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Plant module size influences the intra-tree distribution and abundance of a shoot-boring sawfly in young balsam fir

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Abstract

Field surveys were carried out to assess the effects of intra-tree variation in developing shoot length within and among crown levels on the density and abundance of the balsam shoot-boring sawfly, *Pleroneura brunneicornis* Rohwer (Hymenoptera: Xyelidae), in young balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae). Overall, cardinal direction had no influence on shoot-borer density or abundance; however, the highest percentage and abundance of bored shoots occurred on intermediate-sized shoots within the crown (i.e., in the mid-crown and on the distal-lateral and medial-lateral shoots). Comparatively, few shoot borers occurred in the upper or lower crown levels, or on the relatively large terminal shoots within branches. This distribution appears indicative of the higher suitability of intermediate-sized shoots within hosts for either egg lay or larval performance. Results of this study are most consistent with predictions of the 'optimal module size' hypothesis, which posits that herbivore responses to plant module size should reflect the balance of tradeoffs between utilizing relatively large, nutritious shoots vs. small, more easily exploited shoots.

Introduction

Herbivorous insects often vary where they forage within trees in response to heterogeneity in the suitability of resources for egg lay or feeding. Several hypotheses attribute resulting trends in herbivore distribution to intra-plant variations in shoot growth rate or module size, particularly for herbivores whose progeny are constrained to feed within host tissues (e.g., gallers and miners). The 'plant vigor' hypothesis (PVH), for instance, predicts that herbivores should prefer and perform better on relatively large plant modules (e.g., shoots), which tend to possess relatively high concentrations of nutrients and water (Price, 1991, 2003). However, recent studies suggest that some herbivores struggle to exploit the largest, most vigorously growing modules, despite their superior nutritional quality (Flaherty & Quiring, 2008). Such herbivores may instead favor intermediate-sized shoots, balancing tradeoffs between utilizing relatively large, nutritious shoots vs. small, more easily exploited shoots (i.e., the 'optimal module size' hypothesis, OMSH) (Quiring et al., 2006; Flaherty & Quiring, 2008).

Although the PVH and OMSH have been tested extensively using insects that induce galls (i.e., abnormal growths in the plant tissue that serve as a chamber for juvenile feeding) (Price, 2003; Quiring et al., 2006), less work has been carried out for other insect guilds that feed within plant tissues (e.g., leaf miners and shoot borers). In this study, we investigated for the balsam shoot-boring sawfly, *Pleroneura brunneicornis* Rohwer (Hymenoptera: Xyelidae), how variation in shoot length within crowns of young, intensively managed balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae), influences shoot-borer distribution and abundance. Although there have been few ecological studies of this relatively obscure sawfly family, the life history and basic biology have been described in detail (Webb & Forbes, 1951; Carleton et al., 2014). This shoot

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borer is mainly an esthetic pest of young fir trees being cultivated for Christmas tree or wreath operations, with a limited impact on tree growth or survival. Adults emerge in the early spring and spend a few weeks laying eggs through the bud cap of tight, unburst buds (Carleton et al., 2014). Within a week or two, newly hatched larvae burrow through the new needles to the shoot apical meristem and proceed to eat a tunnel through the shoot toward its base (Webb & Forbes, 1951). Around mid to late July, the larvae cease feeding, burrow out of the shoot, and drop to the ground where they overwinter as pre-pupae in the soil (Carleton et al., 2014). Although this shoot borer is considered univoltine, studies of close relatives suggest that overwintering pre-pupae may remain in prolonged diapause for up to 2 years (Ohmart & Dahlsten, 1979; Yates & Smith, 2009).

Based on the characteristic hierarchy of shoot growth in balsam fir—with the largest shoots occurring at the branch tips [i.e., terminal (T) shoots; Figure 1] and in the upper crown—the PVH would predict higher densities of shoot borer at the branch tips and upper crown of trees. A strong bias toward south-facing branches might also indicate a bias toward larger shoots, as shoots on the relatively exposed south-facing branches tend to grow more vigorously (Stokes et al., 1995). Alternatively, the OMSH predicts a bias toward intermediate-sized shoot types within branches [i.e., distal-lateral (DL) and medial-lateral (ML) developing shoots; Figure 1] and toward the mid-crown of trees. To test these predictions, we carried out a field study to investigate the effects of crown level, cardinal direction, and shoot type on the distribution of immature shoot borer within crowns of young balsam fir.

