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ORIGINAL ARTICLE

Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California

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ABSTRACT

Aim Native American fire use influenced bark thickness of coastal and island Monterey pine (*Pinus radiata* D. Don) and bishop pine (*Pinus muricata* D. Don) populations.

Methods Basal bark thickness and d.b.h. were measured in two common-garden pine plantations that included all five native Monterey pine populations and nine of 10 native bishop pine populations. One-factor analysis of covariance was used to determine if significant differences in bark thickness existed between island and coastal populations.

Results Bark thickness was measured on 228 Monterey and 42 bishop pines. Bark thickness in coastal and island Monterey pine populations was significantly different. Bark thickness in coastal and island bishop pine populations was not significantly different.

Main conclusions Basal bark was thick in populations where there was a history of Native American burning. Basal bark was thin in two island populations where Native Americans have been absent or distant from the pine populations. While other influences no doubt affect the evolution of lower-bole bark thickness, it appears that frequent anthropogenic fires may be a powerful selection force.

Keywords
Bishop pine, defensive organs, fire ecology, Monterey pine, Native Americans, *Pinus muricata*, *Pinus radiata*.

INTRODUCTION

Fire is a common ecosystem process in many landscapes of western North America. Each landscape has a unique set of properties such as fuel arrangement, load, weather, ignitions, cultural history and topography that will influence fire behaviour and effects. These characteristics will have an impact on the probability that a particular area will be subjected to low-moderate intensity fires, stand-replacement fires, mixed-severity fires, or no fires (Stephens & Ruth, 2005). The type and frequency of fire will have a profound influence on the evolutionary strategies for a given landscape (Keeley & Zedler, 1998).

Plants exhibit adaptive responses to fire, and there may also be selection for specific physiological or life-history strategies in the post-fire environment (Mutch, 1970; Sannikov, 1981; McCune, 1988; Jackson *et al.*, 1999; Schwilk & Ackerly, 2001). Fire-induced injury of plants can be separated into three categories: (1) injury to roots, (2) crown injury, and (3) cambium injury (Ryan *et al.*, 1988; Brown & Smith, 2000). Trees and shrubs can be killed to ground level by stem girdling, independently of crown or root injury (Ryan *et al.*, 1988; Stephens & Finney, 2002). Fire resistance of tree stems is most closely related to bark thickness (Martin, 1963; Jones *et al.*, 2004).

Lightning and Native American ignitions

Before humans inhabited Alta California in the early Holocene, lightning was the most common ignition source (Keeley & Zedler, 1998). Lightning-ignited fires are rare near the Pacific coast of North America (Keeley, 2002), in contrast to the regional population pattern for native peoples before Euro-American contact (Krech, 1999).

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Native Americans in Alta California routinely burned grasslands, savannas and forests to increase the yield of crops including grasses, geophytes, forbs and acorns (Lewis, 1982; Blackburn & Anderson, 1993; Keeley, 2002). Native Americans in Baja California also used fire to manage resources, but information on their uses of fire is limited (Stephens *et al.*, 2003).

There is considerable debate on the degree to which Native Americans altered vegetation distribution, and whether they had any influence on plant traits (Keeley, 2002). Some contend that Native American fire use had a dramatic and widespread impact on our landscapes (Lewis, 1982; Blackburn & Anderson, 1993; Bonnicksen, 2000), but Vale (2000) contends that Native American uses of fire primarily affected ecosystems in the more mesic eastern USA. Information on individual species' responses to anthropogenic fire is rare. This study will explore the idea that past Native American burning may have been a selective force in some western North American pine populations.

Coastal and island pine populations

Monterey pine (also known as radiata pine) (*Pinus radiata* D. Don) and bishop pine (*Pinus muricata* D. Don) are unusual in Alta and Baja California in that they have populations on or near the coast (within 20 km of the ocean) and on islands in the Pacific Ocean (Fig. 1). These two species have been classified as adapted to infrequent stand-replacement fires (McCune, 1988; Keeley & Zedler, 1998). Common characteristics of such species are cone serotiny and thin bark. Species such as ponderosa pine (*Pinus ponderosa* Laws) have been classified as fire resistors because they can survive frequent surface fires due to thick bark that insulates their cambium.

