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Change in the periodicity of a cyclical forest defoliator: An indicator of ecosystem alteration in Western Canada

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ABSTRACT

The western spruce budworm (*Choristoneura occidentalis* Freeman = *C. freemani* (Razowski), Lepidoptera: Tortricidae) (WSB) is a recurrent defoliator of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and other conifers in western North America. Repeated defoliation causes timber depletions, which often require control using pest management programs involving combinations of aerial sprays with biological controllers (*Bacillus thuringiensis*) and other tactics. Anticipating the recurrence cycle of this periodic defoliator is important for forest management planning, which needs to consider budworm-caused depletions in timber supply analyses, and for risk management and control. We studied the historical periodicity of outbreaks at the western edge of the insect's distribution, on southern Vancouver Island, British Columbia, using the methods of dendrochronology applied to a living Douglas-fir chronology spanning 734 years (1281–2014 CE) and a floating chronology dating from 1863 to 1528 before the Common Era (BCE). To separate the growth fluctuations due to budworm defoliation from climatic fluctuations in the living chronology, we compared the temporal growth patterns of Douglas-fir with those of the non-budworm host western red cedar (*Thuja plicata* Donn ex D. Don), which is sympatric with Douglas-fir in this area. We concluded that before the 1930s, outbreaks were frequent, severe, and often spatially synchronized. Following the 1930s, periods of growth reductions indicative of outbreaks were present at the same frequency, but were less severe and not as synchronized as before. We provide evidence to suggest that periodic budworm disturbances on southern Vancouver Island have persisted through the centuries but that this regime has gradually shifted outside its historic range at about 1930. We concluded that although WSB is still present in this setting, population levels have not reached detectable outbreak levels for the last 90 years. We hypothesized that the absence of budworm outbreaks in the last 90 years is a response to the drastic ecosystem changes in this region caused by exploitation and fragmentation of the virgin forests, to possible changes in climate and to the accidental introduction of novel budworm predators into the ecosystem.

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) occurs widely in southern British Columbia (BC) and is one of the world's most important and valuable timber trees. The coastal variety (*P. menziesii* var *menziesii*) ranges from west-central BC southward, along the coast, to central California, growing either in extensive pure stands or, at the edge of its western range, mixed with Sitka spruce *(Picea sitchensis* (Bong) Carr*)*, western hemlock *(Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn ex D. Don). Coastal Douglas-fir is a fast-growing tree, commonly reaching diameters of over 180 cm and ages of over 500 years in old growth forests (Hermann and Lavender, 1990). Starting in the mid-1800s, ecosystems containing coastal Douglas-fir forests on southern Vancouver Island (British Columbia Ministry of Environment, Lands and Parks, 1999) were extensively modified, first by high-grading (removal of the largest trees in a stand) and later by clearcutting (BC Ministry of Environment, Lands and Parks, 1999). Today these once great forests are highly fragmented due to harvesting and urbanization.

Outbreaks of native insects are natural recurring disturbance processes, which are integral to ecosystem functioning, causing shifts in species composition, creating coarse wood debris and providing snags that serve as habitat for wild life, among other functions (Axelson et al., 2018). Insect outbreaks, defined as sudden increases in population above equilibrium levels, pose major problems when their severity threatens forest productivity and other forest values, such as recreation and carbon sequestration. The western spruce budworm (WSB, *Choristoneura occidentalis* Freeman = *C. freemani* Razowski (Razowski,

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2008) (Lepidoptera: Tortricidae), a native insect, is an important disturbance agent of conifers, reaching periodic outbreak levels in western North America. The caterpillars of this species eat the new foliage of host trees, causing tree growth loss, lumber defects and, after several years of severe defoliation, tree mortality (Furniss and Carolyn, 1977; Alfaro et al., 1982; Alfaro and Maclauchlan, 1992). WSB populations reach outbreak levels over large geographic areas, with isolated populations often displaying strong periodicity and temporal synchrony (Alfaro et al., 2014; Flower et al., 2014; Axelson et al., 2015).

Douglas-fir is the principal tree species defoliated by WSB in BC, but other tree species are also susceptible, including Engelmann spruce, *Picea engelmannii* Parry ex Engelm., and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt (Furniss and Carolyn, 1977). WSB outbreaks affect BC's economy. Between 1990 and 2011 the defoliated area in BC exceeded 800,000 ha (ha) annually (National Forestry Database, http://nfdp.ccfm.org/data/compendium/html/comp_41e.html), although since 2011 the total outbreak area in the province has declined. During outbreaks the expected damage through growth loss and mortality is high enough to justify the need for annual spray operations aimed at protecting the industry's timber supply in selected areas (Maclauchlan and Buxton, 2012). Outbreak events may last only one or two years, or they can persist for more than ten years (Maclauchlan et al., 2006). Recent studies in central BC show that WSB outbreaks re-occurred numerous times over the past several centuries, with a mean return interval of about 28 years (Alfaro et al., 2014; Axelson et al., 2015). Consequently, WSB outbreaks are described as pseudo-periodic, that is, they are cyclical, but with variable periodicity (Swetnam and Lynch, 1993). The intensity, geographic extent and periodicity of outbreaks are thought to be mainly influenced by climate, budworm predator fluctuations and changes in host distribution due to forest fires and anthropogenic disturbances (Nealis, 2016; Harvey et al., 2018).

