



# Stand structure interacts with previous defoliation to influence herbivore fitness

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## ABSTRACT

The intensity and duration of *Neodiprion abietis* outbreaks have recently increased in forests of North America that were precommercially thinned more than a decade earlier. We tested the hypotheses that changes in stand structure following thinning increase the fitness (i.e., survival rate  $\times$  fecundity) of *N. abietis* by either (a) increasing foliar availability and/or quality (i.e., increased availability of primary metabolites and/or reduced foliar defenses) or (b) by reducing any negative effects on foliar quality and/or availability resulting from herbivory that occurred during the preceding season(s). Effects of thinning and previous herbivory on *N. abietis* and its host plant (*Abies balsamea*) were determined through (i) a manipulative field experiment that evaluated the effects of experimental defoliation on *N. abietis* in a thinned stand, (ii) a manipulative field experiment that examined the effects of thinning on *N. abietis* in undamaged and naturally defoliated stands, and (iii) a field survey to estimate survival of *N. abietis* in natural populations.

Defoliation caused reductions in the availability of different-aged foliage available to larvae and in the fitness of a subsequent *N. abietis* generation feeding on defoliated branches, but decreases in fitness were smaller in thinned than unthinned stands. In thinned stands, defoliation was associated with increases in foliage production and foliar contents of monoterpenes and nitrogen, as well as with a decrease in foliar contents of water. Conversely, only small changes in plant growth and foliar contents of nutrients and secondary chemicals were observed in defoliated unthinned stands. This suggests that deleterious effects of defoliation on sawfly fitness were offset by an increase in the foliar content of nitrogen, a primary compound known to improve larval growth in sawflies, which supports the hypothesis that thinning moderates negative effects of previous defoliation on sawfly fitness. The present study demonstrates that forestry practices that alter stand structure by reducing tree density may increase herbivory by affecting the way trees respond to insect attack, even after crown closure, with consequences on the buildup of herbivore populations in attacked trees.

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## 1. Introduction

Recent increases in the area devoted to intensive forest management in North America have been accompanied with changes in the levels of defoliation attributable to insects. Indeed, during the last two decades, many outbreaks of insects formerly known as secondary pests have occurred in North American plantations and in naturally regenerated stands, where the densities of plants have been reduced by planting practices or precommercial thinning, respectively (Quiring, 1990; Piene et al., 2001; Nealis and Turnquist, 2010). Precommercial thinning (hereafter referred to simply as thinning) is a cutting treatment applied to immature stands to concentrate growth on a prescribed (smaller) number of retained stems, which also increases illumination, soil tempera-

ture, decomposition, and mineralization (François et al., 1985; Wickman and Torgersen, 1987; Thibodeau et al., 2000). Thinning is one of the principal silvicultural methods used to increase the yield of stands beyond the best that might be achieved under natural conditions (Smith et al., 1997). It is widely accepted that changes in stand structure resulting from thinning can increase the survival and reproductive performance of insect defoliators, particularly in the years immediately following the thinning treatment (Mason et al., 1992; Avtzis and Bombosch, 1993; Bauce, 1996). This phenomenon has been associated with increased foliar growth and a reduction in some leaf defenses (Bauce, 1996). Less is known about herbivore response at crown closure, several years after thinning treatments.

Changes in stand structure, such as that caused by thinning, may result in different levels of herbivory by insects (Crook et al., 1979; Piene, 1989; Mason et al., 1992), which may in turn influence subsequent generations of defoliators. The size, growth rate, and survival of herbivores feeding on previously defoliated trees often decreases due to reductions in the quality and/or availability

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of foliage (Benz, 1974; Haukioja and Niemelä, 1977; Leather et al., 1987). Conversely, by reducing some host-plant defenses (reviewed by Karban and Baldwin (1997)) or modifying the time of budburst (Quiring and McKinnon, 1999; Carroll and Quiring, 2003), previous defoliation can also increase host-plant suitability for some herbivores. On average, trees in closed, previously thinned stands are less likely to die from competition with adjacent trees (i.e., self-thinning) and have bigger and denser crowns than trees in unthinned stands (Zahner and Whitmore, 1960; Maguire, 1983; Westoby, 1984). Thus, the increased level of resources per tree and tree size in thinned versus similarly aged unthinned stands could increase tree tolerance to defoliation and alter the effects of previous herbivory on foliage availability and/or nutritional quality for subsequent generations of defoliators.

In North America, balsam fir sawfly (*Neodiprion abietis* [Harris], Hymenoptera: Diprionidae) outbreaks have recently increased in area and duration in thinned balsam fir (*Abies balsamea* [L.] Mill) forests (Moreau, 2006), even though thinning treatments often took place more than a decade earlier. We have previously shown that thinning alters the strength of bottom-up forces (i.e., effects of the plant resource) acting on *N. abietis* (Moreau et al., 2006a), which may explain, in part, changes in outbreak dynamics. Here, we test two hypotheses that could explain this result: (H<sub>1</sub>) Increased foliar quality and/or availability caused by thinning increases sawfly fitness. If after crown closure, thinning still promotes higher growth rates and reduces foliar defenses as in the initial years following thinning treatments (Bauce, 1996), then in the absence of previous defoliation by herbivores, (i) *N. abietis* fitness (i.e., survival rate × fecundity), foliage availability, as well as foliar contents of primary metabolites will be higher and (ii) foliar defenses will be lower in closed, previously thinned than in unthinned stands. (H<sub>2</sub>) Thinning moderates negative effects of previous defoliation on sawfly fitness. As discussed above, if previous defoliation by herbivores reduces foliar quality and/or availability for subsequent generations of *N. abietis*, and thinning dampens the negative effects of previous defoliation on sawfly development, then interactions will be detected between previous defoliation and thinning on sawfly fitness and on foliar chemistry. The two hypotheses are not mutually exclusive.