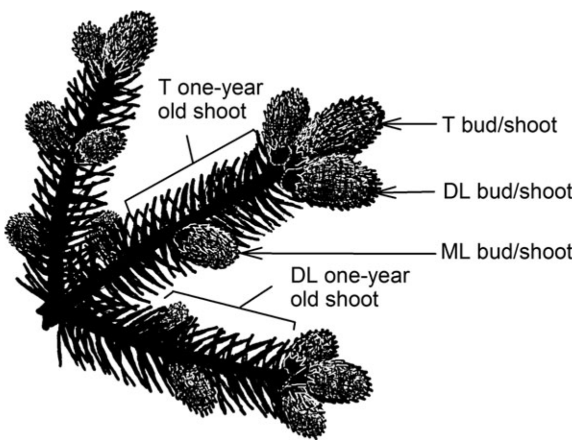

Figure 1 Schematic representation of a balsam fir branch with terminal (T), distal-lateral (DL), and medial-lateral (ML) developing shoots on the terminal and distal-lateral 1-year-old shoots at the branch tip.

Material and methods

Site characteristics

Field surveys were carried out in each of three stands of young, managed balsam fir in three locations, Upper Gaspereau (N46 15.957, W65 51.007), Keswick Ridge (N45 59.456, W66.53.192), and McGivney (N46 20.419, W66 33.794). Shoot-borer population densities in each of these three sites were, respectively, relatively high (4.37 ± 0.36 individuals per developing shoot), moderate (3.51 ± 0.38), and low (1.09 ± 0.21) (Carleton et al., 2014). In past years, these stands had been groomed as potential Christmas tree plantations; however, no trees had been pruned for at least 3–5 years prior to our study and our study trees had since regained relatively normal crown structure with clear dominance of apical shoots. In general, trees were 1–4 m high and were spaced a minimum of 2–3 m apart.

Field sampling

In 2013, from 15 to 23 July, we selected 15 trees in each site, haphazardly selecting trees that had some signs of previous sawfly damage. Within each tree, we collected a full, dominant branch from each of four cardinal directions (north, east, south, west), in the upper, mid, and lower crown (in total 12 branches per tree) and transported them on ice back to the laboratory for processing. At the time of branch collection, there was visible evidence of shoot-borer damage throughout the crown and larvae were approximately mid-instar (Carleton et al., 2014). On each branch, we counted the shoots attacked by shoot borer and identified their position as either terminal (T), distal-lateral (DL), or medial-lateral (ML) (Figure 1). After all attacked shoots were assessed, we then counted the remaining shoots on the branch. To determine what the potential length of shoots would have been in the absence of shoot-borer attack, on 20 August 2013 (after all developing shoots had ceased elongating), we returned to our study trees and collected two branches in each of three crown levels with no evidence of previous attack. Only a subset of trees in each site could be assessed for shoot length. On these branches, we measured the length of a T, DL, and ML shoot on both the T and one DL shoot of the previous year (Figure 1).

Statistical analysis

Due to low occurrence of shoot-borer damage in site 3 (i.e., 1.09 ± 0.21 shoot borers per branch), it was dropped from analyses. We wanted to model two dependent variables (% shoots damaged and shoot length) and three main effects of interest (fixed effects of cardinal direction, crown level, and shoot type); also included in the model were the random effects of site and tree. We proceeded with separate analyses of variance for each dependent variable. Initial analyses on % bored shoots per branch (independent of shoot type) showed no significant effect of cardinal direction on shoot-borer density (G = 6.10, d.f. = 3, P = 0.11) and there was no significant crown level*direction interaction (G = 12.20, d.f. = 6, P = 0.06), and thus cardinal direction was dropped from subsequent analyses. Effect of cardinal direction on shoot length could not be assessed as shoot length was only measured on one branch per crown.

To determine the effects of crown level and shoot type (i.e., T, DL, and ML) on shoot-borer damage, we modeled the proportion of damaged shoots using a quasibinomial GLMM with logit link with site and tree included as random effects. To reduce problems with zero over-inflation, data from the various shoot types were summed across branches within each crown level (from the four cardinal directions), which increased the number of bored shoots in each category. The effect of crown level and shoot type on shoot length was determined using a linear mixed model (LMM), with site and tree as random effects.