Three native populations of Monterey pine occur on the Alta California coast and two populations are located on Guadalupe and Cedros Islands off Baja California (Fig. 1). Bishop pine occurs in 10 separate native populations (Fig. 1). Seven coastal populations occur in Alta California and one in northern Baja California. Two bishop pine populations are located off the coast of southern Alta California (Fig. 1).

The objective of this study was to determine if coastal and island Monterey and bishop pine populations had different basal bark thicknesses. The hypotheses to be tested were that: (1) population location (island or coastal) will not significantly affect the investment in basal bark, and (2) bark thickness is independent of exposure to frequent, low-intensity fire.

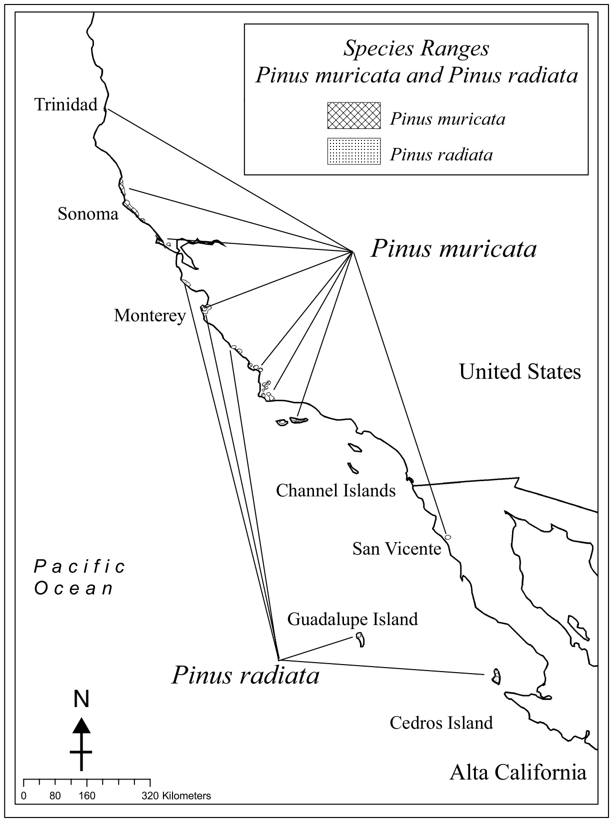

Figure 1 Distribution of Monterey pine (*Pinus radiata* D. Don) and bishop pine (*Pinus muricata* D. Don) and the origins of sampled populations (only the bishop pine population in Monterey was not included in this analysis).

METHODS

Study location

Our study was conducted in two common-garden plantations at the University of California Russell Reservation, located 26 km east of San Francisco, California (latitude 37°55′ N, longitude 122°8′ W). The climate is Mediterranean with a summer drought period that extends into the autumn. Winter and spring receive the majority of precipitation that averages 61 cm. The use of common gardens is critical because it isolates the effects of genetic differences among populations, since all trees experience a similar environment.

Monterey and bishop pine plantations

The first plantation used in the study was planted in 1968 and is the California coastal closed-cone pine plantation (CCCCP) (Kinloch & Libby, 1997). The CCCCP plantation included 20 randomly planted seedlings from each native Monterey and bishop pine population.

The second plantation used in this study was planted in 1982 with Monterey pine and is the western gall rust plantation (WGRP) (Old *et al.*, 1986). The WGRP plantation has five blocks with 20 seedlings from each population planted in each block. Tree position was chosen randomly in the WGRP plantation, and tree spacing was 2×2 m. The WGRP and CCCCP plantations are located within 400 m of each other, and have similar topography and soils.

Bark and tree measurements

In this study, bark thickness was measured at four positions on the thick plates of the bark rather than in the bark fissures. The fissures subtend only a small fraction of the stem surface and, if heated enough, local lesions would occur only under the fissures. However, in order for girdling of the entire cambium to occur, cells must be thermally damaged under the thick plates as well as under the fissures (Jones *et al.*, 2004).

Bark thickness (to the nearest mm) was measured at 10 cm above the ground surface in the four cardinal directions (N, S, E, W) using a bark gauge. The contour method to evaluate bark thickness may be more accurate (Adams & Jackson, 1995), but is destructive and could not be used in the common gardens. Bark thickness was measured near the ground because this would be the area most affected by surface and ground fires. The diameter of each tree was measured at 1.47 m above the ground (d.b.h.). Tree bark thickness was the average of measurements in the cardinal directions.

