



Original article

Interspecific variation in resistance of two host tree species to spruce budworm

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ABSTRACT

Woody plants regularly sustain biomass losses to herbivorous insects. Consequently, they have developed various resistance mechanisms to cope with insect attack. However, these mechanisms of defense and how they are affected by resource availability are not well understood. The present study aimed at evaluating and comparing the natural resistance (antibiosis and tolerance) of balsam fir (*Abies balsamea* [L.] Mill.) and white spruce (*Picea glauca* [Moench] Voss) to spruce budworm, *Choristoneura fumiferana* (Clem.), and how drainage site quality as a component of resource availability affects the expression of resistance over time (6 years). Our results showed that there are differences in natural resistance between the two tree species to spruce budworm, but it was not significantly affected by drainage quality. Balsam fir exhibited higher foliar toxic secondary compounds concentrations than white spruce in all drainage classes, resulting in lower male pupal mass, survival and longer male developmental time. This, however, did not prevent spruce budworm from consuming more foliage in balsam fir than in white spruce. This response suggests that either natural levels of measured secondary compounds do not provide sufficient toxicity to reduce defoliation, or spruce budworm has developed compensatory mechanisms, which allow it to utilize food resources more efficiently or minimize the toxic effects that are produced by its host's defensive compounds. Larvae exhibited lower pupal mass and higher mortality in rapidly drained and subhygric sites. Drainage class also affected the amount of foliage destroyed but its impact varied over the years and was probably influenced by climatic variables. These results demonstrate the complexity of predicting the effect of resource availability on tree defenses, especially when other confounding environmental factors can affect tree resource allocation and utilization.

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1. Introduction

Woody plants regularly sustain biomass losses to herbivorous insects (e.g. Schowalter and Lowman, 1999). Consequently, they have developed various resistance mechanisms that permit them to cope with insect feeding, and which confer upon them resistance to attack by these organisms (e.g. Mattson et al., 1988a). This resistance has two components, *i.e.*, defense and tolerance (Haukioja and Koricheva, 2000; Bauce et al., 2001). Defense refers to the negative effects that the plant can exert upon the insect, either

through deterrence using some defensive trait (antixenosis: toughness of plant structures, thorns, phenology) or adversely affecting insect performance (growth, fecundity or survival) with chemical compounds (antibiosis) that are consumed while the insect feeds upon the plant (Bauce et al., 2001; Larsson, 2002; Agrawal, 2011). Tolerance, in turn, refers to the capacity of the plant to endure insect damage without serious damage or a substantial decrease in plant fitness (Strauss and Agrawal, 1999; Haukioja and Koricheva, 2000; Bauce et al., 2001). This capacity should be central to woody plant resistance because trees are “apparent,” *i.e.*, easily found by herbivores, given their large size and long lifespan, and because their defense mechanisms cannot completely eliminate the damage that can be incurred by consumers (Feeny, 1976). Even though woody plant mechanisms of resistance to insect defoliators have been subjected to numerous and extended studies, the complexity of the interaction between

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woody plants and insect defoliators remains poorly understood since the characteristics of these kinds of plants (long lifespan, large size, architectural complexity, and frequent short period of leaf growth) preclude their extensive study under experimental laboratory conditions (Haukioja, 2005, 2006).

Resource availability, through its effects on antibiosis and plant tolerance, can determine the damage that herbivores potentially can inflict upon plant performance and, ultimately, plant fitness. Several hypotheses have been proposed to explain the effects of resource availability on plant defense. First, the resource availability hypothesis (RAH) suggests that plants growing on low-resource or stressful sites exhibit slower growth rates and, therefore, have higher levels of constitutive defense and lower levels of induced defense than plants growing on more productive sites because the cost of replacing lost tissue is higher under low resource conditions (Coley et al., 1985). Second, the carbon-nutrient balance hypothesis (CNB) predicts that plants growing on low-resource sites should produce more carbon-based defenses than plants growing on high-resource sites. Nutrient deficiency elevates the carbon-nutrient ratio, thereby increasing the amount of carbon that is available for synthesizing carbon-based defenses (Bryant et al., 1983). Third, the growth-differentiation balance hypothesis (GDB) postulates that growth of plants on low-resource sites is limited by nutrient deficiency; therefore, photosynthates that otherwise would be exported to sink tissues are used in differentiation processes, such as the production of secondary compounds (Herms and Mattson, 1992). It is further assumed that plants growing in high-resource sites show higher tolerance to herbivory than those growing in less productive sites (Bryant et al., 1983; Coley et al., 1985; Hawkes and Sullivan, 2001). Nevertheless, previous studies have reported contradictory results (Hawkes and Sullivan, 2001). According to Wise and Abrahamson (2007), these contradictory results can be explained by the fact that labeling the environment as low-resource or high-resource does disentangle the complex and interactive effects of different resources (light, water, nutrients) on plant tolerance, leading to confusing or misleading interpretations.