To test both hypotheses, we examined the independent and interacting effects of previous defoliation and thinning on *N. abietis* fitness and *A. balsamea* foliar availability and quality in a series of manipulative field experiments and a regional survey in western Newfoundland, Canada. Our first manipulative field experiment determined indicators of *N. abietis* fitness and evaluated the effects of previous branch-wide defoliation on *N. abietis* fitness in a single thinned stand located on the periphery of an ongoing *N. abietis* outbreak. Our second manipulative field experiment examined the effects of thinning on *N. abietis* fitness and *A. balsamea* foliar chemistry in undefoliated and naturally defoliated stands located within the outbreak area. Even though balsam fir branches exhibit a high level of autonomy (Sprugel et al., 1991), branch-wide defoliation can have a different effect on branch growth and foliar chemistry than tree-wide defoliation (Honkanen and Haukioja, 1994). Consequently, effects of treatments on branch growth and foliar chemistry were only studied with naturally defoliated trees. Results from manipulative field studies were then compared to population-level estimates of *N. abietis* survival.

## 2. Material and methods

### 2.1. *N. abietis* life cycle

In western Newfoundland, natural populations of *N. abietis* are univoltine. In late summer/early fall, females oviposit into

current-year and occasionally older foliage (Carroll, 1962). Mated females can produce offspring of both sexes through selective fertilization of eggs, whereas unmated females only produce male offspring. Eggs hatch in the spring, 2–4 weeks after budburst. Larvae preferentially feed on old needles of balsam fir (Moreau et al., 2003) throughout the crown (Anstey et al., 2002). Male larvae have five instars and complete development within 30 days, whereas females can have five or six instars and complete development in about 35 days (Carroll, 1962). Last instar larvae generally spin a cocoon directly on the foliage, pupate inside it, and emerge as adults 2–3 weeks later.

### 2.2. Manipulative field study on effects of experimental defoliation by *N. abietis*

In 2001, twenty dominant or co-dominant trees were selected in a thinned stand (49°5'35.3"N, 57°30'5.5"W) without any significant densities of defoliators or visible damage by herbivores. The stand was located on the northern edge of a current *N. abietis* outbreak (see Moreau (2006)) and was composed of naturally regenerated balsam fir (over 90% of the basal area) growing at a density of 2100 trees per hectare. The mean tree age ( $\pm$ SEM) was  $23 \pm 2$  years. The understory was composed mainly of *Dryopteris spinulosa* ([O.F. Muell] Watt), *Cornus canadensis* (L.) and *Clintonia borealis* ([Ait.] Raf). The moss layer was dominated by *Dicranum majus* (SM.), *Hylocomium splendens* ([Hedw.] Schimp. in B.S.G.) and *Pleurozium schreberi* ([Willd. ex Brid.] Mitt).

Two 8–10 year-old mid-crown branches were selected in the southwestern quadrant of each tree. Natural enemies were removed from selected branches according to methods described by Moreau et al. (2006a). For each of the 20 trees, one of the two branches, assigned at random by picking a number out of a hat, was experimentally defoliated by tying to the branch one to three short (<2 cm) sections of shoots, containing a total of 60 *N. abietis* larvae. This number of larvae per branch corresponds to the average number of larvae required to cause severe defoliation in mid-crown branches (Parsons et al., 2005). The methods used to collect shoots with newly-emerged, first-instar larvae are described in Moreau et al. (2006a). Shoots with larvae were not placed on branches assigned to the “undefoliated” treatment. To exclude other defoliators, predators and parasitoids and to prevent larval dispersal to other branches, sleeve cages (1 × 0.75 m) made of fine-mesh cloth were placed around all study branches. Sleeve cages enclosed twigs bearing all of the most recent 8 years of foliage. Visual inspections of the cages revealed that 75% of larvae had moved from cut shoots onto study branches after 24 h and that more than 95% had moved after 36 h. As soon as all larvae had spun a cocoon, cages were removed from branches and cocoons discarded.

The performance of *N. abietis* larvae on undefoliated and experimentally defoliated branches was evaluated in 2002. Before egg hatch in spring 2002, the ratio of the number of needle scars to the sum of needles and needle scars (hereafter referred to as the percentage of needles missing) for the first 8 classes of needle age was visually estimated using 10% classes for every shoot on undefoliated and experimentally defoliated branches according to methods described by Parsons et al. (2005). Undefoliated branches did not contain a full complement of foliage (i.e., 0% needle missing; Fig. 1a) before *N. abietis* feeding, due primarily to decreasing needle retention with needle age. Twenty first instar larvae were caged on each undefoliated and experimentally defoliated branch using the method described above. This number of larvae per branch corresponds to the average number of larvae per branch observed in the early and late phases of outbreaks (Moreau, 2004). Cages were removed when all larvae had spun cocoons. The percentage of needles missing was recorded using the method described above.

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