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Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Evaluating spatial patterns of drought-induced tree mortality in a coastal California pine forest



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ARTICLE INFO

Article history: Received 17 September 2013 Received in revised form 6 December 2013 Accepted 18 December 2013 Available online 9 January 2014

Keywords: Tree mortality Coastal fog Drought-stress Remote sensing Random Forest

ABSTRACT

In a coastal, fog-influenced forest on Santa Cruz Island in southern California, we observed mortality of Bishop pine (Pinus muricata D.Don) trees following a brief (2 year), yet intense, drought. While anecdotal evidence indicates that drought-induced Bishop pine mortality has occurred in the past in the stand we studied, this is the first attempt to capture the spatial distribution of mortality, and begin to understand the environmental drivers underlying these events. We used high spatial resolution remote sensing data to quantify the spatial extent of tree mortality using a 1 m true color aerial photograph and a 1 m LiDAR digital elevation model. We found the highest density of dead trees in the drier, more inland margins of the forest stand. We used the Random Forest decision tree algorithm to test which environmental variables (e.g., summertime cloud frequency, solar insolation, and geomorphic attributes) would best separate live and dead tree populations. We also included tree height as a variable in our analysis, which we used as a proxy for overall tree size and potential rooting distribution. Based on the Random Forest analysis, we generated a map of the probability of survival. We found tree survivorship after drought was best explained by the frequency of summertime clouds, elevation, and tree height. Specifically, survivorship was greatest for larger trees (~8-10 m tall) in more foggy parts of the stand located at moderate elevation. We found that probability of survival was lowest at the inland extent of the stand where trees occur at the upper limit of their elevation range (~400 m). The coexistence of these main factors with other landscape variables help identify areas of suitable habitat for Bishop pines across the stand, and extend our understanding of this species' distribution.

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1. Introduction

Across the western United States, widespread increases in tree mortality rates have been observed in recent decades (van Mantgem et al., 2009). Many experimental, observational, and modeling studies attribute tree mortality to drought stress in response to regional warming (Anderegg et al., 2012; Allen et al., 2010; Williams et al., 2010; Adams et al., 2009; Breshears et al., 2005; Allen and Breshears, 1998). To date, the geographical scope of studies of tree mortality in the American West has been limited to continental, montane climates (Hanson and Weltzin, 2000). Much less is known about the extent and frequency of drought-induced mortality events in coastal forests.

The maritime influence on weather and climate in coastal forests is assumed to buffer coastal ecosystems from extreme climate fluctuations, and therefore help maintain a stable distribution of species over time. However, we observed extensive mortality of a coastal pine species, Bishop pine (*Pinus muricata* D.Don), following a brief, yet intense, drought period at the southern extent of its range in California, where they are at the climatic margin that can support the species (Fischer et al., 2009; Williams et al., 2008).

Throughout the Pliocene and Pleistocene, when the California climate was considered to be more mesic compared to today, with year-round precipitation, Bishop pine, and closely related Monterey pine (Pinus radiata), were more widely and evenly distributed along the California coast (Raven and Axelrod, 1978). Bishop pine populations are currently restricted to a small number of stands scattered along the fog-belt of coastal California and northern Baja California (Lanner, 1999). The reduction of suitable habitat for Bishop pine (and similar coastal forests) since the late Pleistocene is attributed to the onset of xeric Mediterranean climate conditions (warmer temperatures, and reduced seasonal precipitation, occurring predominantly during the winter). However, summer precipitation from fog drip, and potentially foliar uptake of fog water (Limm et al., 2009; Limm and Dawson, 2010), is thought to enable Bishop Pines to persist along the coast and offshore islands (Raven and Axelrod, 1978).

Fog water inputs to a forest, and its effects on the water relations of trees, are spatially heterogeneous because deposition of

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fog water and shading effects of fog are controlled by a variety of factors that range from the landscape to canopy scale. Fog is commonly defined as a low-stratus cloud that intercepts land. The mechanisms by which fog ameliorates the water stress of trees largely depend on their relative position to the fog layer. Shading effects, which reduce evapotranspiration, will benefit trees that are below the fog layer (Fischer et al., 2009). Plants immersed in the fog layer benefit from direct water inputs because fog droplets deposit on leaves and drip to the ground increasing shallow soil moisture (Carbone et al., 2012; Fischer et al., 2009; Corbin et al., 2005; Dawson, 1998; Ingraham and Matthews, 1995; Harr, 1982; Azevedo and Morgan, 1974; Vogelmann, 1973). Moreover, vegetation type, and canopy structure of a forest, has been shown to strongly influence fog water deposition (Ponette-Gonzalez et al., 2010; Hutley et al., 1997). For instance, direct fog water inputs decrease from the windward edge of the forest to its interior (Weathers et al., 1995), negatively impacting the water status of trees that receive less fog-water inputs in the interior (Ewing et al., 2009). Such edge effects can also impact recruitment rate of trees, and ultimately forest structure (Barbosa et al., 2010; del-Val et al., 2006). In short, the effect of fog on the growth and persistence of tree species in fog-influenced ecosystems is strongly mediated by the spatial heterogeneity of the landscape, namely topographic variation and forest structure (Uehara and Kume, 2012; Gutierrez et al., 2008; Cavelier et al., 1996; Vogelmann, 1973). Since the influence of summer cloud shading and fog drip/ immersion on the moisture regime of forested ecosystems vary spatially, it is reasonable to hypothesize that the risk of droughtinduced mortality in a fog-influenced forest would follow suit.

