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Survival and growth of balsam fir seedlings and saplings under multiple controlled ungulate densities

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ABSTRACT

Tree species composition in forests can be strongly modulated by high densities of cervid herbivores ultimately leading to local extirpation of species. To establish which cervid densities are compatible with the recruitment of a browse sensitive tree species, seedlings and saplings should be surveyed under variable cervid densities rather than in their presence or absence alone. We studied the growth and survival of different demographic stages of balsam fir (*Abies balsamea*) on Anticosti island (Québec, Canada) under controlled densities of white-tailed deer (*Odocoileus virginianus*). In a seven-year experiment using deer enclosures, we followed the life stage and fate of individually tagged balsam fir seedlings/saplings under forest cover and forest logged at the start of the experiment. Almost no regeneration into the sapling stage (>30 cm) was observed under ambient deer densities after 7 years and decreased survival and growth were observed under an experimental deer density of 15 km^{-2}. However, mortality at $\leqslant$15 deer km^{-2} decreased over time and with age and stem height, converging towards mortality observed at 0 deer km^{-2}. Given the relatively high stem density of saplings at 15 deer km^{-2} 7 years after the start of the treatment, our data indicate that at this density considerable balsam fir regeneration may occur, although the ultimate contribution of balsam fir to the canopy remains uncertain. The notion that small seedlings are most vulnerable to deer browsing and that balsam fir recruitment rapidly decreases after logging suggests that maintaining low deer densities is most crucial immediately after a stand-initiating disturbance (e.g. logging).

1. Introduction

Large vertebrate herbivores can have strong top-down effects on the abundance of targeted plant populations. The magnitude of herbivore impacts on plant fitness depends on two types of resistance traits, either avoidance or tolerance based (sensu Belsky et al., 1993). Tolerance is the capacity of a plant to maintain fitness through growth and reproduction after sustaining herbivore damage (Rosenthal and Kotanen, 1994). Avoidance traits are traits that decrease consumption or the chance of consumption by herbivores. Resistance of plants to herbivores may change with demographic stages, since individuals may change in palatability or compensatory abilities (Boege and Marquis, 2005). In addition, the presence of palatable or unpalatable neighbouring plants influences the foraging decisions of herbivores. Such indirect avoidance is known as avoidance by association (e.g. Hjältén et al., 1993; Bee et al., 2009). The combined effects of individual resistance traits and associations are here termed inclusive resistance.

In ecosystems with long-lived plants such as forests, the inclusive resistance of different demographic stages may be of crucial importance for the survival of tree populations. Many forests worldwide nowadays have dense cervid herbivore populations scarcely regulated by predators, raising concerns about the conservation of key tree species in such ecosystems (Côté et al., 2004). In order to understand herbivore impacts on tree species composition of forests and to develop realistic management scenarios, experimental studies should assess the effects of variation in herbivore densities on the regeneration of tree species. The rare experiments dealing with multiple different deer densities have either focused on general patterns of succession (Tilghman, 1989; Horsley et al., 2003) or exclusively on the seedling stage (Tremblay et al., 2007). To obtain a more mechanistic understanding of the sensitivity of plant populations to deer, we need to study herbivore effects on different demographic stages (e.g. Knight et al., 2009). Hence, we need to test the effects of different deer densities at seedling stages as well as later stages during forest regeneration and quantify survival and transitions to later stages.

One such system in which cervid densities are exceptionally high is Anticosti Island, Québec, Canada. The island, free of large predators, exhibits unusually high densities of introduced white-tailed deer (*Odocoileus virginianus*). This circumstance allows for

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rigorous testing of the possible effects of elevated herbivore densities on boreal forest plant communities. Deer, introduced near the end of the 19th century, reached high densities in the 1930s and remained abundant ever since. From this time onward the dominant tree species on the island, balsam fir (*Abies balsamea*), decreased in abundance and has been gradually replaced by white spruce (*Picea glauca*) (Potvin et al., 2003). The demise of balsam fir may ultimately cause a setback to white-tailed deer itself, as it has become staple food for deer on Anticosti Island (Tremblay et al., 2005; Lefort et al., 2007). Because white spruce is far less palatable than balsam fir (Sauvé and Côté, 2007), eradication of balsam fir may deprive deer from a critical winter resource. In a previous paper, Tremblay et al. (2007) have shown using an enclosure experiment with controlled deer densities, that the seedling bank of balsam fir, although chronically browsed, can withstand fairly high levels of herbivory (15 deer km^{-2}). Here, we extend our investigation to the period of recruitment of seedlings to the sapling stage (stems taller than 15 cm) up to 7 years after a stand-initiating disturbance. We hypothesized that growth and survival of balsam fir is a function of deer density and is modulated by changes in inclusive resistance over time.

