Fire on the California Islands: Does it Play a Role in Chaparral and Closed Cone Pine Forest Habitats?

Mary C. Carroll[1], Lyndal L. Laughrin[2] and Ann C. Bromfield[2]
[1]Santa Barbara Botanic Garden, Santa Barbara, CA 93105
[2]Santa Cruz Island Reserve, University of California
Santa Barbara, CA 93106

Abstract - Despite the importance of fire in the maintenance of chaparral and closed-cone pine forests on the mainland, there have been only three documented lightning-caused fires in such habitats on the islands during the past 140 yr. We examine evidence for prehistoric fires, as well as the post-fire response of chaparral vegetation to human-caused fire on Santa Catalina Island. In addition, results of seed germination comparisons between island and mainland chaparral species suggest that, although island seeds exhibit a vigorous response to heat and fire treatments, some species also show significant germination under control conditions.

Introduction

The occurrence of wildfires at regular intervals in California's chaparral and coastal forest habitats has been well-documented (Muller *et al.* 1968; Hanes 1971, 1977; Byrne *et al.* 1977; Keeley 1981; Kilgore 1981), for most Mediterranean-type ecosystems throughout the world (Mooney & Conrad 1977). Numerous studies have described characteristics that enable chaparral and closed cone pine species to tolerate fires, including fire-stimulated germination (Sweeney 1956; Keeley & Keeley 1981), retention of seeds on the plant during fire-free intervals (Lotan 1975; Perry & Lotan 1979; Gill 1981) and development of protected, dormant buds (below ground or under thick bark) that can sprout after fire (Keeley & Zedler 1978; James 1986; Keeley *et al.* 1986). At the ecosystem level, fire has been regarded as a major mechanism for soil nutrient mineralization (Rundel & Parsons 1980; Schlesinger 1985).

Although the frequency of chaparral fires in prehistoric times has been the subject of controversy, the present frequency is often cited as 20-40 yr for a given area (Muller *et al.* 1968; Hanes 1976; Minnich 1983). Evidence of large wildfires every 20-40 yr also is provided by charcoal deposition in varved sediment cores from the Santa Barbara Basin (Byrne *et. al.* 1977; Byrne 1979). Recent charcoal deposits in such cores are known to coincide with major fires in Santa Barbara and Ventura Counties. Material deposited from 735-1,520 A.D. indicated fire-free intervals of about 40 yr, followed by major fire events.

Fire-dependent plant associations such as chaparral, coastal sage scrub and closed cone pine forests occur on both the mainland and offshore California Islands. Yet, prior to this study, there had been no documentation of any naturally occurring fires (*e.g.*, ignited by lightning) on any of the California Islands. The lack of such fires in appropriate habitats on the California Islands contrasts sharply with the mainland record, even though the same genera, and in many cases, the same species predominate in island scrub and forest habitats. Man-caused fires have occurred on the islands, but no data are available on post-fire succession or the demography of these island populations.

The purpose of this study was to evaluate the potential for natural fire ignitions on the islands. In addition, since many mainland chaparral taxa exhibit increased seed germination following fire, the second focus of this study was to compare germination responses of selected populations of mainland and island chaparral species.

Methods

Fire History: A survey of historical literature was made to document fire occurrences on the California Islands. In addition, dozens of island residents, employees and researchers were interviewed regarding their knowledge of previous lightning ignitions and fire history in general. Comparisons were made between natural fire frequencies on the islands and those on the mainland by utilizing fire records for the Los Padres National Forest.

Response of Island Vegetation to Fire: We established study sites in two recently burned areas on Santa Catalina Island during September, 1984 and April-May, 1985. These sites are located on the northeastern side of the dominant ridge of the eastern part of the island, and both have predominantly north-facing exposures. Both sites are named for beaches at the mouths of the nearest canyons. The fires at both sites were human-caused; the White's Landing site burned on 18 June 1984, and the Pebbly Beach fire occurred on 2 July 1985. The site at White's Landing is located 7.75 km north of Avalon and 0.8 km east of Blackjack Mountain at an elevation of 335 m. The area is underlain by andesite of Miocene age (Rowland 1984). The unburned vegetation at this site was dominated by exotic grasses intermixed with coastal sage scrub and chaparral species. The burn covered approximately 12 ha. Disturbances at this site included grazing by feral pigs, feral goats and bison, as well as rooting by pigs.

