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Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: A multi-century dendrochronological record

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ABSTRACT

Douglas-fir forests in the interior Pacific Northwest are subject to sporadic outbreaks of the western spruce budworm, a species widely recognized as the most destructive defoliator in western North America. Outbreaks of the western spruce budworm often occur synchronously over broad regions and lead to widespread loss of leaf area and decrease in growth rates in affected stands. In spite of the ecological and economic significance of this defoliator, the mechanisms controlling this species' population dynamics are still not fully understood. We used dendrochronological methods to reconstruct three centuries of western spruce budworm outbreaks at thirteen sites along a transect running from central Oregon to western Montana and compared the outbreak reconstructions with regional drought history. The reconstructions reveal repeated western spruce budworm outbreaks that sometimes persisted more than a decade and were significantly synchronous among sites. Synchrony was higher in the second half of the record, possibly due to changes in forest composition and structure brought about by land use practices. Across stands and regions, there was a moderately strong relationship between initiation of synchronous outbreaks and periods of transitional climate conditions in which moisture availability was below average prior to outbreak initiation, but above average in the first few years of an outbreak. There was a weak relationship between cessation of outbreaks and one or more years of high moisture availability. Outbreaks tended to occur near the end of droughts. The association between climatic variability and outbreak dynamics observed across this transect indicates that climate is an important driver of western spruce budworm outbreaks. Other factors that we did not test, but that may influence outbreak dynamics include stand structure, forest composition, predation, and phenological synchrony between larvae and host trees. Future changes in western spruce budworm outbreak dynamics will be determined by a combination of changing climate, interactions with other disturbance agents, and changing forest composition and structure. Our results suggest that western spruce budworm outbreaks will likely intensify if drought frequency increases in the future.

1. Introduction

Outbreaks of phytophagous insects are important drivers of forest dynamics through their effects on primary productivity, nutrient cycling, and succession. In the mixed-conifer forests of the interior Pacific Northwest, the dominant defoliating insect species is the western spruce budworm (*Choristoneura occidentalis* Freeman; Fellin and Dewey, 1982; Wickman, 1992). The larvae of this species feed primarily on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) trees. Defoliation by the western spruce budworm leads to reduced growth rates and mortality of limbs or entire trees (Alfaro et al., 1982; Ferrell and Scharpf, 1982). Outbreaks of this insect may also predispose host trees to subsequent infestations by other insects and pathogens (Alfaro et al., 1982; Ferrell and Scharpf, 1982; Hadley and Veblen, 1993). Outbreaks often extend over multiple states and may continue for well over a decade (Swetnam, 1986; Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995; Ryerson et al., 2003). In 1986, at the peak of its last major outbreak, western spruce budworm affected more than 5.2 million hectares in the United States (Hofacker et al., 1987). Resurgence in the total area defoliated by the western spruce budworm starting in 2009 indicates that a widespread outbreak may be occurring for the first

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time since the 1980s (Man, 2012). In spite of the ecological and economic significance of this species, its outbreak patterns, population dynamics, and responses to climatic variability are not fully understood.

Western spruce budworm populations often fluctuate synchronously over broad spatial scales, but the causal mechanisms of this synchrony are not fully understood (Peltonen et al., 2002). Analysis of synchrony patterns can offer insights into the mechanisms driving disturbance patterns over broad spatial scales and aid in predicting and responding to future disturbances. Synchrony of western spruce budworm populations is usually attributed to rapid dispersal of adult moths, the influence of exogenous forces such as climatic variability (the Moran effect; Moran, 1953), or a combination of the two (Myers, 1998; Cooke et al., 2007).

Climatic fluctuations, particularly changes in moisture availability, have been suggested as an important driver of western spruce budworm outbreaks (Hard et al., 1980; Thomson et al., 1984; Campbell, 1993; Swetnam and Lynch, 1993; Ryerson et al., 2003). However, different methods of quantifying climatic influences have yielded inconsistent results. Several studies based on dendrochronological reconstructions of outbreak events have found that they tend to occur during periods of high moisture availability (Swetnam and Lynch, 1993; Ryerson et al., 2003). In contrast, studies of modern observed western spruce budworm outbreaks have generally reported a tendency for outbreaks to occur following periods of low moisture availability (Hard et al., 1980; Thomson et al., 1984; Campbell, 1993). These contradictory results reflect a broader uncertainty regarding the role of climate in triggering outbreaks of herbivorous insects. Three competing hypotheses have been used to explain observed patterns of moisture availability associated with insect outbreaks. According to the *plant stress hypothesis*, drought or other abiotic stressors can trigger insect outbreaks through an increase in the nutritional quality of foliage due to the concentration of nitrogen or other beneficial nutrients or chemical compounds (White, 1984; Mattson and Haack, 1987). Alternatively, the *plant vigor hypothesis* proposes that the quality and/or quantity of foliage improves when moisture levels are high, thus benefiting some herbivorous insects (Price, 1991). More recently, the potential importance of the temporal variability, rather than simply the magnitude, of moisture stress was highlighted in the *pulsed plant stress hypothesis* (Huberty and Denno, 2004; Mody et al., 2009). The pulsed plant stress hypothesis proposes that intermittent plant stress may be particularly conducive to herbivorous insect outbreaks (Huberty and Denno, 2004; Mody et al., 2009).