Significance of fixed effects in GLMMs was determined using likelihood ratio (LR) tests. GLMMs were fit using the 'glmmPQL' function from the 'MASS' library (Venables & Ripley, 2002) in R version 3.0.3 (R Development Core Team, 2014). Models using LMM were run using the 'lmer' function from the 'lme4' library (Bates et al., 2014).

Results

For each dependent variable we detected a significant effect of crown level and shoot type (Table 1). The crown level* shoot type interaction had a marginally non-significant effect on % of shoots bored and was dropped from the model to test the main effects using LR tests. The interaction, thought marginally non-significant, is largely due to fewer ML shoots being attacked in the lower crown.

Table 1 Summary of analyses examining the effects of crown level (upper, mid, lower) and shoot type (terminal, distal-lateral, medial-lateral) on the percentage of shoots bored and shoot length in two young stands of balsam fir in 2012

Dependent variable	Fixed effects	Test statistic	P
% shoots bored	Crown level	G = 16.4 (d.f. = 2)	<0.001
	Shoot type	G = 14.4 (d.f. = 2)	<0.001
	Interaction	G = 9.2 (d.f. = 4)	0.056
Shoot length	Crown level	$F_{2,120}$ = 47.1	<0.001
	Shoot type	$F_{2,120}$ = 65.9	<0.001
	Interaction	$F_{4,120}$ = 6.0	<0.002

In both sites, the highest mean % of bored shoots within trees occurred in the mid or lower crown (Figure 2A and B). Within all crown levels, but particularly in the upper crown, most of the bored shoots were either DL or ML, and comparatively few bored shoots were found at the tips of branches (i.e., on T shoots) (Figure 2A and B). Mean shoot length in both sites, in contrast, decreased from the upper to lower crown and from the T to ML shoots within each crown level (Figure 2C and D).

Discussion

Our study indicates that the balsam shoot-boring sawfly is highly responsive to variation in shoot length within its host. In general, the highest shoot-borer densities occurred in the mid or lower crown, and tended to favor the moderately sized DL or ML shoots. Relatively few bored shoots occurred in the upper crown or on T shoots, as would be predicted by the PVH. Overall, the apparent tendency of this shoot borer to favor intermediate-sized shoots, both within and among crown levels, is most consistent with predictions of the OMSH.

The OMSH has been traditionally used to explain distributional patterns of galling insects, including several galling adelgids (Quiring et al., 2006; Flaherty & Quiring, 2008). For gallers, it has been argued that selection of intermediate-sized shoots reflects tradeoffs between the nutritional benefits of feeding vs. the challenges of overtaking the apical meristem to induce a gall on relatively large modules (Quiring et al., 2006; Flaherty & Quiring, 2008). Gall induction is clearly not required for shoot-boring sawfly success; however, there may be other factors that diminish the suitability of relatively large shoots, such as higher concentrations of harmful allelochemicals or a more vigorous resin response to damage (Kapler & Benjamin, 1960). Alternatively, natural enemies could also influence shoot selection, although past studies examining this hypothesis for gallers have often failed to find a connection (e.g., Santos et al., 2008). At present, it remains uncertain what the specific mechanisms are causing this shoot borer to favor intermediate-sized shoots over relatively large or small shoots.

Although our study did not include foliar chemical analyses, several past studies have shown significant variation in insect performance and/or shoot nutritional chemistry among both crown levels and shoot types within young conifers. Johns et al. (2010), for instance, found that higher larval survival of a free-feeding sawfly in the upper vs. lower crown of young black spruce, *Picea mariana* (Mill.) BSP, was correlated with 21% lower

