3.3. Browsing probability

Browsing was under 10% for all stock types. Accordingly, attempts to model browsing probability were unsuccessful when all treatments and their interactions were included as explanatory variables. For all seedlings, independently of the stock type treatment, the relative risk of being browsed during a given growing season increased with seedling height at the end of the previous growing season (Fig. 3).

3.4. Seedling competitive environment

The first axis of the PCA of the vegetation communities around planted balsam fir expressed a gradient from plant species resistant (positive value) or not (negative value) to browsing (25.6% of the variance explained, Fig. 4). No clusters matching either the fencing treatments or the stock types could be identified. Percent PAR reaching the upper-half of seedlings was not influenced by fencing ($F_{1,5}$ = 2.05, p = 0.21). Small stock seedlings received about 13% less light (72% ± 3) than medium (85% ± 3, t_{10} = 3.80, p = 0.009) and 15% less than large stock types (86% ± 3, t_{10} = 4.26, p = 0.004; $F_{2,10}$ = 10.9, p = 0.003).

3.5. Seedling biomass and foliar nutrient concentrations

Large stock seedlings had the largest current year and total biomass at the end of the third growing season (13 g ± 3 and 72 g ± 7 respectively, Table 3), followed by medium stock (7 g ± 3, t_{19} = 1.85, p = 0.07 and 54 g ± 7, t_{19} = 3.10, p = 0.02 respectively) and small stock seedlings (5 g ± 3, t_{19} = 2.44, p = 0.02 and 34 g ± 7; t_{19} = 6.13, p < 0.001 respectively). The biomass of current-year needles was consistent with this finding; large stock seedlings had almost two to three times as much biomass as medium and small stock sizes (17 g ± 2 vs. 9 g ± 2; t = 3.73, p = 0.02; and 5 g ± 2; t = 5.13, p < 0.01; respectively). Foliar nutrient concentrations were similar across stock types (Appendix B). Fencing enhanced Mg foliar concentration of leader's needle by 20% compared to unfenced conditions (1.38 g kg^{-1} ± 0.07 vs. 1.12 g kg^{-1} ± 0.07).

4. Discussion

After 3 growing seasons, medium stock size seedlings had a performance similar to large stock seedlings that were almost twice their biomass at the onset of plantation. The competitive performance of seedlings was thus not directly proportional to their initial size, as we suspected, but this was not related to a higher apparency and browsing risk of large stock size seedlings; survival and growth were similar for seedlings exposed to or protected from browsing by while-tailed deer. Thiffault and Roy (2010) have reported that medium size white spruce seedlings (similar in size to those used in the present study) can withstand a moderate level

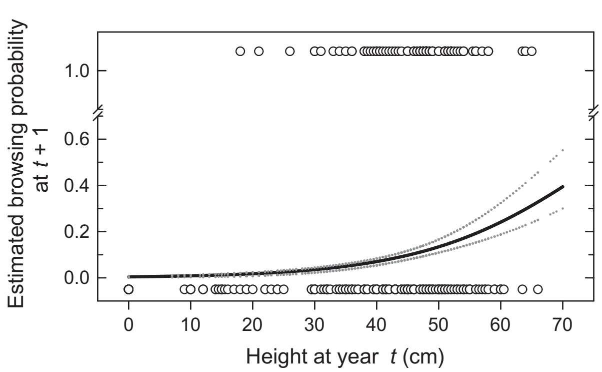

Fig. 3. Estimated probability of being browsed for planted balsam fir seedlings (*Abies balsamea*) in unfenced plots submitted to white-tailed deer (*Odocoileus virginianus*) herbivory (n = 288) during a given growing year as a function of their height at the end of the previous growing year (odds ratio = 1.07; c = 0.746). Top and bottom circles represent occurrences of browsed (top) and non-browsed (bottom) seedlings. Dash lines represent 95% confidence limits.

