SCIENTIFIC NOTE

Production of epicormic buds by Douglas-fir in central British Columbia, Canada, following defoliation by western spruce budworm (Lepidoptera: Tortricidae)

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Western spruce budworm, *Choristoneura freemani* Razowski (= *C. occidentalis* Freeman), is an important defoliator of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in southern British Columbia (Maclauchlan *et al.* 2006). Defoliation by larvae can result in reduced tree growth, top-kill and occasional tree mortality (Alfaro *et al.* 1982). Larvae feed on the new foliage of all ages of trees; mortality is most common in immature and suppressed understorey trees (Maclauchlan and Brooks 2009), but repeated, severe defoliation can kill larger trees.

Flushing of buds late in the season is a proposed mechanism by which conifers can compensate for defoliation (Piene 1989), and increased late bud production may explain why some species or individuals experience greater survival and faster recovery following defoliation (Piene and Eveleigh 1996). The terminology used in the literature for these late-flushing buds varies, but Meier *et al.* (2012) recommend calling them epicormic buds, while sequential buds are those formed during shoot elongation.

The most recent western spruce budworm outbreak in British Columbia extended farther north than had been observed previously. Near the northern edge of that outbreak, my observations suggested that defoliated Douglas-fir had fewer flushed epicormic buds at the end of the summer than might have been expected farther south. At higher latitudes, a short growing season and early frosts may reduce the ability of trees to compensate for defoliation by producing epicormic buds.

In 2010, two-year-old *P. menziesii* var. *glauca* seedlings were obtained from Pacific Regeneration Technologies, Inc. in Red Rock, B.C. Seedlings were planted individually in conical pots of all-purpose potting mix on May 17, when the earliest sequential buds on local Douglas-fir trees began to swell. Third- to fifth-instar western spruce budworm larvae were collected from two sites north of Williams Lake, B.C. (52.266° N, 122.285° W and 52.471° N, 122.434° W) on June 16. Larvae were kept on live foliage in large plastic bags and transported to the University of Northern B.C. (UNBC) in Prince George, B.C. (53.893° N, 122.816° W), then transferred to the experimental seedlings within 48 hr. Each seedling had 18–22 sequential buds at approximately the same stage of development as those of Douglas-fir on campus.

Five treatments (n = 24 each) were applied on the same day as follows.

1. Control: No further manipulation of seedlings.
2. Control+mesh: A white, polyester-netting (BioQuip Products Inc.) cylinder was secured with elastic bands over each seedling.
3. Scissors: All sequential buds were removed at the base with fine scissors.
4. Scissors+mesh: Sequential buds were removed with scissors, and a netting cylinder was secured over each seedling.
5. Larvae+mesh. A netting cylinder was secured over each seedling, and 10 larvae were added. The larvae on each seedling ranged from approximately third to fifth instar, representing the range and distribution of larvae collected at field sites.

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A sixth treatment, larvae on seedlings without mesh, was not possible due to the risks of releasing insects in an area where they are not currently found. Seedlings were randomized within racks and placed outside in the compound of the Enhanced Forestry Laboratory at UNBC. They were watered daily, and pupae were removed twice weekly.

Once all larvae had pupated or died, the mesh bags were removed, and flushing epicormic buds were counted for each seedling. Due to heteroscedasticity and small sample size, treatments were compared using a Kruskal–Wallis rank sum test and a Nemenyi *post hoc* test with chi-squared approximation for independent samples (PMCMR v4.1 package; Pohlert 2014) within the R 3.4.0 statistical programming language (R Development Core Team 2016).

Control seedlings, both with and without mesh bags, flushed no epicormic buds (Fig. 1). Destruction of sequential buds, by either scissors ($P < 0.001$ in all cases) or western spruce budworm larvae ($P = 0.029$), significantly increased numbers of epicormic buds over the control seedlings (Fig. 1). Seedlings defoliated by larvae had significantly fewer epicormic buds than those defoliated with scissors ($P = 0.034$ for scissors, and $P = 0.026$ for scissors+mesh). In most cases, epicormic buds on seedlings with larvae showed feeding damage.