The proportion of dead Bishop pines that followed the recent drought event increased from the coast inland, and mortality was more severe at the margins of the stand. These spatial patterns seemed to coincide with modeled soil water deficit, which included the influence of fog on the water budget of the ecosystem. Specifically, Fischer et al. (2009) found that the combined effects of fog drip and cloud shading can reduce summertime drought stress up to 56% in the Bishop pine stand, and inland locations are particularly sensitive to reduced cloud shading and increased evapotranspiration compared to more coastal areas. While observations and water deficit models may infer that fog inundation and cloud shading are key climate variables explaining spatial patterns of tree mortality in this coastal forest, it is unlikely that a single environmental variable, such as fog frequency, can entirely explain the spatial patterns of tree mortality.

A suite of physical factors, such as landscape features (e.g., soil thickness and type, slope, aspect, elevation, topography, and drainage networks), can generate stress gradients across the landscape (Gitlin et al., 2006) and may explain the distribution of water stress in trees and tree mortality just as well as spatial patterns of climate (Koepke et al., 2010; Ogle et al., 2000). In addition to landscape factors, biotic factors, such as tree size, may help predict mortality within a forest stand (Floyd et al., 2009). While trees at different life stages (for which size can be proxy) may make different physiological adjustments to avoid or tolerate water stress, in general, it has been argued that larger trees with an extensive rooting distribution should be more capable of accessing stable water resources even during dry periods compared to smaller trees, and therefore be less sensitive to drought conditions (Cavender-Bares and Bazzaz, 2000; Dawson, 1996; Donovan and Ehleringer, 1994). In particular, water status of larger, adult Bishop pines is less affected by the summer dry period compared to smaller, sapling trees, which become water stressed by latesummer (S. Baguskas, unpublished data). Understanding how interacting environmental factors explain the spatial patterns of mortality will improve our ability to assess the vulnerability of coastal forests to drought-induced mortality in the future.

Remote sensing is a powerful tool for quantifying the spatial extent of tree mortality, which is often the first step towards elucidating patterns and processes underlying a mortality event, such as drought stress (Allen et al., 2010; Williams et al., 2010; Macomber and Woodcock, 1994), bark beetle infestation (Edburg et al., 2012; Wulder et al., 2006), and the potential impacts on regional carbon budgets (Huang and Anderegg, 2012). While many studies have quantified the spatial extent of tree mortality at regional and landscape scales using moderate-spatial (>30-m ground resolution) resolution remote sensing data (e.g., Meigs et al., 2011; Anderson et al., 2010; Fraser and Latifovic, 2005), a growing number of studies have used high-spatial (<5-m ground resolution) resolution remote sensing data to examine tree mortality at finer spatial scales in order to detect mortality of individual trees (or clusters) within a stand (e.g., Stone et al., 2012; Dennison et al., 2010: Hicke and Logan, 2009: Chambers et al., 2007: Guo et al., 2007; Coops et al., 2006; Clark et al., 2004). Developing a way to possibly make large scale estimates and predictions of tree mortality based on remotely sensed data can help land managers, who are tasked with making decisions about species and land conservation in the future, respond to a future expected to become warmer and drier.

Our research addresses the following questions: (1) What is the spatial distribution of tree mortality observed during the 2007–2009 drought period? (2) What is the correlative relationship between environmental variables, such as climate, landscape features, and tree size, and the spatial distribution of tree mortality? (3) Where is tree mortality likely to occur on the landscape during periods of drought stress?

2. Methods

2.1. Study site

This study was conducted in the westernmost and most extensive (3.6 km²) Bishop pine stand on Santa Cruz Island (SCI, 34°N. 119°45′W), which is the largest of the northern islands in Channel Islands National Park (~250 km², 38 km E-W extension) located approximately 40 km south of Santa Barbara, CA (Fig. 1). The Mediterranean climate along the California coast and islands offshore is characterized by cool, rainy winters and warm, rain-free (yet foggy) summers. While rainfall is highly variable both inter- and intra-annually, on average about 80% of rain falls on SCI between December and March (Fischer et al., 2009). We observed mortality of Bishop pines during water year 2006-07 and 2008-09, when fewer than 25 cm of rain fell (median rainfall is 43 cm) (Fig. A1). In 2009, we observed peak mortality of Bishop pine trees in the field based on the high number of tree canopies with red foliage, and we found that no other plant species exhibited a mortality response like the Bishop pines did.

The Bishop pine stand that we studied exists on complex and rugged terrain ranging from sea level to just over 400 m in elevation. Bishop pines are almost entirely restricted to the wetter, cooler north-facing slopes. There are only a few scattered clusters of trees that exist on the drier south-facing slopes, and those tend to occur in drainages. Steep ridges rise from the Santa Cruz Island fault that runs E–W through the central part of the island. There is a stark ecological and geographical difference between the northern and southern sections of the island. The northern half of the island is composed of Santa Cruz Island volcanics and is sparsely vegetated compared to the southern half, which is mostly metamorphic in origin and supports most of the vegetation (Junak et al., 1995). The habitat for woody vegetation is considered to be more suitable at the center of the largest Bishop pine stand where the canopies are continuous relative to the margins of the

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