THE RELATIONSHIP OF BISHOP PINE CONE MORPHOLOGY TO SEROTINY ON SANTA CRUZ ISLAND, CALIFORNIA

Steven M. Ostoja[1] and Robert C. Klinger[2, 3]

[1]Department of Biological Science, California Polytechnic State University, San Luis Obispo, CA 93407
(805) 756-2788, E-mail:sostoja@polymail.calpoly.edu
[2]The Nature Conservancy, 213 Stearns Wharf, Santa Barbara, CA 93101, (805) 962-9111
[3] Current Address: Section of Evolution & Ecology, University of California, Davis, CA 95616
(530) 752-1092, E-Mail: rcklinger@ucdavis.edu

ABSTRACT

We tested the effect of increasing temperature on the serotiny of Bishop pine cones collected from three stands on Santa Cruz Island. We hypothesized that cone adaptations to the historic fire regime would be more important than adaptations to local site conditions or morphological variation, and that patterns of serotiny between the stands would be similar. Fifty cones from each stand were tested at five different temperatures (30°, 80°, 130°, 180°, 230°C). The number of open scales/cone was related positively to temperature, but there was no significant difference in the percentage of scales opening at temperatures greater than 130°C. Morphological differences in the cones existed between the stands, but there was no significant difference between the stands in the percentage of scales opening at the different temperatures. At intermediate temperatures (130° and 180°C), the percentage of open scales/cone was positively related to cone size, but negatively related to the number of scales/cone. These results indicate that local adaptations are not directly influencing serotiny patterns in the island's Bishop pines, and that variations in fire behavior can lead to potentially different patterns of postfire regeneration.

Keywords: Bishop pine, fire, Santa Cruz Island, serotiny.

INTRODUCTION

Bishop pines and other closely related species are characterized by cones sealed by a resinous coating, which melts when exposed to sufficient heat, resulting in the release of mature seeds. Because of this reproductive strategy, and because these species occur in maritime and insular regions dominated by chaparral and scrub communities, it is assumed that they are adapted to historical periodic fires and may even require fire for successful regeneration (Vogl 1973; Zedler 1986). It is also assumed that the level of serotiny in closed cone pines should mainly depend on the fire regime (Holland and Keil 1995), but other factors such as local environmental conditions or morphological traits may influence serotiny as well (Perry and Lotan 1979; Borchert 1985). For Bishop pine as a species, as well as other closely related pines (Monterey pine *Pinus radiata*, knobcone pine *Pinus attenuata*, and pygmy pine *Pinus contorta bolanderi*), an understanding of the degree of serotiny and the relative influence of different factors on serotiny becomes an important element in understanding the ecology of this species.

Stands of Bishop pine on Santa Cruz Island occur in different edaphic and local climatic conditions, possess different morphological characteristics, and have recent differences in the levels and types of disturbance. A general policy of fire suppression during the ranching era of the nineteenth and twentieth centuries prevented the spread of any large fires on the island, and differential grazing impacts by feral sheep have severely reduced fuel loads in some stands and not others (Hobbs 1980; Carroll et al. 1993; Wehtje 1994). Recently, two of the islands three stands of pines have suffered from a wood engraver beetle population increase (*Ips* sp.), which has led to an accumulation of dense, continuous fuel loads within these stands. Linhart et al. (1967) reported morphological variations in cones between the stands, and Hobbs (1980) noted differences among soils and local climate. These local ecological differences could result in cones from different stands opening at different temperatures as a result of varying fire intensities (Gauthier et al. 1996) and potentially different responses to fire by the cones as a result of morphology.

In the long-term absence of fire, a stand of trees may become senescent as individual trees lose vigor and produce fewer and fewer new cones. Observations we made in the stands over the last eight years indicated that cones were opening and seedling regeneration was occurring in all three despite the absence of fire, but how this compared to potential regeneration following a fire was unknown. In addition, the form of the response of the cones opening at different temperatures was unknown. Several possibilities exist, including a direct linear response with increasing temperature; a linear response up to a threshold temperature (beyond which relatively few scales opened); or a stepwise response to multiple ranges of temperatures, where the percentage of scales that opened remained constant within each range.

The goal of this study was to identify the response of Bishop pine cones to varying temperatures, determine whether this pattern was characteristic of the different stands, and relate morphological characteristics of the cones to the patterns we observed in the scales opening. We hypothesized that if morphology or local environmental conditions had modified the response of the cones to the historic fire regime, then we would expect to see different patterns of scales opening between the different stands or among cones of different sizes. Alternatively, if adaptations to the historic fire regime were more important than adaptations to local conditions, then we did not expect to see differences between stands in the proportion of open scales at different temperatures.