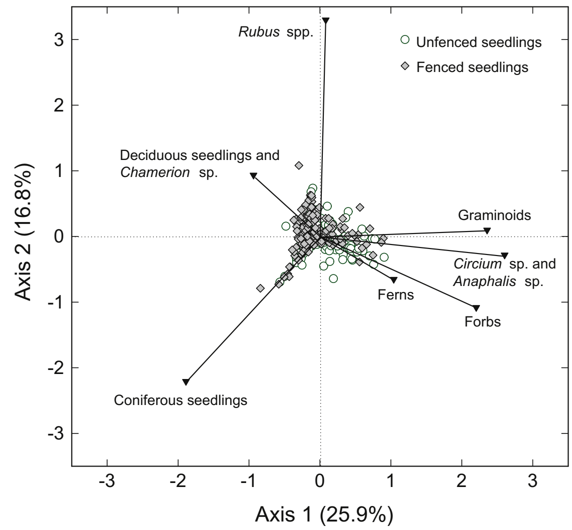

Fig. 4. Principal components of the vegetation communities around planted balsam fir (*Abies balsamea*) seedlings (n = 288) under 2 browsing regime (fenced and unfenced) by white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, QC, Canada. Axes 1 and 2 have a cumulative R^2 of 42.7. Vectors for plant functional groups (see Appendix A) reveal that axis 1 represents vulnerability of species to browsing with preferred species having negative scores. No cluster related to either the stock type or the fencing treatment could be identified.

of competition, whereas large seedlings perform better than smaller stock in highly competitive environments (Jobidon et al., 2003). Similar conclusions were drawn for *Pinus elliottii* Engelm. (South and Mitchell, 1999) and *Picea sitchensis* (Bong.) Carr. (South and Mason, 1993). Yet, in the Anticosti context, medium stock seedlings experienced marginally lower mortality rates than the larger ones (almost twice as low). Nevertheless, survival remained higher than 80%, thus precluding the need for fill-planting to compensate low stocking (Dancause, 2008).

The small stock seedlings remained smaller than seedlings from the other stock types over the entire study period, but from the second growing season and thereon, their leader growth was comparable to that of the medium and large stock. Small stock seedlings also had a consistently smaller diameter than other stocks, and both larger seedling types maintained similar diameter growth. Many authors have demonstrated that height growth is not a reliable indicator of early competition (e.g. Morris et al., 1990; Jobidon et al., 1998), whereas radial increment is rapidly impaired when light availability is reduced by competitors. Our results suggest that, regardless of the presence/absence of deer, competition level on the planting site was not sufficient to elicit a clear competitive advantage for the large seedling stock type over the medium stock type. However, it was important enough for the smaller stock seedlings to be negatively influenced. Indeed, the h:d ratio of the medium stock seedlings was at first similar to the h:d of small stock seedlings, but after one growing season, it had decreased to a level similar to that of the large stock seedlings, supporting that both stock types have competed equally well in this environment (Opio et al., 2000). Still, after 3 growing seasons, the h:d ratios of all seedling types were under 50, a value that is far below levels judged to be critical in terms of competitive status and tree stability (Jobidon, 2000).

We predicted that when exposed to browsing, larger seedlings would have a higher apparency, resulting in higher browsing probabilities. Indeed, the browsing probability increased as a function of the preceding year's height, which suggests a selection by deer for taller seedlings, regardless of stock type. Close et al. (2009) found a similar pattern; foliage browsing of *Eucalyptus globulus* Labill. by small mammals (European rabbits, *Oryctogalus cunilus*,

Table 3
Contribution of browsing exposure (fenced or unfenced) and seedlings stock type (small, medium or large) on variation in foliar and woody biomass of balsam fir (*Abies balsamea*) seedlings three years after plantation on Anticosti Island, QC, Canada ($n = 72$). We measured the biomass of needles and woody parts separately. For needles, we controlled for seedling part (current year needles on leader, current year needles, previous year needles). The effects of experimental treatments were modeled using general mixed linear models. d.f. = numerator/denominator degrees of freedom. Square brackets indicate nested factors.

