Forest Ecology and Management 307 (2013) 333–340

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

Julie Faure-Lacroix [a], Jean-Pierre Tremblay [a,b,*], Nelson Thiffault [b,c], Vincent Roy [c,1]

[a] Département de biologie & Centre d'études nordiques, Université Laval, 1045 ave de la Médecine, Québec, QC G1V 0A6, Canada
[b] Centre d'étude de la forêt, 2405 rue de la Terrasse, Pavillon Abitibi-Price, Université Laval, Québec, QC G1V 0A6, Canada
[c] Direction de la recherche forestière, Ministère des Ressources naturelles, 2700 rue Einstein, Québec, QC G1P 3W8, Canada

ARTICLE INFO

Article history:
Received 28 January 2013
Received in revised form 15 July 2013
Accepted 17 July 2013
Available online 15 August 2013

Keywords:
Anticosti
Balsam fir
Exclosure
Competition
Plantation
White-tailed deer

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).

* Corresponding author at: Département de biologie & Centre d'études nordiques, Université Laval, 1045 ave de la Médecine, Québec, QC G1V 0A6, Canada. Tel.: +1 (418) 656 2131x3629; fax: +1 (418) 656 2043.

E-mail addresses: julie.faure-lacroix.1@ulaval.ca (J. Faure-Lacroix), jean-pierre.-tremblay@bio.ulaval.ca (J.-P. Tremblay), nelson.thiffault@mrn.gouv.qc.ca (N. Thiffault), vincent.roy@rncan-nrcan.gc.ca (V. Roy).

1 Present address: Natural Resources Canada, Canadian Forest Service, Centre de foresterie des Laurentides, 1055 rue Du P.E.P.S., Québec, QC G1V 4C7, Canada.

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.07.031

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

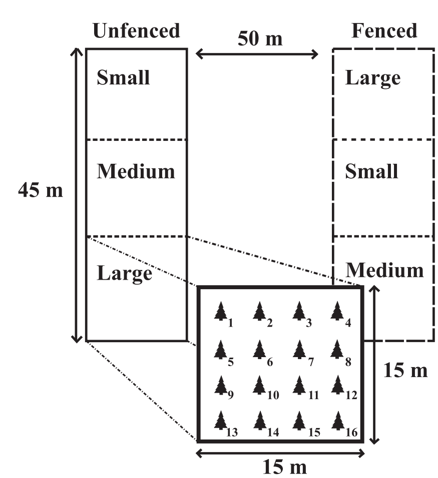

Fig. 1. Design of one block out of 6 from a split-plot experiment testing the performance of planted balsam fir (*Abies balsamea*) seedlings with different initial stock sizes subject to herbivory by white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, QC, Canada. Within each fenced or unfenced 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.