From a conservation and management perspective, determination of the relative degree of serotiny between the different populations helps in the development of appropriate fire management plans for the species and the communities they occur in. This understanding includes the prediction of how different populations can be expected to regenerate in response to specific climatic and disturbance events. If the response of Bishop pine cones to varying fire effects is determined, then steps may be taken to more completely understand the fire ecology within this ecosystem where the natural fire regime has been altered.

STUDY LOCATION

A general description of Santa Cruz Island is given in Junak et al. (1995). There are three separate stands of Bishop Pines on Santa Cruz, commonly referred to as the east (or Chinese Harbor), north (or Pelican Bay), and west (Christy) stands (Linhart et al. 1967). The three stands occur in different soil types and differ considerably in floristic structure and composition, but all are on sites exposed to maritime influences and occur where fog is common in the summer (Minnich 1980).

The east stand occurs on the north and south maritime facing slopes in the isthmus of the island. The stand is divided into two subsections; a north facing zone overlooking Chinese Harbor and a south-facing zone overlooking Yellowbanks (also known as Los Pinos del Sur). The elevation ranges from 100 to 300 m. Soils in both zones are derived from the Monterey Shale Formation, and tend to be shallow and relatively well drained. Bishop pines are not uniformly distributed in the stand, but are scattered in relatively discrete patches. The stand has a dense layer of shrubs, including *Quercus parvula, Q. pacifica, Arctostaphylos viridissima, Adenostema fasciculatum, Lotus dendroideus, Mimulus longiflorus,* and *M. flemingii*. Herbaceous species are relatively uncommon in most parts of the stand, and the organic litter layer is deep and relatively uniform in extent.

The north stand occurs from Twin Harbors to Prisoners Harbor, but pine trees reach their greatest density in the Pelican Bay region, roughly midway between the other two harbors. Trees in this area occur in a relatively uniform distribution, but become more scattered towards Prisoners Harbor. The elevation ranges from 50 to 250 m. Soils are derived from basalt formations, and tend to be very shallow and rocky. Much of the physiognomy is a result of 100 years of overgrazing by feral sheep (Hobbs 1980; Wehtje 1984). The north stand is more open than the east or west stands; the shrub layer is relatively low and open, and comprised predominantly of *Arctostaphylos tomentosa, M. flemingii, Q. pacifica,* and *Q. parvula*. Ground cover is mainly bare ground, with relatively little herbaceous cover or organic litter.

The west stand occurs from Centinela pass to Cañada Christy and Sierra Blanca ridge, with the densest concentration of trees occurring towards the upper parts of Cañada Cervada and Cañada Sauces. The trees tend to occur relatively uniformly throughout the stand, although discrete clumps of trees occur on the outer parts. The elevation ranges from 100 to 500 m. The soils are highly variable in depth, and are derived from three different geologic formations: Willows diorite, Blanca volcanics, and Santa Cruz Island schist. The west stand is the most diverse of the three in floristic composition and structure. There are relatively few shrubs in parts of the stand where soils are shallow and well drained, but in most parts the shrub layer is extremely tall and dense and the litter layer is deep. Species richness is high, and includes *Q. pacifica, Q. parvula, Heteromeles arbutifolia, Cercocarpus betuloides, Ceanothus arboreus, M. longiflorus, Arctostaphylos glauca, A. tomentosa, L.dendroideus,* and *Adenostema fasciculatum*. Herbaceous species include *Lilium humboldtii, Dichelostemma capitatum, Calochortus albus, Silene laciniata,* and *Sanicula hoffmannii.*

METHODS

We collected 150 cones in the summer of 1995 and stored them in paper bags in a cooler at 5°C. Five cones were randomly selected from each of ten trees in each stand. Trees were selected to be relatively uniform in age and size class. Because prior classification of pines into two species on Santa Cruz has been rejected (Linhart et al. 1967; Junak et al. 1995), and because cones with characteristics of the two varieties can occur on the same tree (R. Klinger, pers. obs.), we did not attempt to stratify the cones by forma.

From each cone the maximum length, width at widest point, weight, and the number of scales were recorded. Scales were counted on a randomly selected quarter of each cone. One of the five cones from each tree was randomly selected for exposure to a different temperature setting ranging from 30°C to 230°C in 50° increments (30°, 80°, 130°, 180°, or 230°). Any cone selected for any specific heat treatment which had any degree of scale separation was not included in the analysis (n=4).

