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Impact of the first recorded outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata*, in southern California and the extent of its distribution in the Pacific Southwest region

Tom W. Coleman [a,*], Michael I. Jones [b,1], Béatrice Courtial [c], Andrew D. Graves [d], Meghan Woods [e], Alain Roques [c], Steven J. Seybold [f]

[a] USDA Forest Service, Forest Health Protection, San Bernardino, CA 92408, United States
[b] Department of Entomology, University of California, Davis, CA 95616, United States
[c] INRA, UR633, Zoologie Forestière, F-45075 Orléans, France
[d] USDA Forest Service, Forest Health Protection, Albuquerque, NM 87102, United States
[e] USDA Forest Service, Forest Health Monitoring, Davis, CA 95618, United States
[f] USDA Forest Service Research, Pacific Southwest Research Station, Davis, CA 95616, United States

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ABSTRACT

The Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* McDunnough (Lepidoptera:Erebidae: Lymantriinae), is a native western North American defoliator of true fir, *Abies* spp. Mill., and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. We investigated the population genetics and impact associated with the first recorded outbreak of DFTM in southern California (USA), and report the first collection of DFTM in Baja California Norte, Mexico. This latter population is similar genetically to populations from Washington, USA and British Columbia, Canada. We assessed forest stand characteristics, levels of defoliation, and mortality of white fir, *Abies concolor* Lindl., associated with the DFTM outbreak in the Transverse Mountain Ranges of southern California. We compared these data to those from southern California non-outbreak stands of *A. concolor*, and from virgin stands with an *A. concolor* component in the Sierra San Pedro Martir National Park (Mexico). Total stand density (ha^{-1}) was significantly higher (22%) in non-outbreak stands than in outbreak stands. However, outbreak stands had significantly higher mortality of *A. concolor* than non-outbreak stands [whether expressed as density (70%) or basal area (m^2 ha^{-1}) (32%)]. Total stand and *A. concolor* density and basal area for living and dead trees were significantly lower in the Sierra San Pedro Martir National Park than in southern California. Dead *A. concolor* comprised >95% of all tree mortality in both outbreak and non-outbreak areas in southern California, which corresponded to a mean 20% basal area loss of *A. concolor* associated with DFTM feeding injury within the outbreak area. The mean level of defoliation of *A. concolor* by DFTM was 39%, and 62% of all dead *A. concolor* were associated with DFTM defoliation. In stands with high levels of defoliation, larval feeding and tree mortality were also noted in Jeffrey pine, *Pinus jeffreyi* Grev. & Balf. The amount of dead *A. concolor* basal area associated with the fir engraver, *Scolytus ventralis* LeConte (Coleoptera: Scolytidae), in non-outbreak stands was 96% greater than in outbreak stands. Using the U.S.D.A. National Insect and Disease Risk Map software, a total of 13,534 ha were predicted to be at risk to basal area loss from future DFTM outbreaks on national forest lands in southern California. Changes in forest management practices and fire suppression policies likely led to an increase in the density and continuity of DFTM's preferred host in southern California and to a southward shift in the historic range of DFTM outbreaks.

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1. Introduction

Changes in forest land management objectives and practices have subsequently increased the economic and ecological significance of native forest insect species in Asia, Europe, and North America (Nilsson, 1976; McFadden et al., 1981; Dahlsten and Rowney, 1983). Timber management practices leading to greater forest stand densities, off-site plantings, and even-aged monocultures have resulted in higher levels of activity and impact of native bark beetles, defoliators, and regeneration pests (Graham, 1956; Sartwell and Stevens, 1975; Smith, 1976; Knight and Heikkenen, 1980; Wermelinger, 2004; Chen and Tang, 2007; Grodzki, 2008;

* Corresponding author.
E-mail address: twcoleman@fs.fed.us (T.W. Coleman).
[1] Current address: 135 Illick Hall, 1 Forestry Dr., Syracuse, NY 13210, United States.

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Schaupp et al., 2008). Furthermore, successful wildfire suppression policies in North America have altered the composition and structure of forests and led to new forest pest impacts (Baker, 1992; McCullough et al., 1998; Taylor, 2001; Parker et al., 2006).

Similar shifts in forest stand composition occurred throughout California (USA) following timber harvesting, fire suppression, and grazing in the late 1800s and early 1900s (Leiberg, 1899; McKelvey and Johnston, 1992; Taylor, 2004). Following these anthropogenic disturbances, shade-tolerant species, like true firs, *Abies* spp. Mill., increased in density, and there was a reduction in the number and distribution of age and size classes of these species (North et al., 2007). As a result, white fir, *Abies concolor* Lindl., now represents a greater component of forest stands in California (Parsons and DeBenedetti, 1979; Minnich et al., 1995).

The Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* McDunnough (Lepidoptera: Erebidae: Lymantriinae), is a native defoliator found throughout coniferous forests of western North America (Furniss and Carolin, 1977; Brookes et al., 1978). Larvae of the DFTM feed preferentially on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and grand fir, *Abies grandis* Lindl. in old-growth pine–fir forests (Brookes et al., 1978). Outbreaks of this insect have also occurred in subalpine fir, *A. lasiocarpa* [Hook] Nutt., along the northern edge of its range (Hansen, 1995). At the southern extent of the range of the moth (Arizona, California, Nevada, and New Mexico), *A. concolor* is the primary host (Brookes et al., 1978; Wickman et al., 1981). Since the early 20th Century, DFTM outbreaks were recorded every decade in the western USA (Wickman et al., 1973; Berryman, 1978; Shepherd et al., 1988; USDA FHTET, 2013). High levels of defoliation by DFTM during outbreaks can cause reductions in growth, top-kill, and tree mortality across all size classes of host conifers (Wickman et al., 1981; Alfaro et al., 1987). When population densities are elevated at high-use recreation sites, urticating hairs from larvae can cause human discomfort and health concerns, commonly known as "tussockosis" (Perlman et al., 1976). Tree mortality associated with DFTM feeding has occurred frequently following complete defoliation (>90% needle loss) of a tree (Wickman, 1978). However, top-kill can occur when 50–90% of the crown is injured by caterpillars (Wickman, 1978). Low level defoliation by DFTM rarely kills host trees, but injury can predispose trees to attack by either the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, or the fir engraver, *Scolytus ventralis* LeConte (both Coleoptera: Scolytidae, *sensu* Bright, 2014) (Wickman et al., 1981; Wright et al., 1984).