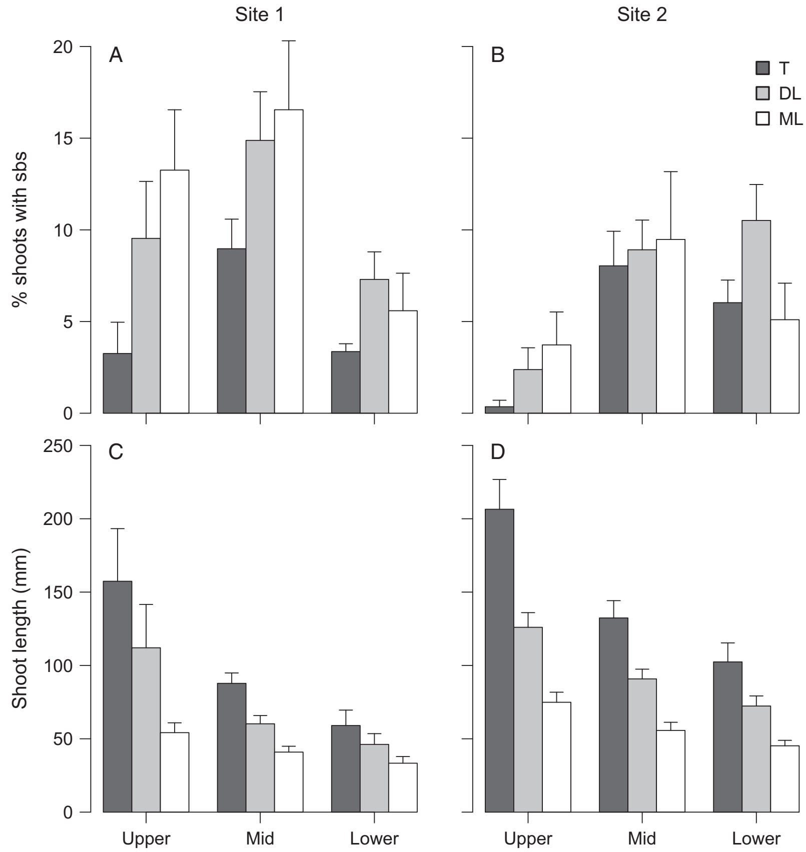

Figure 2 Mean (+ SE) (A, B) percentage of developing shoots damaged by shoot-boring sawfly (sbs), and (C, D) shoot length on terminal (T), distal-lateral (DL), and medial-lateral (ML) shoots in the upper, mid, and lower crown of young balsam fir in two sites.

monoterpene content in the upper crown, despite only a 10-mm difference in average length between the two crown levels. Similarly, larval spruce budmoth (*Zeiraphera canadensis* Mutuura & Freeman) accrue significantly higher survival, wing length, and developmental rates when allowed to develop in the upper vs. lower crown and on T/DL vs. ML shoots in young white spruce, *Picea glauca* (Moench) Voss (Carroll & Quiring, 1994). Although these two examples involve free-feeding larvae, several studies of galling adelgids report similar preference and performance responses to relatively fine-scale variations in shoot length (McKinnon et al., 1999; Flaherty & Quiring, 2008). These studies reinforce results of our present study suggesting that even relatively small intra-tree variations in shoot length may exert strong selective pressure on herbivore foraging behaviors.

It is important to note that our study does not allow us to identify whether the trends observed reflect adult egg lay preference or progeny survival. In our study, adult females may have been very selective of where they laid eggs, selecting intermediate-sized shoots, perhaps due to leverage constraints on oviposition (cf. Floate & DeClerck-Floate, 1993) or to confer performance benefits to progeny (Johns et al., 2009, 2010). Alternatively, the adult shoot borers could have laid eggs indiscriminately, with progeny laid on intermediate-sized shoots simply surviving better than those laid on relatively small or large shoots. Regardless of the mechanism, the tendency of most shoot borers to occur most frequently on intermediate-sized shoots seems indicative of some adaptive benefits.

Results of our study also have implications for developing a relatively precise sample unit for estimating population density. Sampling any particular cardinal direction for this shoot borer does not appear to be important; however, sampling in the mid-crown is likely to provide the most stable estimates of shoot-borer damage. Based on this sample unit, it should be possible to develop more sophisticated sampling regimes to monitor shoot borers as part of an integrated pest management program (Carleton et al., 2013) and to study its population ecology (Ostaff & Quiring, 2000; Johns et al., 2006, 2009).

Support for the PVH has been particularly strong among galling tenthredinid sawflies feeding in deciduous trees such as willow; indeed, the preference of tenthredinids for large plant modules is striking at nearly 86% (Price, 2003). However, a review of non-tenthredinid gallers from a broad range of insect taxa indicates a bias toward intermediate or small shoots in nearly half of the species studied, as predicted by the OMSH (Quiring et al., 2006). The shoot-boring sawfly most resembles this latter group in its intra-tree distribution, due perhaps to analogous challenges associated with exploiting relatively large or small shoots. Further study will be needed to determine whether such constraints promote similar trends in other species of shoot-boring sawflies or in shoot borers from other insect taxa.

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