Fixed factors	Total seedling biomass			Current year biomass					
				Total			Needles only		
	d.f.	*F*	*p*	d.f.	*F*	*p*	d.f.	*F*	*p*
Fencing (F)	1/5	0.09	0.78	1/5	0.11	0.75	1/5	0.32	0.60
Stock Type (T)	2/19	18.81	<0.0001	2/19	19.23	<0.0001	2/19	5.35	0.01
F(T)	2/19	1.23	0.31	2/19	1.15	0.34	2/19	0.68	0.52
Seedling Parts (P)	–	–	–	–	–	–	2/29	43.26	<0.0001
F[P]	–	–	–	–	–	–	2/29	0.32	0.58
T[P]	–	–	–	–	–	–	4/29	4.86	0.02
F[T[P]]	–	–	–	–	–	–	4/29	0.73	0.50

Common brushtail possum, *Trichosurus vulpecula* and red-bellied padelemon, *Thylogale billardierii*) was higher for larger seedlings compared to smaller seedlings, but differences were less perceptible after a culling session. Even though we observed that taller seedlings had a higher browsing risk than smaller seedlings, we did not detect any difference in the browsing probability among stock types. This points to a limitation of our study; as we could not control deer density within the large management enclosure where our study was conducted, we think that the lack of stock type effect is due to a relatively low deer density, even in the unfenced treatment, following intensive culling. Tremblay et al. (2007) reported a browsing-related mortality rate under 7% for small (<10 cm) natural seedlings at local densities lower than 15 deer km^{-2} showing that small balsam fir seedlings are seldom browsed at deer densities such as estimated in our study area. Taller seedlings may however suffer a higher browsing rate as suggested by the cumulative browsing reaching 30% for unfenced seedlings at the end of the third growing season.

Seedlings planted in non-fenced plots showed little benefit from any competition release that deer could have induced by browsing neighboring vegetation. Aside from the trend for lower height of seedlings within unfenced plots at the third growing season, no significant difference could be found between growth of seedlings in fenced and unfenced plots. Percentage of full light reaching the seedling upper-half was also similar across treatments. Moreover, nutrient concentrations were similar for protected and unprotected seedlings (except for Mg, but concentrations for all treatments exceeded the threshold causing needle chlorosis in *Picea abies* ([0.24 g kg^{-1}]; Ingestadt, 1959), further suggesting similar levels of competition for nutrients across treatments. The evidence for scarce competition and lack of difference between fenced and unfenced plots can be related to the chronic heavy browsing pressure sustained over many decades in our study area prior to forest harvesting, deer culling and planting (Tremblay et al., 2005). The field layer of balsam fir forest appears relatively resilient to overbrowsing (Tremblay et al., 2006), but chronic browsing has been shown to trigger alternative successional trajectories (Tanentzap et al., 2011; Nuttle et al., 2013). The delay before the establishment of aggressive competitive vegetation can also be increased due to previous browsing pressure if browsing resistant species such as *P. glauca* are not already present on the site (Tremblay et al., 2006).

Overall, our results revealed prominent effect of bottom-up control over top-down control on seedling growth. In fact, we found little support for a top-down controlled system, but rather evidenced that a biological limit to gains in performance is reached given seedling size and the competitive environment (South and Mitchell, 1999). Depending on the level of competition, increasing initial seedling size does not ensure increased performance. In this case, competition mechanisms appear sufficient to create an advantage of large over small seedlings, but not enough to differentiate medium from large stock types. The browsing pressure may lower this limit to gaining in performance, as suggested by the increased browsing probability and the lowered current foliar biomass for large seedlings, compared to the smaller stock types.

5. Conclusion

Our results suggest that in balsam fir dominated forest previously submitted to heavy browsing pressure by white-tailed deer, medium stock type seedlings provide the best short-term cost/benefit balance for restoration planting operations. The extensive history of chronic heavy browsing pressure in this system appears to have influenced the competing vegetation complex in such a way that medium stock seedlings perform as well as larger ones during the establishment phase. The medium stock size seedlings performed better than the small stock seedlings in this context, and represent savings in terms of production/handling/planting costs, compared to large stock seedlings (Thiffault, 2004). Further monitoring and mid- to long-term economical analyses are necessary to verify if these early responses are indicative of future growth and financial performances in such ecosystems. Unless deer density drastically increases in this management enclosure, differences between stock types should remain minimal in the short terms. However, the life expectancy of the management enclosures is 10–12 years (Beaupré et al., 2004). It remains uncertain how the increase in deer density that will follow fence removal will affect plantation success. Many factors will influence the response of the established seedlings, including deer abundance, the height and constitutive defense of the saplings (Boege and Marquis, 2005) and the height and composition of the neighboring vegetation (Palmer et al., 2003).

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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.2013.07.031.

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