Spruce budworm (*Choristoneura fumiferana* [Clem.]) is one of the most destructive pest insects in North America (Mattson et al., 1988b). During its last outbreak in eastern Canada, the budworm accounted for losses to the forest products industry of 44 million m³ of wood per year (Sterner and Davidson, 1982). Budworm hosts include balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), red spruce (*P. rubens* Sarg.), and black spruce (*P. mariana* [Mill.] BSP). A clear hierarchy of host species susceptibilities exists, with balsam fir being the most susceptible, followed by white spruce, red spruce, and black spruce as the least susceptible (Henningar et al., 2008). Differences in susceptibility may be due to the more rapid shoot growth, greater development, and greater foliage per unit area exhibited by white spruce compared to balsam fir, resulting in reduced defoliation of the former (Greenbank, 1963). Nevertheless, previous work has proposed that differences in host nutritional quality, the quantity of secondary compounds (antibiosis) (Greenbank, 1963; Thomas, 1989; Delvas et al., 2011; Fuentealba and Bauce, 2012c) and tolerance (Fuentealba and Bauce, 2012b; Bauce and Fuentealba, 2013) may also play an important role in plant resistance in the spruce budworm-host tree system.

A greater understanding of the mechanism of resistance of host trees to insects and the effect of resource availability on these mechanisms would allow us to improve our knowledge about plant-insect relationships and the effect that these have upon the population dynamics of key insect pests, which in turn will help us to develop better control methods for reducing the damage to the forest industry that is caused by insects (Hanover, 1975). The present study aimed at evaluating and comparing the natural

resistance (antibiosis and tolerance) of the two main host tree species of spruce budworm, viz., balsam fir and white spruce, and how site drainage qualities as a component of resource availability can affect the expression of resistance in these conifers. Given that induced defense in the aforementioned hosts does not seem to play an important role in resistance against spruce budworm (Mattson et al., 1991), we focused on constitutive defenses. Balsam fir (Hix et al., 1987) and white spruce (Wang and Klinka, 1995) are best adapted to growing in well-drained sites, which provide adequate nutrients and moisture that support vigorous tree growth. This enhances the ability of these species to withstand and recover from defoliation (Bélanger et al., 1995). The first objective of this study was to evaluate drainage site quality effects on the expression of resistance of host trees to spruce budworm attack. To facilitate this assessment, we evaluated balsam fir and white spruce tolerance and antibiosis along a gradient of drainage quality and the effect that these mechanisms of resistance exert on spruce budworm performance. The information obtained from this study will allow us to better understand interspecific variation in resistance among the host tree species studied and how their resistance is affected by drainage quality as a component of resource availability. This knowledge in turn may help to develop specific silvicultural treatments adapted to better protect these host tree species according to their level of resistance to spruce budworm.

2. Methods

2.1. Natural history

Balsam fir extends from Newfoundland to Alberta (Frank, 1990). Being a shade tolerant species, balsam fir regenerates best under tree cover but it can occasionally establish at the beginning of a succession (Dix and Swan, 1971). Although balsam fir has the ability to establish on a wide variety of substrates because it can rapidly develop its root system and its taproot is deep, allowing this species to reach moister soil strata (Bakuzis and Hansen, 1965), it is better adapted to grow on well-drained sites (Hix et al., 1987). Furthermore, its large seeds limit its dispersal capacity; therefore, individuals tend to establish at relatively short distances from parent trees (Galipeau et al., 1997). White spruce occurs across Canada, from Newfoundland to Northwest Territories (Nienstaedt and Zasada, 1990). It can grow on diverse sites but it exhibits its best growth on well-drained sites (Wang and Klinka, 1995). Furthermore, its seedlings are more susceptible to desiccation and to herbaceous competition than balsam fir seedlings which may complicate white spruce establishment and increase seedling mortality (Bakuzis and Hansen, 1965; Nienstaedt and Zasada, 1990). Given the size of its seeds (4 times smaller than that of balsam fir), white spruce is able to colonize distant sites, enabling it to have great establishment density at the beginning of the succession (Galipeau et al., 1997).

These two conifers can be attacked by several types of insects during their lifetime (Frank, 1990; Nienstaedt and Zasada, 1990; Alfaro and Fuentealba, 2015) but none of them can inflict more damage than spruce budworm. The current outbreaks of this insect damaged more than 6 million hectares in the province of Quebec in 2015 (MFFP, 2015). Differences in tree resistance to spruce budworm attack has been historically attributed to differences in budbreak development (Greenbank, 1963) (see introduction). However, more recent studies have found that secondary compounds such as monoterpenes, tannins and phenols can negatively affect spruce budworm performance and, therefore, be implicated in tree resistance. For example, some monoterpenes can negatively affect spruce budworm survival, food ingestion, developmental time, and pupal mass (Mattson et al. 1991; Bauce et al. 1994; Bauce,

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