In enclosures established in a mosaic of forest cover and clear cuts, we maintained four different deer densities: 0, 7.5, 15 deer km^{-2} and ambient deer density (27–56 deer km^{-2}). This allowed us to quantify regeneration of balsam fir both under canopy (advance regeneration) and after a stand-initiating disturbance. We predicted that (a) browsing on balsam fir increases with deer density, (b) growth and survival of balsam fir seedlings is hence negatively affected at a higher density of white-tailed deer, and (c), that recruitment into the sapling stage and subsequent survival is less affected than seedling recruitment, given changes in inclusive resistance to herbivory. To this end, we recorded recruitment, survival, stem height and branch number of almost 6000 individually tagged balsam fir seedlings/saplings each autumn from 2002 until 2009. We also monitored browsing damage incurred by deer. Past research has shown that the regeneration of browse sensitive tree species can be severely reduced by cervid herbivory (e.g. Long et al., 2007; Olesen and Madsen, 2008; Stroh et al., 2008). Most of these studies compared herbivore presence with total absence (but see Horsley et al., 2003). Such designs are certainly helpful in establishing which species are most vulnerable and whether or not they can recover in the absence of herbivory. However, in order to understand the limits of herbivore resistance, regenerating vegetation needs to be exposed to multiple different densities of herbivores.

2. Methods

2.1. Study area

The experimental site was located on Anticosti Island (7943 km^2) in the Gulf of St. Lawrence, Québec, Canada (49°06′–49°95′N, 61°67′–64°52′W). The climate on Anticosti is maritime with a mean air temperature of −13.6 °C in January and 14.8 °C in July and a mean annual precipitation of 328 cm as snow and 610 mm as rainfall (Environment Canada, 2005). The dominant boreal forest cover is part of the eastern balsam fir – paper birch (*Betula papyrifera*) region (Saucier et al., 2009). Approximately 200 deer were introduced to Anticosti Island in 1896 and 1897. The deer population became abundant ca. 30 years after the introduction and remained at high density thereafter (~20 km^{-2}, Potvin and Breton, 2005). Other herbivores on the island are snowshoe hare (*Lepus americanus*) and rare moose (*Alces alces*) (Potvin et al., 2003). No natural predators are present although black bear (*Ursus americanus*), a possible predator of white-tailed deer fawns (Mathews and Porter, 1988), has been sighted occasionally until the 1990s (Côté, 2011). However, each year in autumn at least 8000 deer are hunted on the island (Rochette and Gingras, 2007).

2.2. Experimental design

We conducted a controlled browsing experiment to investigate the relationships between deer density and balsam fir forest regeneration dynamics in interaction with timber harvesting. The browsing treatment included four levels of deer density (0, 7.5, 15 deer km^{-2} and ambient density). Each level was applied to two types of forest cover: (1) even-aged clear cut, logged at the start of the experiment (2001), and (2) uncut forest both with >70% canopy closure by mature balsam fir forest overstorey before the beginning of the experiment. All deer densities and forest cover types were replicated within three blocks, each composed of four adjacent or close proximity experimental units. The enclosures were built of 3 m high wire game fencing and their surface area was 10 ha for the 0 deer km^{-2}, 40 ha for the 7.5 deer km^{-2} level (3 deer per enclosure) and 20 ha for the 15 deer km^{-2} treatment level (3 deer per enclosure). Effects of ambient deer density were estimated in a 40 ha area, where we estimated deer density from pellet counts at 27 deer km^{-2} in blocks B and C, and 56 deer km^{-2} in block A (see Tremblay et al., 2006 for details). The browsing treatment was repeated during eight consecutive years (2002–2009, y0–y7).

Wild deer were captured in the vicinity of the experimental blocks each May, relocated in the enclosures and culled in November. Both in May and in November there was generally substantial snow cover on the ground (>20 cm). Mainly yearlings (11–12 months old at the time of capture) but also adults were distributed evenly among the experimental units. We used multiple control procedures to maintain the target densities, including lethal and non-lethal drives and checking for tracks in the snow before stocking. All deer were fitted with VHF collars (Lotek Wireless Inc., Newmarket, Ont., Canada) during the course of the experiment. All animal handling protocols were approved by the Université Laval Committee of the Canadian Council on Animal Care (2008017-2).

In June of y0, before the first application of the browsing treatment, we randomly selected 20 circular plots (0.5 m^{-2}) for each combination of deer density and forest cover in each block (n = 480 plots). We used numbered glass rods to tag all balsam fir seedlings that had passed the cotyledon stage and were less than 10 cm tall and had a single unbrowsed stem per plot (n (y0) = 3300 seedlings). We removed seedlings that did not meet those criteria and woody debris to obtain homogeneous conditions. We monitored the height and status of tagged seedlings and the emergence of new seedlings during annual visits in September from y0 to y7 as: (1) alive and unbrowsed, (2) browsed, (3) browsed-to-death, (4) dead from unknown causes, (5) new seedlings past the cotyledon stage, (6) newly emerged seedlings with browsing damage or (7) lost to the experiment (e.g. due to windblown trees damaging plots). Browsing by deer leaves shredding marks that are easily discernible from the sharp cuts made by snowshoe hare. Browsing damage by snowshoe hares was only very rarely observed in our experiment. From the autumn of 2002 until autumn 2009 we obtained 29,988 observations on 5933 tagged seedlings.

2.3. Deer density and seedling growth

To estimate growth of seedlings under the different herbivore pressures, we compared the length of stems over time since the seedlings were tagged across the different cover types and deer densities. Because no transformation of individual stem heights