In a laboratory oven each randomly selected cone was subjected to a specific temperature setting for a period of 25 minutes. To account for temperature fluctuations, the oven was preheated for the desired setting for 30 minutes prior to cones going into the oven chamber. To insure accurate temperature readings, three laboratory thermometers were also used both during the duration of the preheating period and during duration of each actual run. At the end of each run the cones where removed and set out at room temperature for a period of 20 minutes. We felt this was representative of the period of time when a fire has passed, yet cone response is not complete. Each cone was then reweighed, inverted to remove the seeds, and open scales counted. Only scales that were thought to be sufficiently open for seed displacement were considered open scales.

For each cone we calculated the percentage of scales that opened, then tested differences between stands and temperatures with a 2-way ANOVA with one nested factor (trees within stands). We used a Tukey test for post-hoc comparisons. We tested differences between stands in cone size (height) and the number of scales/cone with a MANOVA with the same nested factor as in the 2-way ANOVA. All cones were included in the analysis. We tested the relationship between the percentage scales open/cone and the size and number of scales/cone with multiple linear regression analysis. We tested this relationship for temperatures >30°C because very few scales opened at this temperature. Each temperature was analyzed separately.

Prior to accepting the results of any statistical test, we performed a residual analysis to test assumptions underlying parametric ANOVA. The number of scales/cone was square root transformed for the MANOVA test. Two cones were identified as outliers in the 2-way ANOVA and omitted from the analysis. We dropped one outlier from the 130° analysis, two from the 180° analysis, and one from the 230° analysis in the multiple regression tests. Cases with missing data (scales already opened) were also omitted from the analyses.

RESULTS

We computed a Pearson correlation matrix to assess redundancy among the variables we measured for each cone (Table 1). Height, width, and weight were strongly correlated with each other, therefore we selected height and the number of scales as the variables we would use in statistical tests. We selected height because the data had a more normal distribution than width and weight.

There was a significant relationship between temperature and the percentage of open scales/cone ($F=327.08$, $df=4,102$, $p=0.000$). Cones tested at 30°C had significantly fewer open scales than all other temperatures; <1% of the scales opened at this temperature. Cones tested at 80°C had significantly fewer open scales than the three higher temperatures, but there was no significant difference between 130°, 180°, and 230° (Figure 1). There was no significant difference in the percentage of scales opening between the different stands ($F=0.71$, $df=2,102$, $p=0.49$) or in an interaction between stands and temperature ($F=1.15$, $df=8,102$, $p=0.34$).

There was a significant difference in cone size and the number of scales/cone between the three stands (Wilks Lambda=0.286, $F=51.68$, $df=4,238$ $p=0.000$). There was no significant difference in the number of scales/cone between the north and east stands ($F=0.099$, $df=1,120$, $p=0.754$), but cones from the north stand were 27% larger than cones in the east stand ($F=4.24$, $df=1,120$, $p=0.042$). Cones from the west stand were significantly larger and had significantly more scales than cones in either of the other stands (Wilks Lambda=0.296, $F=141.83$, $df=2,119$, $p=0.000$). Cones from the west stand were 33% larger and had 35% more scales than the other two stands (Figure 2).

There was no significant relationship between cone size or the number of scales/cone and the percentage of open scales/cone for the 80° and the 230° tests. There was a significant positive correlation between cone size and the percentage of open scales/cone and a significant negative correlation with the number of scales/cone and the percentage of open scales/cone for 130° and 180° (Table 2).

Table 1. Pearson correlation coefficient matrix between four variables measured on Bishop pine cones from Santa Cruz Island, CA.

	Height	Width	Weight	Scales
Height	1.000			
Width	0.813	1.000		
Weight	0.840	0.895	1.000	
Scales	0.541	0.594	0.626	1.000

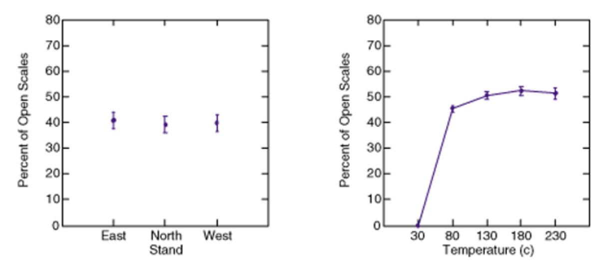

Figure 1. The percentage of scales opening on Bishop pine cones as a function of temperature and stands from which cones were collected. Santa Cruz Island, California, 1995.

