Indirect host-mediated effects of an exotic phloem-sap feeder on a native defoliator of balsam fir

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ARTICLE INFO

ABSTRACT

Since its introduction from Europe, balsam woolly adelgid [*Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae)], a phloem-sap feeder, has spread throughout the balsam fir [*Abies balsamea* L. (Mill.)] forests of eastern Canada. Trees under *A. piceae* attack develop "gout" and differ from unattacked trees in physiology, morphology, growth, and chemistry. The native and eruptive eastern spruce budworm [*Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae)] also attacks fir, causing severe defoliation during outbreaks. While balsam woolly adelgid and budworm feed at different times and on different host tissues, such spatiotemporally separated herbivores may still interact via host-mediated indirect effects. We examined the relationship between gout and the performance of developing budworm larvae in balsam fir dominated stands in western Newfoundland. We tested for adelgid–budworm interactions in unthinned and precommercially-thinned (∼20 years past) stands, because the host's growing condition can affect foliage composition and herbivore performance.

Budworm attained lower pupal weight when reared on trees with high levels of gout. In unthinned stands moderate gout reduced budworm survivorship, but there was no such effect in thinned stands. Gout did not affect budworm sex ratio. Although our data are consistent with interactions mediated by foliage quality (rather than quantity), and although budworm survivorship was associated with several aspects of foliage chemistry (Mg and N, positive; monoterpenes, negative), we were unable to identify specific host quality changes underlying the adelgid–budworm interaction. Our study demonstrates that *A. piceae* attack is an important factor influencing budworm performance, and it should be considered when analyzing budworm population dynamics and when developing management protocols for forests impacted by *A. piceae* attack.

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1. Introduction

Spatially or temporally separated herbivores exploiting shared hosts may interact indirectly when they alter the quantity or quality of available host tissues. Such interactions can be either facilitative or competitive (e.g., Denno et al., 1995; Karban and Baldwin, 1997; Heard and Buchanan, 1998; Ohgushi, 2005; Kaplan and Denno, 2007; Tabuchi et al., 2011), and the interacting herbivores can have more-than- or less-than-additive effects on their hosts (Morris et al., 2007). Host-plant mediated competition is likely when one herbivorous species reduces the performance of another by inducing changes in plant physiology, phenology, morphology, defensive chemistry, or nutritional value (Karban and Baldwin, 1997). Such indirect competition has been observed more frequently in systems that include introduced species than in all-native systems (Denno et al., 1995), perhaps because herbivore impacts are expected to be more severe in evolutionarily novel associations (Heard and Kitts, 2012). As introduced species become established and spread globally, host-plant mediated interactions between herbivores may become increasingly important in structuring communities (Masters and Brown, 1997) and in shaping best management practices. In a forestry context, examples may include interactions between hemlock woolly adelgid and elongate hemlock scale on hemlock (invasive/invasive; Preisser and Elkinton, 2008), between brown spruce longhorn beetle and spruce budworm on spruce (invasive/native; S.B. Heard et al., unpubl. data), and between balsam woolly adelgid and

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spruce budworm on balsam fir (invasive/native, and the topic of this paper).

In Atlantic Canada, most balsam fir [*Abies balsamea* L. (Mill.)] stands now show signs of feeding by the exotic balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), which was introduced to eastern North America approximately 100 years ago (Kotinsky, 1916; Quiring et al., 2008). While even large populations of *A. piceae* need not greatly impact their native host, European silver fir [*Abies alba* (Mill.)] (Balch, 1952; Ragenovich and Mitchell, 2006), North American *Abies* spp. show a hypersensitive reaction when fed upon by this adelgid. The reaction includes stunting of terminal shoot growth and abnormal swelling of buds and nodes (Balch, 1952), which have led to description of the condition as "gout". These visible effects are accompanied by exaggerated cell growth in the bark and cambium, inhibition of bud production, and reduced photosynthetic capacity (Balch, 1952). Thickening of cell walls and reductions in tracheid pit apertures disrupt water conduction to the crown of the tree (Balch, 1952; Ragenovich and Mitchell, 2006). Severe and continued gout can cause branch, crown and even tree mortality (Balch, 1952), but shorter-term effects are felt as well: *A. piceae* attack alters branch growth and chemistry of one-to-four-year-old balsam fir foliage (Grégoire et al., 2014). *A. piceae* may well have other impacts on its host trees, which would be correlated with the occurrence of gout, and therefore we emphasize that, in what follows, we use gout as a proxy for *A. piceae* attack history and impacts more broadly.