The DFTM is univoltine and male moths fly typically from July to November, when mating occurs (Wickman, 1963). Flightless females can lay up to 150–200 eggs in a single egg mass, which is deposited on the cocoon from which the female emerged. Populations overwinter in the egg stage, and egg hatch is synchronized the following year with bud burst and shoot elongation of host trees, which occurs from May to early June (Brookes et al., 1978). Larvae complete four to six instars during the summer months. First-instar larvae migrate to the tops of trees where they feed preferentially on new foliage or balloon to other host trees within the stand to feed (Brookes et al., 1978). Late-instar larvae typically consume older foliage and will feed throughout the crown when population densities reach outbreak levels. Pupation occurs from late July to August on foliage with eclosion occurring 10–18 d later (Wickman et al., 1981).

Outbreaks of DFTM can persist for three to four years in forest stands, and population densities can increase and decrease dramatically during the outbreak cycle (Wickman et al., 1973; Hansen, 1995). Increases in densities of insect natural enemies, the naturally occurring nuclear polyhedrosis virus (NPV), and the loss of suitable host material can contribute to population collapse (Wickman et al., 1973; Mason et al., 1983; Otvos et al., 1987). Fire suppression activities have transformed pine–fir forests to true fir- and Douglas-fir-dominated stands across the native range of DFTM, which has increased the likelihood of outbreaks (Wickman et al., 1981).

Historically (1916–1984), DFTM outbreaks in California were limited to the Sierra Nevada Mountain Range (Shepherd et al., 1988; Fig. 1). However, in 1996 an outbreak on *A. concolor* was recorded in the southern Sierra Nevada, and, in 2009, high-levels of defoliation of *A. concolor* by the DFTM were first detected in the Transverse Mountain Ranges of southern California on the San Bernardino National Forest (San Bernardino Co.). The DFTM had been collected in the 1950s, 1960s, and 1970s on the Angeles and San Bernardino National Forests, but no outbreak was ever reported (Natural History Museum, Los Angeles Co., USDA Forest Service Hopkins U.S. System Index, 1929–1955; Wickman et al., 1973, 1981; Shepherd et al., 1988). These collections also represented the southernmost recorded collection of the species in the Pacific Southwest region of North America.

This first recorded DFTM outbreak in southern California provided an opportunity to compare the forest stand characteristics and impact associated with this event to previous outbreaks in the western USA. It also allowed us to compare these characteristics and impacts with those in similar, nearby lightly infested or uninfested forest stands in California and in Baja California Norte, Mexico. At the latter location, no previous timber management and limited fire suppression activities had occurred (Maloney and Rizzo, 2002; Stephens and Gill, 2005). We also compared mitochondrial DNA sequence similarity of DFTM from populations in southern California and Mexico to populations along the northern edge of its distribution (Washington, USA and British Columbia, Canada) to verify DFTM species status in these isolated populations in the Transverse Mountains and Sierra San Pedro Martir (Fig. 1). We predicted basal area loss from future DFTM outbreaks in southern California by assessing forest stand measurements collected in this study with the U.S.D.A. National Insect and Disease Risk Map software (Krist et al., 2013). The risk model is a multi-criteria geographic information system (GIS) application built on ArcGIS technology that can account for regional variations and can be applied at varying landscape scales (ESRI Inc., Redlands, CA, USA). As an outcome of the risk analysis, spatial predictions were made for future DFTM population increases so that stand thinning prescriptions could be developed to reduce short- and long-term negative impacts from future outbreaks.

2. Methods

2.1. Genetic analyses

Larvae from the Pacific Southwest region were collected on foliage and bark surfaces of *A. concolor* and stored in 99% ethanol at −80 °C (San Bernardino National Forest) or −2 °C (Baja). These larvae and those from a northern site (10 specimens: San Bernardino National Forest, N 34.22425°, W 116.87723°; 7 specimens: collected on *P. menziesii* from the Okanagan National Forest, WA, USA N 48.575°, W 120.258333°; and 2 specimens: Sierra San Pedro Martir National Park, Baja California Norte, Mexico, N 30.99863°, W 115.55489°) were subjected to population genetic analysis. Whole genomic DNA was extracted from individual specimens by using a Nucleospin® Tissue XS Kit (Macherey-Nagel, Düren, Germany). Genetic variation was examined by amplifying a 658 bp fragment of the mitochondrial gene (mtDNA) for cytochrome oxidase c subunit 1 (COI) with the polymerase chain reaction (PCR). Reactions were performed in 25 μl volumes containing 2 μl of DNA template (concentration around 30 ng/μl), 1x PCR Buffer without $MgCl_2$ (Sigma, St. Louis, MO, USA), 2.5 mM $MgCl_2$, 400 μM of each dNTP, 1 U REDTaq Genomic DNA polymerase (Sigma), and 1 μM each of