REGENERATION OF BISHOP PINE (*PINUS MURICATA*) IN THE ABSENCE AND PRESENCE OF FIRE: A CASE STUDY FROM SANTA CRUZ ISLAND, CALIFORNIA

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ABSTRACT

Remnant stands of overaged Bishop pine (*Pinus muricata*) on Santa Cruz Island suffered catastrophic mortality rates during the pronounced California drought episode of 1986-1991. This pine is generally characterized as a fire-obligate species. Natural fires are, however, quite exceptional on the Channel Islands, and the life span of Bishop pines does not exceed 60 to 80 years. How then has this population persisted over centuries and millennia? We established circular census plots of 0.1 acre in size surrounding tall pine snags in three pine patches. We counted all seedlings and saplings and recorded their ages. The results showed that the dying and dead pine stands were substantially regenerating in the absence of any wildfire. An out-of-control prescribed fire — fanned by Santa Ana winds— burned most of the eastern pine patch in December 1994; it provided a rare opportunity to evaluate the impact of the fire factor on this pine population. This event consumed most living and dead biomass above the surface. The hypothesis of a resilient 'pyrofugal' species is proposed that evades post-Pleistocene fire regimes in landscapes where natural wildfires are rare.

Keywords: Bishop pine, *Pinus muricata*, closed cone pines, Santa Cruz Island, fire ecology, island biogeography.

INTRODUCTION

The Bishop pine (*Pinus muricata*) is a member of a small set of closed cone pines that are generally considered to be fire-dependent for regeneration and long-term persistence. In this paper we report and discuss data on the natural regeneration on Bishop pines on Santa Cruz Island, the largest of the California Channel Islands, where natural wildfires have been exceedingly rare in historic time. Based on anecdotal qualitative information from brief visits of Bishop pine stands on the island, we developed the following research hypothesis: Bishop pines of Santa Cruz Island do not require periodic fire events for seed germination and stand regeneration. Our specific objectives were to seek answers to the following questions:

1. How much stand regeneration occurs with and without the presence of wildfires?

2. What are the mechanisms of seed availability, dispersal, and germination in the Bishop pine?

3. What is the role of fire in the evolution and ecology of coastal pine species?

CLOSED CONE PINES AND FIRE

In closed cone pines the cones do not open and release their seeds right after maturation; instead the cones are serotinous or 'late-opening' and retain the seeds in the tree canopy or inside the cone for many years. Viable seed was taken from cones of lodgepole pine (*P. contorta* var. *latifolia*) 75 years after cone maturation (Agee 1993:133). The high ambient temperatures of a fire burning through the crown of a serotinous pine melts the resin seal of the closed cones, and "they open soon after" (Agee 1993:134). In the introduction to their review of California closed cone pine and cypress taxa Vogl et al. (1977:295) state: "The major species are intimately related to fire, characterized by a closed-cone habit or by serotinous cones, whereby the ovulate cones remain sealed after maturity, usually accumulating on the tree until opened by fire." In California, there are three principal species with closed cone characteristics, knobcone pine (*P. attenuata*), Monterey pine (*P. radiata*), and Bishop pine (*P. muricata*).

Knobcone pines occur in California on apparently infertile, acid, and dry substrates that may also contain toxic elements; such substrates limit and reduce the growth and presence of other plant species. Stands of this pine generally occur where they are exposed to marine air; the substrate (often serpentinite) has a high water-retaining capacity. Cones of this pine remain unopened and attached to the trunk, usually for the life of the tree. Detached cones and those on fallen branches and pine snags also remain closed. "Only rarely do the heavy, wooden cones open without fire. Reproduction is also absent in decadent stands where the majority of trees are senescent or dying" (Vogl et al.

1977:330). Fire-opened cones shed their seeds to the ash-covered surface; the seedbed is rich in minerals and offers high insolation. The trees have a short life span of around 50 years, rarely 100 years. Fire frequency is 33 to 50 years due to favorable fuel conditions, relatively dry sites, and the proximity of other fire type communities.

Monterey pines occur naturally within 8 km of the coast of central California, from sea level to 300 m. There is no clear understanding of the physical or biotic factors limiting this highly successful commercial timber tree to its restricted range. The cones remain on the trees for years, but open and close several times during this period, producing a light seed rain that results in small numbers of pine seedlings. In one study, the latter were thin, small, and had sparse needles (Vogl et al. 1977). By contrast, strong and healthy seedlings were found after a recent surface burn. Fires that produce optimum conditions for reproduction "are not as often the catastrophic types common to the other species, but are more frequently surface fires in which parent trees survive" (Vogl et al. 1977:347).