Tree growth varies annually depending on climatic events and forest disturbances, such as insect defoliation. This variation is recorded in tree ring-width series as sequences of narrow or wide rings. Different types of forest disturbances cause recognizable patterns in the ring-width series, which can be analyzed using dendrochronological methods, to reconstruct the disturbance history of a locality Dendrochronology has been used to study outbreak population recurrence of many insects (Speer 2010), including WSB in central BC (Campbell et al., 2006; Alfaro et al., 2014; Axelson et al., 2015; Harvey et al., 2018) and in the western United States (Swetnam and Lynch, 1993; Ryerson et al., 2003; Flower et al., 2014).

The tree-ring signal that indicates past WSB disturbance was described in detail by Swetnam and Lynch (1989; 1993) for the western United States and by Alfaro et al. (1982) for the dry interior of BC. Typically, rings in affected trees narrow progressively with every additional year of defoliation, until they reach a minimum increment that depends on defoliation intensity and the number of years a tree has been defoliated (Alfaro et al., 1982; Axelson et al., 2015). Once an outbreak ends and defoliation ceases, the ring-widths in the surviving trees progressively increase over several years, eventually reaching pre-outbreak increments or even larger. Increased growth following outbreaks likely occurs in response to stand thinning due to tree mortality (Alfaro et al., 1982). The cause-effect relationship between defoliation and ring-width reductions usually lags one or more years (Alfaro et al., 1982, Mason et al., 1997).

Severe outbreaks of western spruce budworm on southern Vancouver Island were first noted between 1909 and 1911 (Harris et al., 1985) (referred to in this paper as the 1910s outbreak) (Hewitt, 1911a; Hewitt 1911b; Wilson, 1911). A second outbreak was reported from 1925 to 1930 (1930s outbreak) (Mathers, 1931) (Fig. 1). More precise monitoring of WSB outbreaks in BC started in the 1950s, when the Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service initiated systematic ground and aerial surveys. While WSB moths have consistently been collected at sites on southern Vancouver Island (Van Hezewijk (*in prep*.)) over the intervening years, there are no reports of infestations reaching outbreak levels since the 1930s.

There are several hypotheses for the absence of outbreaks over the last 90 years on southern Vancouver Island. Thomson and Benton (2007) suggested that a regional warming trend has disrupted the synchrony between WSB and the timing of bud flushing in Douglas-fir. Other possible explanations include changes in Southern Vancouver Island ecosystems, including a reduction in the amount and extent of available host material due to logging and land-use changes, or the introduction of novel budworm predators or parasitoids into the community (Van Hezewijk (*in prep*.)). An alternative explanation is that the two outbreaks recorded in the early 1900s were themselves anomalous within a region that generally may not be prone to budworm outbreaks.

Anticipating the recurrence cycle of this periodic defoliator is important for forest management planning, which needs to consider budworm-caused depletions in timber supply and for risk management and control. In this paper we use dendrochronological methods to establish the historic range of variability in WSB outbreak recurrence on southern Vancouver Island, the western edge of this forest defoliator range. Our objective was to determine whether the absence of outbreaks in modern times, corresponds to an interruption of a regular long-term cycle and determine if the two documented outbreaks constitute a rare phenomenon in this region.

Several studies have used insects as bioindicators to quantify environmental change, such as the effects of natural or anthropogenic disturbances on ecosystems. Annual population levels of various insect pests, usually measured indirectly by recording the annual amount of visible damage, are often used as an indicator to measure the health of Canadian forests (Natural Resources Canada 2018). Other examples include the use of ground beetle (Coleoptera: Carabidae) population measurement to indicate habitat alteration since they are quickly affected by anthropogenic activities such as urbanization, forest fragmentation, overgrazing by livestock and pollution (Avgın and Luff, 2010; Esch et al. 2016). In this paper we use the of western spruce budworm to determine if forest ecosystems of southern Vancouver Island are functioning within the historical range of variability in terms of frequency and intensity of outbreaks.

2. Methods

2.1. Study area and tree-ring data

We looked for signals of budworm defoliation in Douglas-fir tree-ring chronologies from southern Vancouver Island, which were corrected by subtracting the annual growth of a sympatric tree species that is not a host to WSB. The principle is that tree rings of sympatric tree species respond synchronously to regional climate fluctuations, but differently to species-specific disturbances (Speer, 2010). This proxy chronology retains the budworm signal as a significant difference between host and non-host species. Tree-ring samples from the sympatric non-budworm host WRC were collected from various locations on southern Vancouver Island. A regional master non-host chronology was developed and its annual ring widths subtracted from the corresponding host ring-width of every Douglas-fir chronology.

2.2. Study area, data collection and chronology development

Annual ring-width data were collated at 12 sites on southeastern Vancouver Island, ranging from Rocky Point in the south, to Gabriola Island in the north (Fig. 1, Table 1). This region has a long history of timber harvesting and a large portion of the region has been modified by human activities. The present-day forested area is primarily composed of second- or third-growth stands comprised of Douglas-fir, with minor amounts of red alder, western red cedar, western hemlock, grand fir, and western white pine (Nuszdorfer et al., 1991). Four of the sample stands consisted of pristine old growth (i.e., not previously harvested) (Rocky Point, Saddle Dam, Rithet West and Rithet East). The sample