The current ubiquity of *A. piceae* in the fir stands of eastern Canada and its marked influence on the morphology and physiology of fir trees suggest that it could have important effects on the performance of other herbivores with which it shares hosts. Balsam fir is a primary host for many native herbivores, among which the eastern spruce budworm (*Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae); henceforth, just "budworm") is of particular importance to ecology, harvesting, and management of eastern Canadian forests. Budworm is an oligophagous, eruptive herbivore common in eastern North America (Blais, 1983; Royama, 1984). It causes widespread defoliation, tree mortality and economic losses during outbreaks (e.g., Hennigar et al., 2011; Zhao et al., 2014). Budworm larvae feed primarily on buds and current-year foliage of balsam fir and white spruce [*Picea glauca* (Moench.) Voss] but also cause measurable defoliation in red [*P. rubens* (Sarg.)] and black [*P. mariana* (Mill.)] spruce (Hennigar et al., 2008). In general, past studies of budworm dynamics (Morris, 1963; Royama, 1984; Gray, 2008), impact (MacLean and Ostaff, 1989; Piene, 1989; Nealis and Régnière, 2004; Campbell et al., 2008), and management (Crook et al., 1979; Bauce, 1996; Hennigar et al., 2011) have been carried out in apparently *A. piceae*-free stands. As a result, little is known of how *A. piceae* will interact with budworm and whether *A. piceae* could influence budworm outbreak dynamics.

Interplant competition can affect foliage quality, which can then influence herbivore performance (e.g., Awmack and Leather, 2002; Lamontagne et al., 2002; Kumbaşli et al., 2011). In managed forest landscapes, major reductions in competition between trees are achieved by the silvicultural practice of precommercial thinning (hereafter, just "thinning") to increase forest yield (e.g., Koga et al., 2002). Thinning of balsam fir [*Abies balsamae* (L.) Mill.] can either increase (Kumbaşli et al., 2011) or decrease (Bauce, 1996) the performance of insect defoliators. Whether thinning might also influence interactions between herbivore species attacking different tissues remains unknown; however, we previously demonstrated that both thinning and *A. piceae* gout affect bud and shoot growth in fir (Grégoire et al., 2014), and hence they may have interactive effects on budworm. We carried out field experiments to test the hypothesis that *A. piceae* gout would reduce budworm performance on fir, perhaps by reducing branch growth and altering foliage chemistry. We also tested the hypothesis that thinning would modify the adelgid–budworm interaction.

2. Materials and methods

2.1. Effects of gout, budworm density, and thinning on defoliation and budworm performance

We studied adelgid–budworm interactions in mature balsam fir stands in western Newfoundland, Canada. Stand and tree selection are described in detail in Grégoire et al. (2014). Briefly, stands were dominated by balsam fir and black spruce >40 years old, with scattered white birch (*Betula papyrifera* Marsh.) and a ground cover primarily of mosses. In 2008 and 2009, we selected four pairs of stands based on the presence of *A. piceae* populations and gout damage, and on the absence of significant herbivory by other insects. One stand of each pair had been thinned (in 1986–1989, ~20 years before our study); the other was unthinned. Thinned stands had 6000–8500 stems/ha and mean diameter at breast height of 9.6–12.2 cm, while unthinned stands had 10,500–43,000 stems/ha and mean dbh 5.8–8.3 cm. In each stand we chose five otherwise healthy dominant or co-dominant balsam fir trees in each of three gout level classes. "Low" gout trees had no visible trace of swollen nodes; "medium" gout trees had 20–40% of axial nodes and <10% of lateral nodes swollen; and "high" gout trees had >70% of axial nodes and >40% of lateral nodes swollen. We excluded any tree that showed symptoms of herbivory by insects other than *A. piceae*, or had produced cones in the previous or current year (because cone production can reduce resource allocation to foliage; e.g., Morris, 1951).

We chose five mid-crown branches on each tree and randomly assigned each to one of five target budworm densities: 0, 0.25, 0.50, 0.75, and 1 budworm larva per bud. These densities are commonly reached during outbreaks. The zero-budworm branches were used only to confirm that such branches did not suffer defoliation, and we do not discuss them further. We used budworm larvae obtained from the Insect Production Services of the Canadian Forest Service in Sault Ste. Marie, Ontario because we observed no wild larvae at our study sites. We transferred second-instar larvae onto current-year shoots of the study branches on 1 cm^2 pieces of cheesecloth, prior to budburst and approximately 24 h before larvae emerged from their hibernacula. We placed a 1 m^2 sleeve cage of fine mesh over each branch, as in Quiring and McKinnon (1999), to prevent larvae from dispersing and to protect them from natural enemies.

Once >80% of larvae had pupated (mid-July), we cut the branches and transported them, in their sleeve cages, to the laboratory. When pupae developed visible eyespots, we weighed, counted, and sexed them (Jennings and Houseweart, 1978). We estimated defoliation of current-year shoots for each branch using classes of 0%, 1–10%, 11–20%, 21–40%, 41–60%, 61–80%, 81–99%, and 100% defoliation (Parsons et al., 2005). Shoots ≥1 year old did not suffer significant defoliation.

We analyzed five dependent variables: defoliation, and four measures of budworm performance (larval survivorship, sex ratio, male pupal weight, and female pupal weight). We analyzed pupal weight separately by sex because budworm show strong sexual size dimorphism. Because we were not interested in possible variation among trees in susceptibility, we averaged each performance measure across the five replicate trees in each stand to improve fit to distributional assumptions. Because our design was complex, and because we were primarily interested in how defoliation and budworm performance responded to gout and budworm density, we conducted statistical analysis in two main steps.