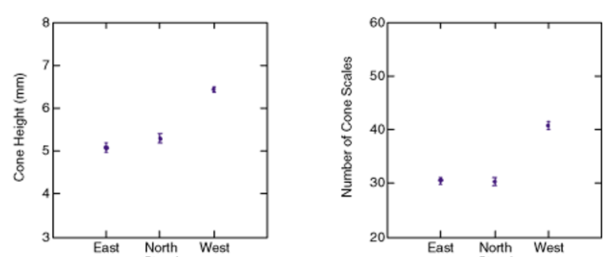

Figure 2. Relationship between the size of Bishop pine cones and the number of scales/cone among three stands on Santa Cruz Island, California.

Table 2. Multiple linear regression tests of the relationship between percent open scales and the height and number of scales/cone from Bishop pines on Santa Cruz Island, CA.

Effect	Coefficient	95% C.I. Lower	95% C.I. Upper	t	p
80°					
Constant	37.46	20.07	54.85	4.42	0
Height	1.7	-1.54	4.93	1.07	0.292
Scales	-0.05	-0.52	0.42	-0.23	0.823
R=0.213, Adjusted R^2 = 0.00					
130°					
Constant	39.72	24.15	55.28	5.25	0
Height	5.69	2.75	8.63	3.98	0
Scales	-0.62	-1.05	-0.19	-2.95	0.007
R=0.627, Adjusted R^2 = 0.347					
180°					
Constant	53.72	35.3	72.26	5.99	0
Height	4.87	1.02	8.72	2.6	0.015
Scales	-0.87	-1.39	-0.35	-3.46	0.002
R=0.578, Adjusted R^2 = 0.281					
230°					
Constant	71.41	52.04	90.77	7.63	0
Height	-1.12	-5.63	3.39	-0.51	0.612
Scales	-0.36	-0.98	-0.27	-1.18	0.25
R=0.399, Adjusted R^2 = 0.086					

DISCUSSION

The results of this study suggest that a serotiny threshold of 80° to 130°C exists for Bishop pines in all three stands on Santa Cruz Island. This similar cone response in all the stands probably indicates the importance of adaptation to a historic fire regime, with local environmental factors having relatively little influence on the response. Studies done on jack pine in the Great Lakes region of North America indicate that adaptations to historic fire regimes (or, alternatively, adaptations over large geographic scales) may be more facultative than obligatory, and populations which are relatively close geographically but occur in sites with different fire regimes can evolve different levels of serotiny (Gauthier et al. 1996). The most likely reasons we do not observe this on Santa Cruz Island is that variations in local factors are not important enough, or have not existed long enough, to override the more important influence of similar temperature and moisture patterns which occur in the maritime areas across the island.

Although Bishop pine cones will open at ambient temperatures, this fraction is very small compared to the proportion opening at higher temperatures. However, increasing temperatures beyond 130°C does not result in a greater proportion of scales opening, indicating that hotter fires may not necessarily benefit seedling regeneration any more than a relatively cool fire would. It is even possible that a hotter fire could result in lower seedling germination if shed seeds were burnt directly in the flame, scorched in the hot ash bed, or rendered inviable if nutrients were volatalized.

Our results show that the cones in the west stand are larger and have more scales than in the eastern or northern stands, which is consistent with the findings of Linhart et al. (1967). This size difference is most likely a function of abiotic factors providing a better habitat, including greater amounts of fog, lower wind velocity and richer soil with greater water holding capacity (Hobbs 1980). As a result, the trees can probably put more resource allocation into reproduction than physiological maintenance.

The influence of cone size on serotiny only at intermediate temperatures may be an interaction between physical mechanisms and evolutionary adaptations. At lower temperatures, there is not enough heat to physically make most cones open, while at high temperatures there is so much heat that opening in all cones will be at a maximum, regardless of size. But in the intermediate temperature ranges, it may be an evolutionary advantage to have larger cones open and release greater absolute amounts of seed than small ones. Larger cones have a relatively lower number of scales open than smaller ones, which probably is related to the surface area of the cone that is exposed to heat. But in terms of absolute numbers, more seeds will be released from the larger cones, thereby increasing the number of seeds that could survive to germinate and become established in the burn area. If this hypothesis were true, it would imply that different patterns of seedling regeneration would occur in each of the stands as either a function of varying fire intensity or as a result of differential morphology following fires of intermediate intensity.