The Bishop pine occurs in California from Humboldt County in the north to Santa Barbara County, and on Santa Cruz and Santa Rosa islands; in Baja California, it is found in two isolated stands on Cedros Island and near San Vicente. This pine is morphologically more variable than other pines; it exists in maritime climates along the coast and up to 400 m above sea level. Frequent fogs and fog drip provide additional moisture to the pines in the often extremely long dry late spring, summer, and fall season. Vogl et al. (1977:337) surmise that this pine "has survived climatic changes since the Pleistocene times because of reduced plant competition on the poor, acid, and often swampy soils, … and possible high water tables." Stands of Bishop pine are "characteristically even-aged, originating after fire.... On rare occasions, old cones open on hot days. …A fire-free period of 80+ year (yr) would also allow trees to succumb to diseases and die without reproducing….Fire appears to be a critical factor in the continuance of *P. muricata*…" (Vogl et al. 1977:337-338).

In their concluding paragraphs, the authors make a strong case for the necessity of fire for the long-term persistence of the closed cone pines: "Since most of these conifers are obligate fire types, fire cannot be eliminated or replaced by any other process….If fire is not reintroduced, these groves and forests will eventually be eliminated…The continuance of these conifers, however, can be assured only by ecological management, which will have to include the reintroduction of fire" (Vogl et al. 1977:349-350).

In summary, the expert assessment of these and other closed cone conifers emphasizes the importance of fire for stand continuance and survival of the species. Reproduction and regeneration without an accompanying fire event is seen as uncommon or rare processes and leading to the development of weak pine seedlings.

PINES AND FIRE ON THE CHANNEL ISLANDS

The effect of fire on the vegetation and pines of the Channel Islands has been investigated by several authors. Hobbs studied the regeneration of all three populations of Bishop pine on Santa Cruz Island in 1977-1978 (Hobbs 1980). She established study sites and counted the number of seedlings in each. No seedlings were found in the sheep-grazed northern population, but pine seedlings were recorded in every sheep-free study site located in the western and eastern pine stands. She questioned the existence of an obligate fire factor by concluding: "Moreover, the fact that abundant regeneration was recorded in the other two populations dismisses the question of whether fire is a necessary agent for opening the cones and distributing seed" (Hobbs 1980:165).

A more detailed mapping of the northern pine population was carried out by W. Wehtje in 1990. Between 1981 and 1988 over 37,000 feral sheep were removed from the central and western part of Santa Cruz Island, and the general area of the northern pine stand was essentially sheep-free by 1985 (Wehtje 1994). Some 65% of the pine seedlings recorded in 1990 were 5 yr or younger. Many of them had recolonized grassy and bare surfaces that had been free of pines as a result of a massive 4800 ha fire that occurred in September 1931 (Hobbs 1980; Carroll et al. 1993), and of serious overgrazing. A small lightning-caused fire in 1987 burned 1.4 ha of the northern study area. Wehtje examined the remaining evidence of this fire as well as charcoal from the earlier fire. Both fires killed many pines, in 1987 "even when only scorched"; he concluded that "Bishop pine appears to be very sensitive to fire damage" (Wehtje 1994:339).

Contrary, therefore, to the almost uniformly positive assessment of the fire factor by many authors, and the pleading for the "reintroduction" of fire by Vogl et al. (1977:350) in the ecological management of close cone forests, the evidence from the two Santa Cruz Island studies does not support the need for fire in Bishop pine persistence and regeneration.

Other research has documented the rarity of lightning-caused fire on the Channel Islands; only three such events have occurred in recorded history compared to some 44 accidental and intentional fires (Carroll et al. 1993). Post-fire analysis of plant succession and richness on Santa Catalina Island shows vigorous resprouting and germination of native island shrubs, trees, and herbs. Germination experiments of both mainland and island chaparral shrubs revealed interesting differences, however. Significant numbers of island seeds exhibited higher germination in unburned control sites than their mainland counterparts. This may reflect an adaptation of island taxa to a lower fire frequency and greater time intervals between fires favoring between-fire seedling establishment (Carroll et al. 1993). No pines were included in these studies.

Bishop pines were found as macrofossils in deposits on Santa Cruz Island dated 14,000 BP. "Abundant" charcoal in Holocene deposits of this island may be have resulted from natural prehistoric fires (Junak et al.1995:35) or from accidental or intentional fires caused by native Americans who were a part of this island ecosystem for the past 7,000 to 10,000 years. We are not aware of any study containing detailed prehistoric fire intensity and frequency data for Santa Cruz Island; thus we are left wondering whether there were large fires every 500 years or so, whether the frequency alternated depending on fluctuating climatic cycles and/or the need or carelessness of Native Americans fishing and harvesting marine resources on the island.