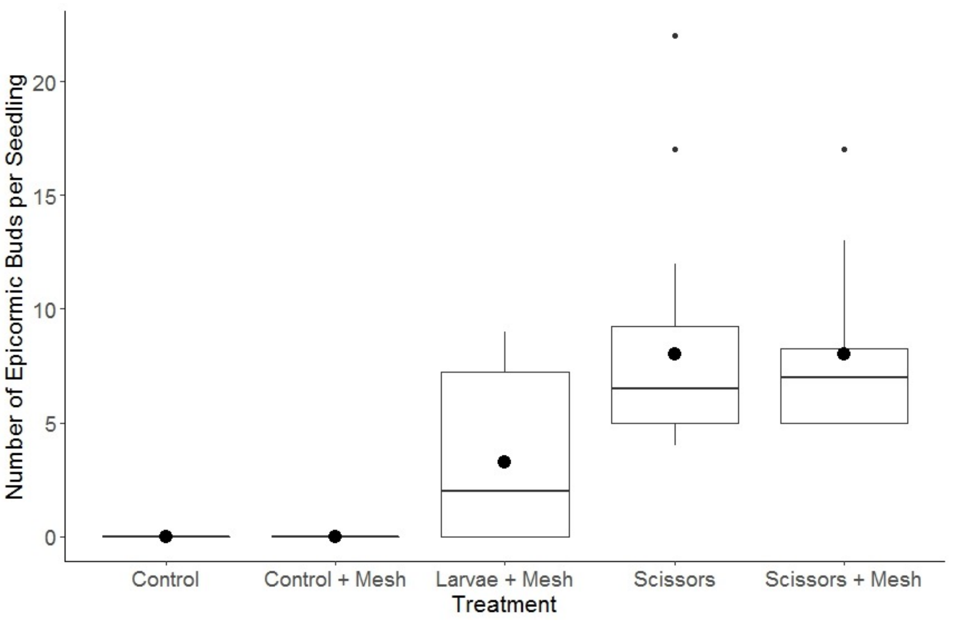

Figure 1. Numbers of epicormic buds per two-year-old Douglas-fir seedling. Control seedlings were not defoliated; other treatments had expanding spring buds removed with scissors or by feeding of third- to fifth-instar western spruce budworm larvae. Treatments including "Mesh" had seedlings contained in white, polyester-netting cylinders. Boxplots portray the median (midbar in the box), the 25th and 75th percentiles (box), lowest and highest points within 1.5x the inter-quartile range (lower and upper vertical lines), and outliers (small circles). Large circles show the mean values.

Seedlings defoliated by any means responded with production of new foliage late in the summer. Seedlings with larvae caged on them had significantly fewer flushing epicormic buds than did seedlings that had been defoliated with scissors. Defoliation by insects can have different impacts than defoliation using scissors (Piene and Little 1990); however, in the current experiment, the apparent reduction in epicormic buds in the budworm-defoliated seedlings may have been due to the continued feeding activity of the larvae. It was not possible to distinguish between sequential and epicormic buds once they had been eaten, as individual buds were not tracked in detail in this experiment.

The larval collection sites north of Williams Lake, B.C., experienced 1,539–1,688 mean annual growing degree days, and 174–180 mean frost-free days from 1961–1990 (http://www.climatewna.com/ accessed 2017). Sites near Monte Creek, B.C., where outbreaks have occurred more commonly, have experienced 1,910 mean annual growing degree days and 207 mean frost-free days from 1961–1990 (http://www.climatewna.com/ accessed 2017). Both the number of growing degree days and the number of frost-free days can vary substantially with location and year; in general, a shorter growing season can be expected in the north and at higher elevations, with a greater risk of early fall frosts, than in the south at lower elevations.

These results suggest that northern trees may experience greater growth losses and potentially higher mortality during western spruce budworm outbreaks than might be anticipated further south. Synchrony between larvae and their host trees is a key component of the population dynamics of this insect; both the beginning and end of the phenological window are important to survival and fecundity (Nealis 2012). The availability of high nutritional–quality buds during later instars could improve the survival and fecundity of larvae at the end of the phenological window (Régnière and Nealis 2016). Depending on location and local weather conditions, however, the short growing season in the north could also result in higher insect mortality in some years.

Further work is needed to investigate the interaction between western spruce budworm larvae and epicormic buds at northern latitudes and at higher elevations. Experiments that track individual buds, compare the effects of natural larval feeding to bud removal later in the season, and examine the impacts on mature trees would all improve understanding of defoliator impacts on northern stands. If field populations of mature trees carry less new foliage late in the summer in the north than they do in the south, the impact of a western spruce budworm outbreak could be more severe in the northern part of the insect's range.

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