The Pebbly Beach site is located 1.75 km east of Avalon at an elevation of 230 m. It occurs on quartz diorite of Miocene age (Rowland 1984). Undisturbed slopes had an almost continuous canopy of chaparral vegetation that was only rarely broken by patches of non-native weedy grasses and forbs. The burn covered an area of 2.4 ha and included both chaparral and disturbed vegetation. Feral goats do not frequent this area, but grazing by the introduced black-tail deer was evident during field reconnaissance.

Four permanent 30 m transect lines were established at each site in 1984 and 1985; two were placed in burned areas and two in nearby analogous unburned vegetation on slopes with similar exposures and gradients. Density and percentage of vegetative cover (% ground surface cover) were recorded for all species within each of 15 1-m^2 quadrats placed alternately along both sides of each transect line. Relative density, cover and frequency were used to determine importance values for each species.

Seed Germination Experiments: Seeds of *Ceanothus megacarpus*, *Dendromecon rigida* and *Lotus scoparius* were collected on the mainland in the Santa Ynez Mountains, Santa Barbara County, CA in 1982 and 1983 from mature shrubs. Seeds from these three species plus those from two island endemic shrubs, *Arctostaphylos insularis* and *Ceanothus arboreus*, were gathered on Santa Cruz Island, Santa Barbara County, CA in 1982, 1983 and 1984.

Germination comparisons were made between one-year old seeds of mainland and island populations of the same species; in addition, seeds of the two island endemic species also were tested. Storage, seed pretreatments and germination media were identical for mainland and island seeds of the same species. Sterilized potting mix was placed in wooden flats and eight replicates of 50 seeds each then were sown from each population of each species. Half of the flats were topped with 40 cm of dried chamise (*Adenostoma fasciculatum*) stems and ignited with a propane torch; the other half were left untreated as controls. After the branches burned and the flats cooled, both control and burned flats were watered with deionized water and incubated for 21 days at 10°C, followed by 10 days at 23°C. Each treatment was repeated three times. Incubation was carried out in the dark except while germination was being scored every 7 days.

In a different experiment the germination response of seeds of mainland and island *Emmenanthe penduliflora* was compared for different heat and media treatments. Seeds of *Emmenanthe* were collected on the mainland 3 km southwest of Newhall, Ventura County, CA, from a one-year-old burn in June 1985 and on Santa Catalina Island, Los Angeles County, CA, from a one-year-old burn at the Pebbly Beach site in June 1985. Seeds from each site were counted into 24 separate lots of 25. The seed lots were given one of three heat treatments prior to sowing: 1) control (no added heat); 2) 80°C for 2 hr or 3) 120°C for 5 min. All seed lots were subsequently sown in 100 X 15 mm Petri dishes containing sterilized potting soil. Half of the lots (8) receiving each heat treatment then were topped with powdered charred wood, prepared by charring *Adenostoma* stems with a propane torch and grinding them in a Wiley Mill to make a uniform powder (Keeley & Keeley 1981); the other half were used as a control. Hence, eight replicates of 25 were used for each heat and charate treatment combination. These dishes were watered with deionized water and incubated in the dark in a manner similar to the previous experiment with seeds sown in flats.

Experiments for all species were analyzed individually with multivariate ANOVA on arcsine-transformed data and significant differences between means were distinguished with the Tukey-Kramer procedure (Sokal & Rohlf 1981).

Table 1. Historical fires on the California Islands (1830-1986). Fires greater than 1 ha are recorded by size range. Fires less than 1 ha in size were not recorded.