The three disjunct stands or populations of Bishop pine (Figure 1) consisted of overaged trees as well as many young saplings and seedlings in the late 1980s. The severe California drought of 1986-1991 in conjunction with a severe bark beetle infestation killed off nearly every tall pine in the denser stands. By 1994, the island landscape had lost the familiar green pine forest patches and gained instead two rather unsightly stands of dead trees in the western and eastern part of the island (Photo 1). In the northern pine patch, however, mature trees grew in isolated clusters; they died as well but their snags did not dominate the landscape due to the presence of evergreen oak and ironwood trees as well as many pine saplings.

In May 1994, we heard rumors of a plan for a prescribed fire in the eastern pine patch. We had looked forward to observe the regeneration process of all pine patches without fire and sheep-grazing; based on the existing database from detailed field-based studies (Hobbs 1980; Wehtje 1994) and abundant qualitative evidence of widespread pine germination (Photo 2) and recolonization, little if any rationale existed for staging an intentional fire event. This provided the stimulus for our research.

Photo 1. Senescent stand of Bishop pine (*Pinus muricata*); western patch, 19 September 1994.

Photo 2. Pine seedling under snag; western patch, 19 September 1994.

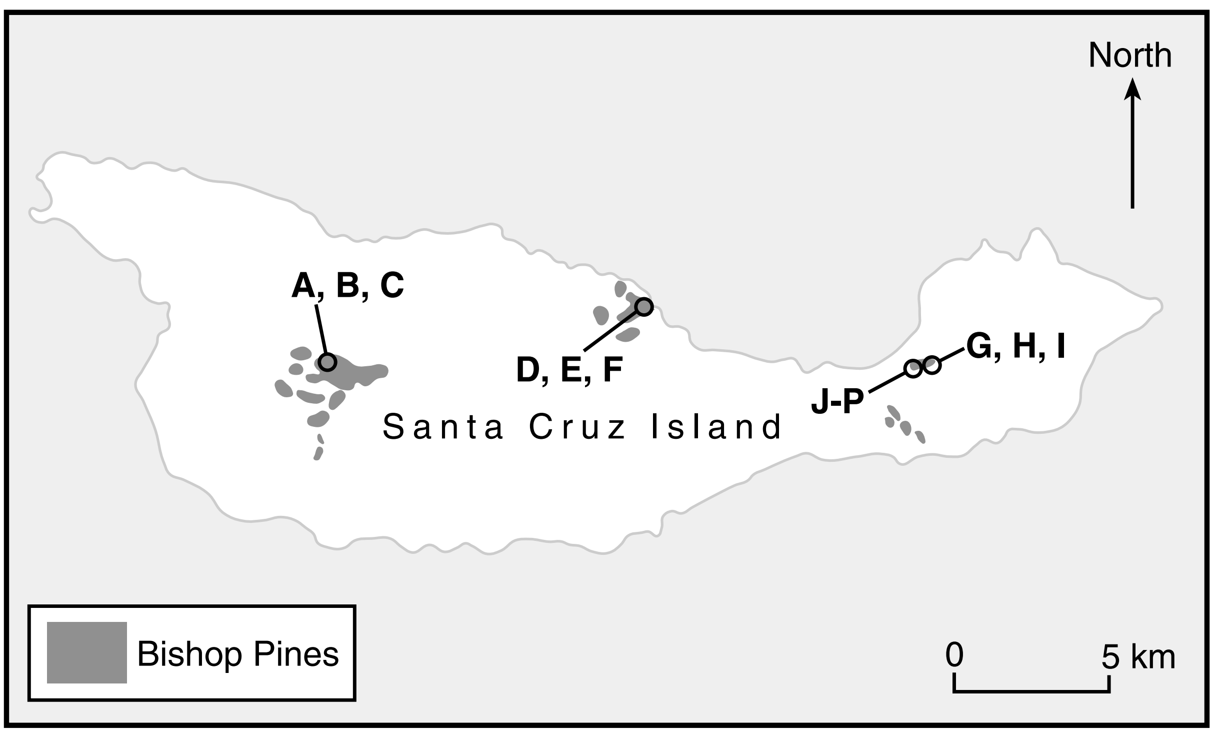

Figure 1. Location of study plots in the Bishop pine stands of Santa Cruz Island. Simplified map from Wehtje (1994).

STUDY SITES AND METHODOLOGY

In September 1994 we established study plots for a quantitative survey of pine regeneration in the northern and eastern pine patches but not in the western patch. On 7 December 1994, a prescribed burn of part of the eastern pine patch was conducted by the Nature Conservancy and the National Park Service. Unfortunately, a strong Santa Ana wind developed the following night, re-igniting the fire and creating a firestorm that burned nearly the entire eastern patch, including our study plots. In June 1998, all study plots were revisited and new plots censused in the western patch as well as in the post-fire habitat of the eastern patch (Figure 1).