In addition to these climatic triggers of outbreak events, there is evidence that land-use changes following Euro-American settlement of western North America have increased the synchrony, as well as severity, duration, and/or frequency, of western spruce budworm outbreaks in many ecosystems (Anderson et al., 1987; Swetnam and Lynch, 1989, 1993; Swetnam et al., 1995). Fire exclusion, logging, and grazing have increased the extent and homogeneity of densely stocked forests composed of tree species favored by the western spruce budworm (Hessburg et al., 1994; Keane et al., 2002). Additionally, the dense, multi-layered forest structure made common by the increase in shade-tolerant saplings makes stands especially vulnerable to western spruce budworm outbreaks, as this structure enables larvae to disperse downwards through the canopy layers with a low risk of falling to the forest floor where they would be more likely to be killed by predators (Maclauchlan and Brooks, 2009).

The relative importance of climatic variability, dispersal, and land-use practices on western spruce budworm dynamics cannot be known without long-term outbreak records covering pre- and post-settlement periods. Efforts to quantify and explain synchrony of western spruce budworm populations are hindered by short historical records, which often only span the full length of a single major outbreak, and the limited geographic coverage of currently available dendrochronological reconstructions. The lack of long-term records has also limited efforts aimed at quantification of the relationship between climatic variability and outbreak dynamics. In this article, we present the results of a dendrochronological study in which three centuries of western spruce budworm outbreaks were reconstructed at sites along a transect running from central Oregon to western Montana. We use this multi-century record, along with observational records from the 20th century, to quantify the spatial synchrony of western spruce budworm outbreaks and to assess the association between moisture availability and the occurrence of outbreaks at multiple spatial scales. This is, to the extent of our knowledge, the first annually-resolved, multi-century analysis of the relationship between climate and the initiation and cessation of western spruce budworm outbreaks. Our analyses focus on answering the following questions:

(1) Over what temporal and spatial scales are western spruce budworm outbreaks synchronous?
(2) What is the relationship between moisture availability and the initiation, cessation, and synchronization of western spruce budworm outbreaks?

2. Materials and methods

2.1. Study area

Our thirteen sites are located along a 600 km longitudinal transect stretching from central Oregon to western Montana (Table 1; Fig. 1). The sites are located at middle elevations (1283–2040 m asl) in mixed-conifer stands dominated by a combination of Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and/or grand fir. Some sites also have minor amounts of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), western larch (*Larix occidentalis* Nutt.), western juniper (*Juniperus occidentalis* Hook.), or Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). We also collected samples from ponderosa pine trees (see discussion of outbreak reconstruction methods below) at 12 nearby monospecific sites. The study area has a continental climate characterized by cold winters and warm summers. According to climate division records from the US Historical Climatology Network (http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp; Oregon climate divisions 7 and 8, Idaho climate division 4, and Montana climate divisions 1 and 2) for the period from 1895 to 2010, the average January and July temperatures are −4.7 °C (range: −7.6 °C to −1.6 °C) and 18.2 °C (range: 17.3–18.9 °C), respectively, and the average annual precipitation is 46.1 cm (range: 39.2–67.4 cm).

2.2. Sampling strategy

We targeted specific sites based on the presence of relatively old Douglas-fir and grand fir ("host") trees, field evidence or archival records of historical western spruce budworm outbreaks, and, where possible, the absence of recent stand-replacing fires and logging or other anthropogenic disturbances. To identify past outbreaks, we compared ring-width series from "host" tree species, those favored by the western spruce budworm, with ring-width series from "non-host" tree species. We used ponderosa pine as our non-host species because it is rarely defoliated by the western spruce budworm (Fellin and Dewey, 1982) and because its radial growth response to climate is similar to that of the primary host tree species, Douglas-fir (Fritts, 1974; Campbell et al., 2006).

At each site, we collected samples from eighteen or more Douglas-fir and grand fir host trees with a diameter of at least 40 cm at breast height (1.4 m) by removing two cores at breast