Island	# of Historical Fires by Range in Size of Fires (hectares)			
	1-9	10-99	100-999	1000+ ha
Anacapa	0	0	0	0
San Clemente	9*	2	1	2
San Miguel	12*	0	2	1
San Nicolas	0	0	0	0
Santa Barbara	0*	4*	1	0
Santa Catalina	21*	3	3	1
Santa Cruz	5	2	0	1
Santa Rosa	0	3	0	0

* estimate due to lack of accurate records

Results

Fire History: Many types of human-caused fires have occurred on the California Islands in the past 140 yr (Table 1). Cause of ignition has varied by island and land-use history. Fires caused by mechanical or electrical equipment have been the most common, and occurred on Santa Cruz, Santa Rosa and Santa Catalina Islands (Daily & Stanton 1981; C. Stanton, pers. comm.; A. Vail, pers. comm.; T. Martin, pers. comm.). Unattended campfires have resulted in wildfires on Santa Cruz and Santa Catalina Islands (Daily & Stanton 1981; T. Martin, pers. comm.). Fires ignited by plane crashes have occurred on Santa Catalina and Santa Rosa Islands (T. Martin, pers. comm.; A. Vail, pers. comm.). Intentional burning was practiced in the 1920s on Santa Barbara Island (Philbrick 1972) and for the past ten years on Santa Clemente Island (J. Larson, pers. comm.; L. Salata, pers. comm.); small fires also have been intentionally set on Santa Cruz and Santa Catalina Islands (Daily & Stanton, 1981; T. Martin, pers. comm.). Military operations have caused fires on Santa Rosa, San Nicolas, San Miguel and San Clemente Islands (A. Vail, pers. comm.; R. Dow, pers. comm.; N. Whelan pers. comm.; F. Ugolini, pers. comm.; J. Larson, pers. comm.; L. Salata, pers. comm.). Arsonists reportedly have been responsible for several fires on San Clemente Island as well (J. Larson, pers. comm.; L. Salata, pers. comm.).