Census of Pine Seedlings

Our research goal was not to establish an accurate figure of seedling density for the entire patch; we wanted to document the natural regeneration potential of mature and senescent Bishop pines. Three study plots were established in each pine patch (plots A -I). At random, we selected the trunk of a large dead pine as the center of each study plot and delineated a circular area around it of 0.1 acre in size. A random selection of study sites irrespective of the presence of snags was avoided for two reasons: 1) there was a scarcity of tall snags with potentially thousands of cones, and 2) we wanted, wherever possible, to establish the origin of any pine seedling counted. In some instances, other snags were nearby, however, and their cones and seeds may also have dispersed into the study plot.

We measured the circumference of each pine at breast height (dBH); we counted every live, diseased, or dead pine seedling standing in a plot. Each pine was aged according to the number of annual whorls present. This method of aging was generally simple and accurate; in rare cases, however, Bishop pines may grow two whorls per year creating an overestimate of age by at most one or two years. We determined site characteristics for each pine seedling's germination site as either bare ground (or grass cover), under snag (beneath pine trunk or downed branches), or under tree/shrub (oak tree/shrub, manzanita, and others).

In 1998, we established seven new study sites (J-P) in the burned section of the eastern patch. No tall pines had survived the fire and we selected at random any standing stem indicating the former presence of a mature pine.

Longer-term Observations of Pine Regeneration

The senior author has photographed and recorded portions of the island's pine patches since 1972. In particular, he became interested in the fate of two solitary pine trees growing out of the stony and denuded ridge of the Sierra Blanca to the SW of the western patch. Their demise and seed release and subsequent growth of young pines was followed with great interest from 1990 to 1999.

Cone Opening, Seed Release, and Germination

We made observations on the presence of open and closed cones on the ground and on branches and trunks of live and dead pines (Photos 3 and 4). In addition, the senior author collected three dozen cones of various sizes, from dead and live branches of pines from the eastern and western patches. Three of the cones had opened by circa 40% at the time of collection from a snag. The others were closed and often covered with lichen.

The cones were put in a plastic bag, sealed, and hidden from the sun and other heat sources. They were then put in a large plastic salad bowl and positioned on a backyard table in West Los Angeles where they were fully exposed to the normal midday and afternoon sun and ambient temperatures. Every few days the bowl was checked for newly opened cones, and all released seeds were collected and stored in small stamp envelopes.

A dozen of the released seeds were placed in standard pine germination tubes, filled with half garden and half potting soil, on 15 November 1998; the tubes were left on a garden table in West Los Angeles and watered twice per week through March 1999. An additional 72 seeds were placed in potting soil on 1 February 1999.

Photo 3. A Bishop pine snag with thousands of closed pine cones, 19 September 1994.

Photo 4. Close-up of a cluster of mature spiky 'razorback' closed cones of dead Bishop pine, 19 September 1994.

RESULTS

All study plots contained pine seedlings in the absence of fire (Photos 5 through 8). In 1994, study plots D-I had a total of 312 live seedlings (max. 187, min. 7/plot) on 0.6 acre of pine-occupied surface (Table 1); this equals 520 seedlings/acre or 1,484 seedlings/ha. The parent trees of these seedlings measured between 72 and 220 cm in circumference. Larger snags had more seedlings around them. Some snags still had closed cones on their branches.

The western pine patch (plots A-C) was censused four years later. It contained more seedlings than the other patches, but 223 out of 334 seedlings were 4 yr or younger; only an average number of 36.7 seedlings/plot were 5 yr or older. We assume that some members of the 5+ yr cohorts perished between 1994 and 1998; still, the general magnitude of pine seedlings appears to have been similar to that of the other plots in 1994.

Figures 2 and 3 show the age distribution of Bishop pine seedlings. Germination and survival rates were highest in the years of 1993 and 1994. The oldest seedlings go back to 1975 in the western patch, 1981 in the northern patch, and 1985 in the eastern patch.

Most seedlings were growing on bare ground or in a low grass cover (Table 2) but a sizable number of seedlings had germinated and survived beneath the canopy of shrubs or live trees belonging to manzanita (*Arctostaphylos* sp.), oak (*Quercus* sp.), or other non-coniferous plants (Figure 4). The lowest germination and survival was recorded for seedlings located under the parental tree's trunk and cone-laden branches (Table 2).

Photo 5. Pine snags and seedlings west of Pelican Bay; northern patch, 21 September 1994.