Statistical analysis

To determine if significant differences ($P < 0.05$) in bark thickness existed between island and coastal Monterey and bishop pine populations, a one-factor analysis of covariance (ANCOVA) was used with Bonferroni multiple pairwise comparisons (Zar, 1999). Basal bark thickness was used as the dependent variable, and site (coastal, island) was used as the independent categorical variable. The d.b.h. was included in the model as a covariate because bark thickness was strongly dependent on tree size. Both d.b.h. and bark thickness exhibited right-skewed distributions and were log-transformed to meet assumptions of parametric statistical analysis (Zar, 1999).

RESULTS

In both plantations, many of the planted trees had died by 2003, mainly because of inter-tree competition. Bark thickness was measured on 228 Monterey pines that included all five native populations (Tables 1 & 2). Bark thickness in coastal and island Monterey pine populations was significantly different ($P < 0.001$ for sites and d.b.h.). The Bonferroni pairwise mean difference was significantly different (coefficient = 0.308, $P < 0.001$).

Bark thickness was measured on 42 bishop pines that included nine of the 10 native populations (Tables 1 & 2). Bark thickness in coastal and island bishop pine populations was not significantly different ($P = 0.836$), although the covariate d.b.h. term was significant ($P = 0.004$). The number of bishop pines measured was smaller because they were only included in the CCCCP plantation, and the height of adjacent Monterey pines was greater, resulting in shading and eventual death of many bishop pines.

DISCUSSION

Lightning-ignited fires have been rare in areas near the coast of Alta California during the last century (Keeley, 2002). The number of coastal lightning-ignited fires in Alta California since the early Holocene is unknown, but fire history studies from this area have identified Native Americans as the primary ignition source (Jacobs *et al.*, 1985; Finney & Martin, 1989; Brown & Swetnam, 1994; Stephens & Fry, 2005).

Table 1 Average (standard error) d.b.h. and bark thickness by populations of island and coastal bishop pine (*Pinus muricata* D. Don) (IBP and CBP, respectively), and island and coastal Monterey pine (*Pinus radiata* D. Don) (IMP and CMP, respectively) from the University of California Russell Reservation, California

Population	*N* (number of trees)	d.b.h. (cm)	Range in d.b.h. (cm)	Basal bark thickness (cm)	Range in basal bark thickness
IBP					
Santa Cruz	3	45.7 (4.3)	39.3–53.8	3.8 (0.1)	3.6–4.0
Santa Cruz*	3	35.7 (1.1)	33.5–37.0	3.4 (0.6)	2.4–4.5
Santa Rosa	1	28.8 (–)	–	3.20 (–)	–
CBP					
Trinidad	3	29.6 (4.0)	25.3–37.5	2.2 (0.4)	1.7–2.9
Mendocino	7	31.8 (2.2)	25.0–41.4	3.7 (0.2)	3.0–4.8
Sonoma	8	39.4 (2.9)	25.8–49.7	3.9 (0.1)	3.6–4.3
Marin	3	30.7 (2.0)	27.8–34.5	4.0 (0.4)	3.2–4.7
San Luis Obispo	1	36.3 (–)	–	2.80 (–)	–
Santa Barbara	6	35.8 (10.2)	15.9–49.5	2.6 (0.4)	1.8–3.2
San Vicente	7	39.1 (3.6)	29.3–50.9	2.7 (0.3)	1.7–3.5
IMP					
Guadalupe	62	30.5 (2.1)	12.5–78.5	1.5 (0.1)	0.3–4.0
Cedros	27	28.3 (3.6)	9.7–70.0	1.3 (0.2)	0.3–3.0
CMP					
Año Nuevo	55	36.2 (2.8)	15.3–93.0	3.1 (0.2)	1.1–6.6
Monterey	49	38.2 (2.6)	12.4–75.2	3.3 (0.2)	0.7–6.6
Cambria	35	43.2 (3.4)	10.6–76.3	3.6 (0.3)	0.7–6.4

*Cones similar to Santa Rosa population.