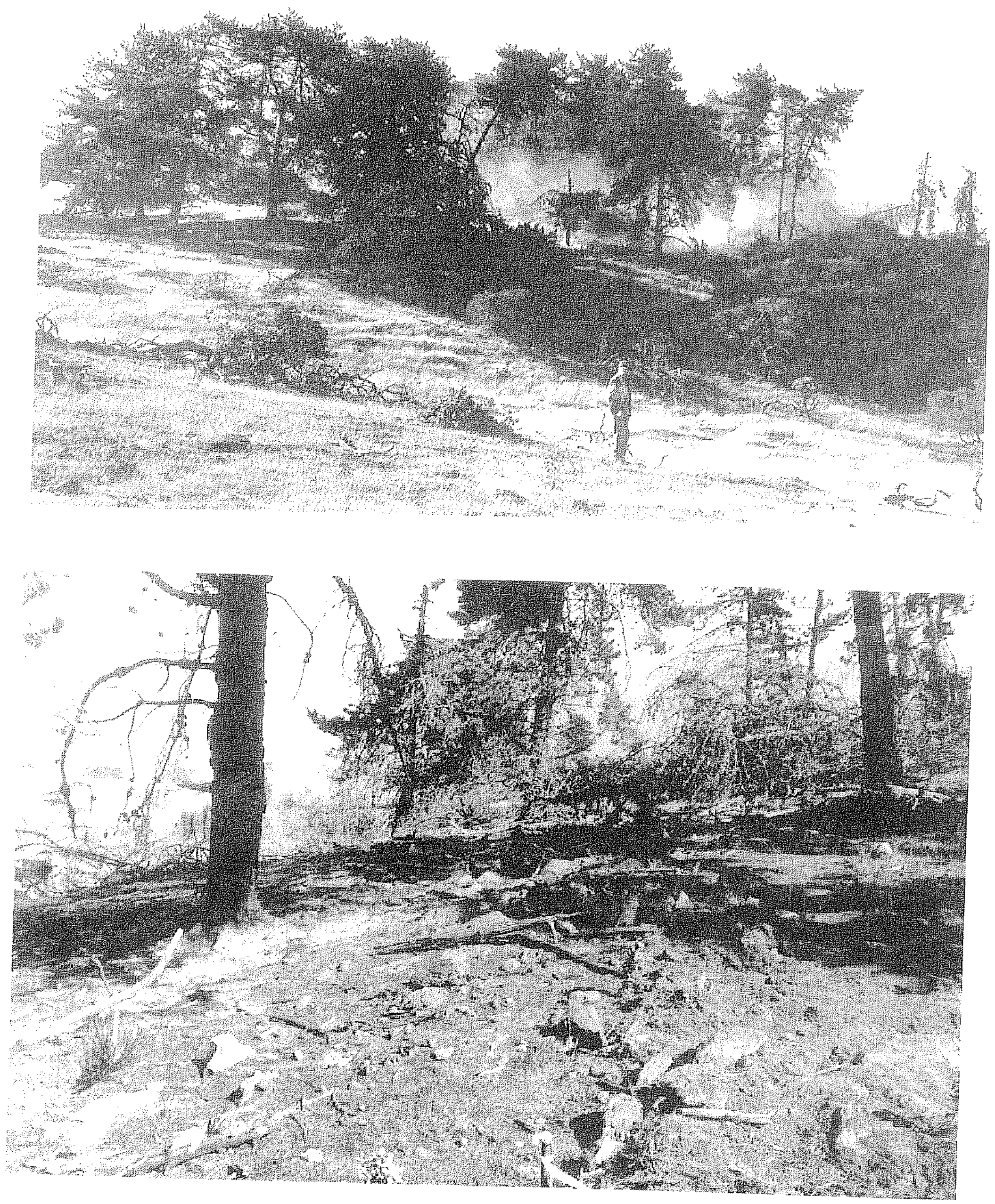

Figure 1. Lightning-caused fire above Pelican Bay, Santa Cruz Island, 25 February 1987. Upper photograph, fire in progress. Lower photograph, detail of burn area.

Table 2. The ten most important species, ranked by importance values for each study site and year. (Habit: A=annual; S=shrub; P=perennial herb; AG=annual grass; *=introduced).

Non-burn			Burn		
Plant Species	Habitat	Importance Values	Plant Species	Habitat	Importance Values
Pebbly Beach-1986			**Pebbly Beach-1986**		
Quercus dumosa	S	84.7	*Heteromeles arbutifolia*	S	36.3
Rhus integrifolia	S	65.4	*Anagallis arvensis*	A*	35.3
Heteromeles arbutifolia	S	45.0	*Festuca megalura*	AG	30.6
Bromus diandrus	AG*	30.0	*Rhus integrifolia*	S	21.2
Marah macrocarpus	P	22.0	*Melilotus indicus*	A*	20.7
Avena barbata	AG*	17.0	*Bromus mollis*	AG*	19.1
Amsinckia intermedia	A	15.0	*Gnaphalium bicolor*	P	16.0
Centaurea melitensis	A*	13.0	*Cytisus linifolius*	S*	12.7
Perezia microcephala	P	9.4	*Bromus diandrus*	AG*	11.4
Keckiella cordifolia	S	6.7	*Rhamnus pirifolia*	S	11.4
White's Landing-1985			**White's Landing-1985**		
Bromus diandrus	AG*	70.1	*Festuca megalura*	AG	68.1
Festuca megalura	AG	38.4	*Bromus diandrus*	AG*	24.0
Hordeum sp.	AG*	24.3	*Opuntia littoralis*	S	22.6
Bromus mollis	AG*	22.7	*Eucrypta chrysanthemifolia*	A	20.3
Amsinckia intermedia	A	17.6	*Erodium cicutarium*	A*	20.2
Avena barbata	AG*	16.8	*Pholistoma racemosum*	A	19.7
Apiastrum angustifolium	A	14.2	*Avena barbata*	AG*	15.1
Rhus integrifolia	S	13.4	*Silene gallica*	A*	11.4
Claytonia perfoliata	A	11.4	*Medicago polymorpha*	A*	8.5
Silene gallica	A*	10.6	*Hordeum* sp.	AG*	6.7
White's Landing-1986			**White's Landing-1986**		
Bromus diandrus	AG*	114.5	*Bromus diandrus*	AG*	62.4
Avena barbata	AG*	63.3	*Avena barbata*	AG*	28.8
Bromus mollis	AG*	15.4	*Bromus carinatus*	AG	26.5
Rhus integrifolia	S	14.5	*Bromus mollis*	AG*	21.9
Hordeum sp.	AG*	9.4	*Silene gallica*	A	17.7
Lupinus bicolor	A	7.9	*Centaurea melitensis*	A*	17.0
Bloomeria crocea	P	5.3	*Festuca megalura*	AG	11.7
Bromus rubens	AG*	4.7	*Salvia apiana*	S	9.6
Silene gallica	A*	4.5	*Medicago polymorpha*	A	7.6
Centaurea melitensis	A*	4.3	*Opuntia littoralis*	S	7.4