Photo 6. Dead pines and oak trees, and pine saplings near Pelican Bay; northern patch, 8 August 1991.

Photo 7. Dead pines dominate the island landscape; eastern patch, 20 September 1994.

Photo 8. Small pine seedlings on bare surface of trail leading through the eastern patch, 20 September 1994.

Table 1. Live Bishop pine seedlings on Santa Cruz Island (1994, 1998).

Age	Plot									Total
	A	B	C	D	E	F	G	H	I	
1	21	11	10	55	1	4	11	8	3	124
2	0	26	10	64	2	3	15	6	2	128
3	4	46	10	31	1	7	9	6	1	115
4	11	53	21	15	3	1	6	1	0	111
5	6	24	20	5	5	1	3	0	0	64
6	2	6	4	3	4	0	0	0	1	20
7	3	5	7	3	5	0	0	1	0	24
8	2	0	4	2	1	1	0	0	0	10
9	3	0	2	2	2	0	0	0	0	9
10	3	1	2	4	1	0	1	0	0	12
11	4	1	0	0	2	0	0	0	0	7
12	0	0	2	0	4	0	0	0	0	6
13	1	0	2	2	0	0	0	0	0	5
14	1	0	0	1	3	0	0	0	0	5
15	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0
17	1	0	1	0	0	0	0	0	0	2
18	1	0	0	0	0	0	0	0	0	1
19	1	0	1	0	0	0	0	0	0	2
24	1	0	0	0	0	0	0	0	0	1
Total	65	173	96	187	34	17	45	22	7	646

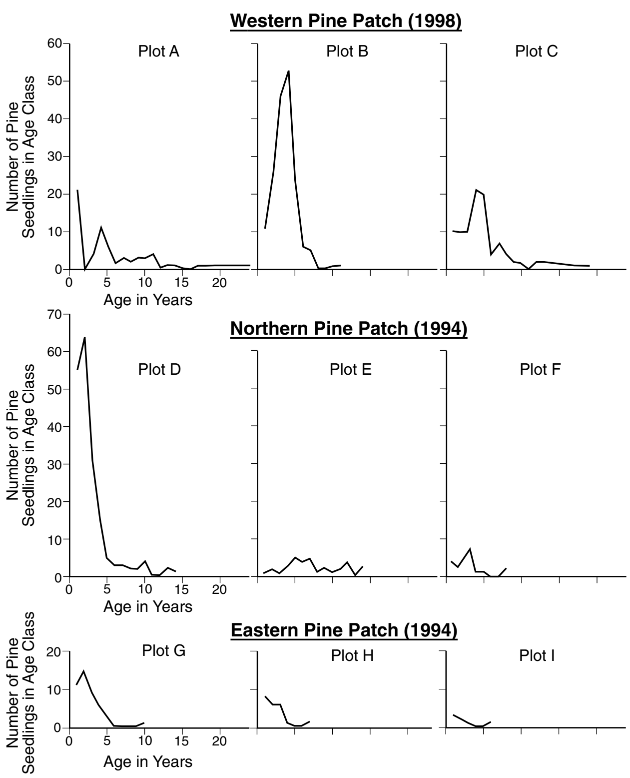

Figure 2. Number of pine seedlings counted per age class in nine study plots.

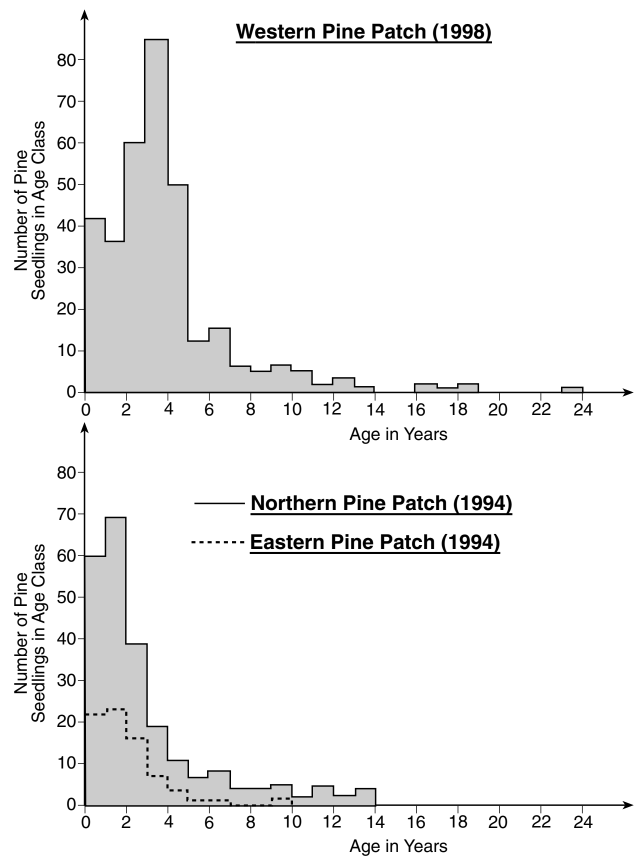

Figure 3. Cumulative total number of pine seedlings counted in the western, northern and eastern pine patch. Note that the western patch was censused four years later than the others.

