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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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