It has been suggested that without fires, closed cone conifers may be at risk of succumbing to parasites and be replaced by other species (Holland and Keil 1995). Because Bishop pines will reproduce without fire, this scenario would probably only happen under extreme conditions. However, it is clear that reproduction in Bishop pines is greater at higher temperatures, and since the community they occur in is characterized by species with fire adaptations (Carroll et al. 1993), it would appear as if some degree of burning within the stands would not have any severe detrimental effect on the species or the community. However, allowing fires to occur in the Bishop pine stands should be approached cautiously. Because of suppression practices over the last 150 years, fuel loads in the western stand are very high and a fire would exhibit extreme behavior. The north stand is recovering from overgrazing by feral sheep, and regeneration is relatively high. Seedlings and saplings are relatively young and could be killed by a fire, therefore fire in this stand is probably inappropriate for another 10 to 25 years. In addition, pine stands have a greater proportion of native species than most other vegetation communities on Santa Cruz, and consideration must be given to what types of nonnative fire following species would colonize the stands after a burn. A high proportion of nonnative species did not invade a prescribed burn in the east pine stand in 1994 (R. Klinger, unpublished data), however this may not be the case in the other stands.

Although we have determined serotiny characteristics of Bishop pines on the island, a great deal of ecological work needs to be done to increase our understanding of factors determining reproductive patterns of the species and community attributes of the stands. Systematically broadening the scope of our knowledge of Bishop pines and the island pine community can contribute substantially to the understanding of ecological and evolutionary adaptations to fire in this and other maritime and insular closed cone conifer forests.

ACKNOWLEDGMENTS

We thank Rashell Ralston for collecting the cones, and technicians in the Biology Department at Cal Poly San Luis Obispo for designing and constructing the oven we used in the temperature trials. Comments from two anonymous reviewers improved the quality of the manuscript.

LITERATURE CITED

Borchert, M. 1985. Serotiny and cone-habit variation in populations of *Pinus coulteri* (Pinaceae) in the southern Coast Ranges of California. Madroño 32:29-48.

Carroll, M. C., L. L. Laughrin, and A. Bromfield. 1993. Fire on the California islands: does it play a role in chaparral and closed cone pine forest habitats. Pages 73-88 *in* Hochberg, F. G. (ed.), The Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Gauthier, S., Y. Bergeron, and J. P. Simon. 1996. Effects of fire regime on the serotiny level of jack pine. Journal of Ecology 84:539-548.

Hobbs, E. 1980. Effects of grazing on the northern populations of *Pinus muricata* on Santa Cruz Island, California. Pages 159-166 *in* Power, D. M. (ed.), The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum Of Natural History, Santa Barbara, CA.

Holland, V. L. and D. J. Keil. 1995. California Vegetation. Kendall/Hunt, Dubuque, IA.

Junak, S., T. Ayers, R. Scott, D. Wilken, and D. Young. 1995. A Flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, CA.

Linhart, Y. B., B. Burr, and M. T. Conkle. 1967. The closed cone pines of the Northern Channel Islands. Pages 151-178 *in* Philbrick, R.N. (ed.), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, CA.

Minnich, R. 1980. Vegetation of Santa Cruz and Santa Catalina Islands. Pages 123-128 *in* Power, D. M. (ed.), 1980. The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Perry, D. A. and J. E. Lotan. 1979. A model of fire selection for serotiny in Lodgepole pine. Evolution 33:958-968.

Vogl, R. J. 1973. Ecology of knobcone pine in the Santa Ana Mountains. Ecological Monographs 43:125-43.

Vogl, R. J., W. P. Armstrong, K. L. White, and K. L. Cole. 1977. The closed cone pines and cypress. Pages 295-358 *in* Barbour, M. G. and J. Major (eds.), Terrestrial Vegetation of California, John Wiley and Sons. New York, NY.

Wehtje, W. 1994. Response of a Bishop pine (*Pinus muricata*) population to removal of feral sheep on Santa Cruz Island, California. Pages 331-340 *in* Halvorson, W. L. and G. Maender (eds.) The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Botanic Garden, Santa Barbara, CA.

Zedler, P. H. 1986. Closed-cone conifers of the chaparral. Fremontia 14:14-17.

SOURCES OF UNPUBLISHED MATERIALS

Klinger, R. C., Ecologist. The Nature Conservancy, Santa Cruz Island Preserve, 213 Stearns Wharf, Santa Barbara, CA. 93101. (805) 962-9111. [Present Address: Section of Evolution & Ecology, University of CA, Davis, CA 95616, (530) 752-1092, rcklinger@ucdavis.edu]. Observations on pine cone morphology, data on prescribed burn in east stand of Bishop pines.