Table 2. Location of live pine seedlings/saplings.

Plot	Plot Type			Total
	Bare Ground	Under Snag	Under Live Shrub/Tree	
A	43	8	14	65
B	84	42	47	173
C	59	22	15	96
D	177	3	7	187
E	31	0	3	34
F	16	0	1	17
G	18	13	14	45
H	9	7	6	22
I	2	3	2	7
Total	439	98	109	646
%	68%	15%	17%	100%

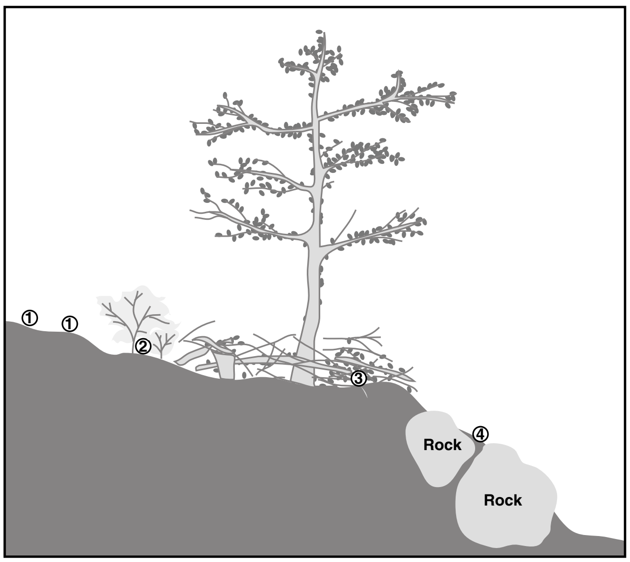

Figure 4. Typical microhabitats for the germination and growth of pine seedlings on Santa Cruz Island: 1) bare surface or grass, 2) under shrubs and trees, 3) under snags and dead branches, and 4) in rock cracks.

The seven study plots on the burned eastern pine patch had a total of nine pine seedlings: three plots had no seedlings at all; the others had 1 (5 yr), 1 (3 yr), 3 (3, 4, 5 yr), and 4 (3, 4, 4, 5) seedlings. The 1994 wildfire had burned everything with the exception of the central lower stems of some of the biggest trees (Photos 9 and 10). Branches, twigs, and all cones on the ground and in the tree canopy of snags and all non-pine vegetation had burned up. On 25 June 1998, the island's plant community was in an early stage of fire recovery. Three oak species were resprouting strongly, *Arctostaphylos* seedlings were abundant, and there were annual and perennial wildflowers and grasses everywhere. But there were practically no pine seedlings. A somewhat tentative re-census of the 1994 study plots (the exact boundaries were unclear as the parent tree snags had disappeared) revealed no surviving pine seedlings.

The examination of pine snags in unburned sections of the island showed that the trees were heavily loaded with cones. More of the latter were opened the longer the tree had been dead. The ridge pines of the Sierra Blanca had been dead at least 5 to 10 years by 1992. They still held unopened cones, but on the steep east-facing slope beneath them, the seeds of these parent trees had already established a new grove of dozens of young pines 5-10 yr old.

A total of 25 mature cones (gray and brown colored) were among those collected from the ground or cut from branches of dead Bishop pines on 23 and 25 June 1998. In the ambient warm summer climate of West Los Angeles (max. daily temperatures 24 to 33°C.) several half-opened cones began to open completely within a few days and to release their seeds. After just 30 days 217 seeds had fallen out, an additional 495 in the next 30 days, and another 224 by 3 October 1998, when all cones had released all their seeds. No force or artificial heat source was used to open any of the cones. A total of 936 seeds were counted (37.4 seeds/cone).

Photo 9. Same trail as on Photo 8 leading through post-fire successional landscape of eastern patch. Note the few charred remains of former pine stand, 25 June 1998.

Photo 10. Successional habitat four growing seasons after wildfire event with *Quercus*, *Arctostaphylos, Mimulus*, and *Lotus* shrubs; eastern pine patch near China Harbor, 25 June 1998.