Table 2 Average (standard error) tree diameter and bark thickness for populations of bishop pine (*Pinus muricata* D. Don) (coastal, CBP; island, IBP) and Monterey pine (*Pinus radiata* D. Don) (coastal, CMP; island, IMP) from the University of California Russell Reservation, California

Parameter	CBP	IBP	CMP	IMP
d.b.h. (cm)	35.4 (1.6)	39.0 (3.0)	38.7 (1.7)	29.8 (1.8)
Basal bark thickness (cm)	3.3 (0.2)	3.5 (0.3)	3.3 (0.1)	1.4 (0.1)
Basal bark thickness from ANCOVA analysis (cm)	3.3 (0.1)	3.4 (0.1)	2.8 (0.1)	1.3 (0.1)

ANCOVA, one-factor analysis of covariance.

The most probable ignition source near the coast of Alta California since the early Holocene is Native Americans. Native Americans inhabited these regions for thousands of years, and used fire as an important management tool (Lewis, 1982; Blackburn & Anderson, 1993). The potential for Native American burning impacts being overshadowed by lightning-ignited fires is greatest in the American south-west, and far less in coastal Alta California (Keeley, 2002).

Island and coastal Monterey pine populations had significantly different bark thicknesses, with trees exposed to regular fire having thicker bark. This observation can be partially explained by Native American burning practices. Native Americans may not have specifically burned coastal Monterey pine forests, but did burn adjacent grasslands, oak woodlands and shrublands for specific purposes. Since there were few barriers to fire spread, many of these fires would burn into adjacent areas, including Monterey pine forests.

The Monterey pine population on Guadalupe Island would rarely have been subjected to fire because pre-European people never inhabited the island (Libby *et al.*, 1968), and there are probably few lightning ignitions. Native American burning practices on Cedros Island are unknown. If Native Americans did use fire on Cedros Island, they would probably have focused their burning in the low coastal hills, well away from the Monterey pines. The coastal hills on Cedros Island contain plants used by Native Americans, and coastal settlements would provide easy access to the abundant marine resources.

There was no difference in bark thickness between coastal and island bishop pine populations. Coastal bishop pine populations were probably subjected to Native American-ignited fires for thousands of years. Island populations of bishop pine occur on Santa Rosa and Santa Cruz Islands off southern Alta California. These islands were inhabited for thousands of years by the island Chumash or their predecessors (Carroll *et al.*, 1993). Fire-history studies reveal that fire was frequent in the interior of the islands (Anderson, 2002). Fire events have increased over the past 5000 years, and this could have been caused by climate change, the effects of Native Americans, or a combination of these factors (Anderson, 2002).

Some pine species live in environments with no predictable fires (Keeley & Zedler, 1998); these are timberline and desertic pines adapted to extreme site conditions. The lack of predictable fire in these environments has resulted in thin bark. The fact that these pines are found on abiotically stressful sites is a powerful argument against extreme temperatures and aridity playing a role in the evolution of bark thickness, and for fire as an important selective agent (Keeley & Zedler, 1998). Timberline and desertic pine species also live in environments that include tree-killing pathogens and bark beetles. The existence of thin bark in these environments makes it doubtful that increased bark thickness has evolved solely as a defence against these organisms.

Bishop and Monterey pines are relatively short-lived (< 100 years) (Stephens *et al.*, 2004), which would result in high forest turnover. Both Monterey and bishop pines can produce viable seed at *c.* 10 years of age (Libby *et al.*, 1968). Native Americans have lived in coastal Alta and Baja California for at least 6000 years, and during this period 60–600 generations of Monterey and bishop pines have become established. Even modest selection pressure for increased bark thickness from Native American burning could have produced the bark characteristics recorded in this study. Since this study did not use methods to isolate the effects of burning, the results should be interpreted as a hypothesis that would benefit from further study.

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BIOSKETCHES

Scott L. Stephens is Assistant Professor of Fire Science at the University of California, Berkeley. He has published on the ecological effects of prescribed fire, the dynamics of forests in north-western Mexico that have a relatively intact disturbance regime, forest fire policy, and the effects of fire and fire surrogate treatments designed to restore western coniferous forests. He has given testimony on fire science and fire policy to the US House of Representatives on three occasions.

William J. Libby is failing his second retirement, having retired from the University of California, Berkeley (Professor of Forestry and Genetics) in 1994, and from the Centre for Advanced Forest Biotechnology, New Zealand, in 1999. While at Berkeley he organized the collections and planted the plantations used in this study. He is currently writing a book on human-caused genetic modifications of forest trees for the Forest History Society, and is a Senior Associate with Zobel Forestry Associates of Raleigh, North Carolina.

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