Germination trials of these seeds are still under way. The first of 12 seeds placed in small soil-filled tubes on 15 November 1998 germinated 60 days later and was a healthy-looking, 2.5 cm tall seedling on 22 January 1999; the second seedling emerged on 9 February 1999. Five seeds from the second batch of 72 seeds had germinated by 30 March 1999. All seedlings had a vigorous appearance.

DISCUSSION

Our results confirm and consolidate the earlier findings of Hobbs (1980) and Wehtje (1994) about the natural regeneration of Bishop pines on Santa Cruz Island: in the absence of feral sheep and cattle, thousands of seeds have germinated and pine saplings have begun to replace the now dead former canopy trees. In 1994, most of the new growth was concentrated in the western and northern patches (Tables 1 and 2); the eastern patch had relatively few pine seedlings because of constant browsing from a few dozen sheep that were still using this area in 1994. Several seedlings in this patch showed signs of sheep damage.

Overall, the young pines looked healthy and survived as would be expected. Many saplings survived the extreme climatic variations of extreme drought years (1986-1991) followed by erratic months of high and low rainfall in the subsequent years until 1998. Under optimal conditions of climate, sun exposure, and surface nutrients, an open pine grove of 25 mature dead pines/ha might produce more than 5,000 seedlings/ha in the 1 to 10 year range. Plot B and plot D are examples of this high regeneration capacity of Bishop pines on Santa Cruz Island after the removal of feral herbivores (sheep, cattle, and most hogs).

These examples of successful regeneration occurred in the absence of fire. Clearly, a hike through the western and northern pine grove today shows the validity of Hobbs' statement that fire is not a necessary agent for regeneration (Hobbs 1980). The thousands of opened cones on pine snags and the groves of pine saplings downhill from isolated groves or solitary trees (as observed on the Sierra Blanca Ridge) are evidence of the normal function of the island's weather factors in accomplishing cone opening, seed release and seed germination and survival.

The observation of the process of cone opening under normal ambient temperatures showed that detached cones may open within days or weeks. A cone that rolls into a crack of dark volcanic rocks (common in the northern pine stand) may experience a surface temperature during a normal, slightly misty summer day (measured on 8 August 1991 by H. S. Walter) that is too hot for the human touch speeding up the drying of cone resin and subsequent opening. Cones on trees are cooled by wind and cooler air temperatures and may need longer to dry up and open. It is therefore likely that trees growing in the relatively coolest, windiest, and foggiest locations should hold on to their closed cones the longest. This explains the long persistence of the isolated pine snags on the Sierra Blanca and can be used to develop a model of the generation change in these Bishop pines (Figure 5).

The parent tree dies as a result of disturbance or senescence but releases its many, many seeds from a huge number of cones gradually over a number of years, perhaps decades. This is part of the 'evader' strategy of plant response to disturbance (Agee 1993:135) that includes "species with relatively long-lived propagules that are stored in the soil or canopy." This has the advantage that seeds from a dead tree become available for germination in subsequent years and seasons under different climatic and other environmental conditions some of which more optimal than others for germination and growth. Figure 5 models a 75-year cycle of generational turnover.

Admittedly, the aftermath of the 1994 wildfire on the eastern patch is a singular case study. It consumed all biomass above the surface, but casual inspection of the burn site revealed no lasting damage to any major vegetation element except Bishop pine (Photos 9 and 10). Oak shrubs, manzanita bushes, and many other plants were 1 to 2 m high and vigorously growing. All live and dead pines were destroyed within the fire's perimeter, including 100,000s of cones and millions of seeds. A very tiny fraction of both of the latter survived. This effect of a true wildfire event corresponds closely, however, to the response of all closed cone pines to catastrophic fires (Vogl et al. 1977; Agee 1993; Wehtje

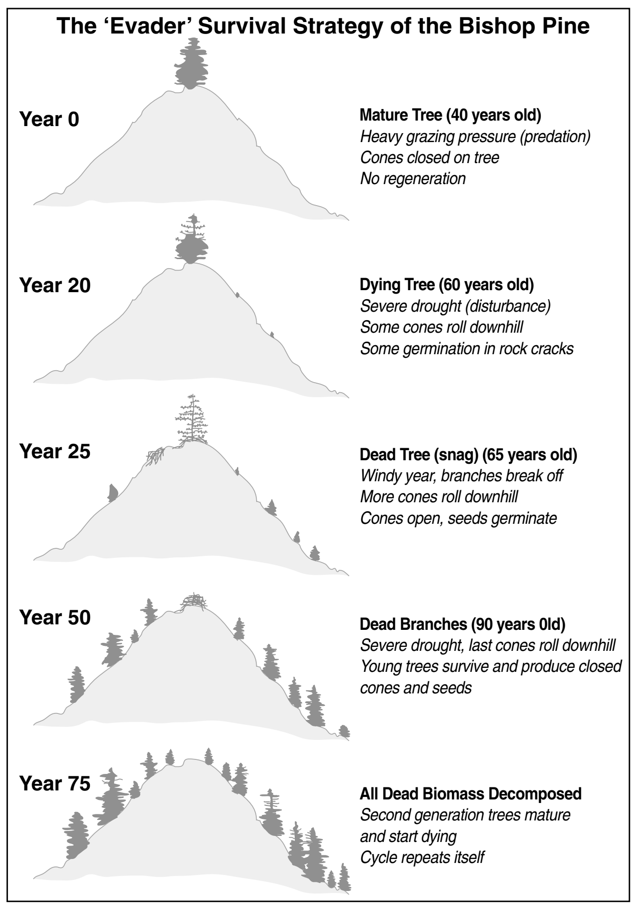

Figure 5. Model of the Bishop pine's natural regeneration cycle in the absence of wildfire.

1994). What seems important to us is the fact that these pines are sensitive to any hot fire. Since the majority of fires in the chaparral and oak-covered slopes of coastal California are usually quite hot — infrequent as they naturally occur — they are likely to kill live and dead pine as well as most cones and seeds. Clearly then, the Bishop pine cannot be called a fire-adapted or -obligate species.

Table 3 shows the probable response of Bishop pines to three different fire-related regimes: no fire, surface fire, and hot crown fire. The latter might spare some cones on green maturing trees with lower fuel loads but would be disastrous at all other times. Benefits to a pine stand accrue only from two regimes. 1) A low burning surface fire would save and open cones in the canopy of young and mature forests; this would cause massive seed release and germination. A recent (1995?) mainland fire near Lompoc may be a case study for this regime type: the burn area was covered with thousands of Bishop pine seedlings in 1998 (D. Kraus, pers. comm.). The resulting forest stand would be even-aged. Older (senescent) forests, however, would lose most of their seeds as trees disintegrate and more and more branches lie close to the surface, exposing them to the flames. 2) The no-fire-regime scenario would also replace the forest, but gradually over perhaps half a tree generation. Succeeding generations of forests would always be uneven-aged, which in our understanding of ecological processes would give them a survival advantage vis-à-vis susceptibility to disease and parasite organisms.

Fire is, of course, a positive factor for germination because the seedbed is enriched by nutrients that may otherwise be unavailable to a pine seed. But that is true for most seeds. Seed scarification by fire is not necessary for germination in the Bishop pine as shown by the spontaneous regeneration on our study plots and by the successful germination of fresh seeds collected from initially closed cones. Fire also reduces ground cover, eliminates potential competitors for water and other resources, and provides maximum exposure to sunlight (Spurr and Barnes 1980). Pines are excellent pioneer species and do very well on overgrazed lands. On Santa Cruz Island, we recorded far more seedlings growing on bare surfaces than under or in the midst of snags and/or live shrubs and trees (Table 2). The probability of a low-intensity surface fire providing these conditions for pine regeneration is, however, extremely low where dead pine fuel and seeds are near ground level. This is usually the case in mature and senescent stands.

Closed cone pines are considered relicts from the Pleistocene (Vogl et al. 1977). They persist in coastal landscapes that do not offer the dry and fire-prone interior environments of the continent. Instead of classifying them as fire-requiring species whose ecological management "will have to include the reintroduction of fire" might it not be closer to reality to classify them as 'pyrofugal' species? Their current habitats, the relatively low plant cover surrounding them, and their maritime climate preferences (low lightning and fire frequency) indicate their survival only in the relatively fire-safest environments of California's brush- and woodlands. They are resilient (Westman 1986) in this Mediterranean-type landscape system because of their fire-evading reproductive strategy. This hypothesis is backed by our observations from Santa Cruz Island. It would be interesting to test its validity beyond the Channel Islands through a study of the natural regeneration of fire-free stands of Bishop and other closed cone conifers in continental settings.

Table 3. Bishop pine stand regeneration and fire.

Pine Age	Fire Factor		
	No Fire	Low Surface Fire	Hot Crown Fire
Pine Stand Young 1 - 20 Years	All cones closed	Some cones survive	All cones consumed
Maturing 20 - 50 Years	All cones closed	Canopy cones survive and seeds germinate	Some cones survive to open and seeds geminate
Senescent > 50 Years	Some cones open and seeds germinate	Canopy cones survive and seeds germinate	Few cones and seedlings survive. Minor regeneration
Dead Stand	Gradual cone opening and full regeneration	Low regeneration. Most cones and seeds consumed by fire	No regeneration. All cones and seedlings consumed by fire

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