In addition, three lightning-cause fires have been documented for the islands. One previously unreported record of lightning-caused fire was uncovered for Santa Catalina Island; a small lightning ignited fire burned 0.1 ha on a ridge above Emerald Bay and Parson's Landing on 1 September 1967 before being extinguished. On Santa Cruz Island, 0.13 ha were burned when a lightning bolt struck a pine tree near Pelican Harbor on 25 February 1987 (Figure 1). This was controlled by the National Park Service and UC Santa Cruz Island Reserve personnel. On 10 July 1988 four lightning strikes were observed touching ground on Santa Rosa Island. One of these strikes burned a small patch (.05 ha) in severely grazed grassland before burning out (A. Fieldson, pers. comm.). Thus, fires have occurred on most of the islands during the past 140 yr, but only three are known to be natural ignitions.

From 1983-1987, six lightning strikes on Santa Cruz Island have been documented, five of which struck bare ridges or communication

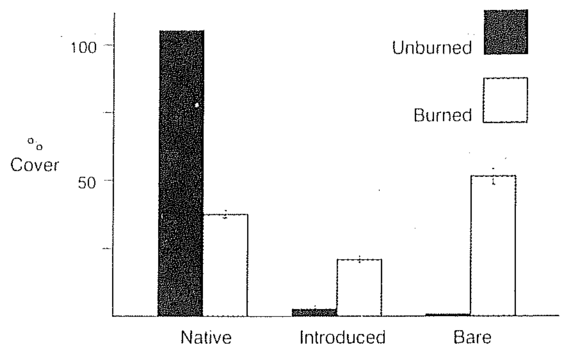

Figure 2. Comparative cover of native plants, introduced plants and bare ground in burned and unburned plots: Pebbly Beach, Santa Catalina Island, 1986.

antennas (T. Green, pers. comm.; P. Schuyler, pers. comm.). Several strikes also have been reported from Santa Catalina Island (Johnson 1972; T. Martin pers. comm.), while electrical storms have been observed over virtually all of the islands (Orr 1968). According to Johnson (1972), a mean of 3.3 lightning centers/yr have been reported off the southern California coast during an 11 yr period, and during a 28 yr period thunderstorms were reported over San Miguel Island on the average of once every 0.8 yr.

By comparison, mainland areas adjacent to the northern Channel Islands had 40 lightning ignited fires during the past 75 yr. These were in the interior mountainous regions of the Santa Barbara and Ojai Ranger Districts. Over the same period there were only four such fires in the coastal Santa Ynez mountain range (Los Padres National Forest, unpub. data).

Response of Island Vegetation to Fire: The results of our observations at the Santa Catalina Island fire sites are summarized in Figures 2, 3 and 4 and Tables 2 and 3. Each site will be discussed separately.

Pebbly Beach (unburned) - Cover in the unburned chaparral was greater than 100% in 1986; most of it consisted of native species (Fig. 2; Table 2), primarily three shrub taxa. Overall species diversity was low (Table 3). A comparison of total importance values for all study areas underscores the predomination of native shrubs in unburned plots at the Pebbly Beach site and the relative lack of herbaceous plants (Table 3). It should be noted that the exotic shrub *Cytisus linifolius* was present in relatively low abundance. Its occurrence in the unburned portion of this area probably represents establishment during some previous disturbance.

Table 3. Summaries of species numbers and total importance values within burned and unburned quadrats at Pebbly Beach and White's Landing, Santa Catalina Island.

	Pebbly Beach		White's Landing			
	Non-Burn 1986	Burn 1986	Non-Burn 1985	Burn 1986	Non-burn 1985	Burn 1986
Species Number						
Total species	11	38	39	37	41	46
Natives	8	26	29	26	26	32
Introduced	3	12	10	11	15	14
Annuals	4	16	28	25	30	34
Perennials	1	9	4	7	2	4
Suffrutescents	1	3	4	3	4	3
Shrubs	5	10	3	2	5	5
Total Importance Values						
Natives	250	183	155	71	188	94
Introduced	60	119	159	225	112	183
Annuals	75	148	276	254	250	218
Perennials	22	40	11	21	5	32
Suffrutescents	9	14	8	3	9	7
Shrubs	204	110	191	18	35	21

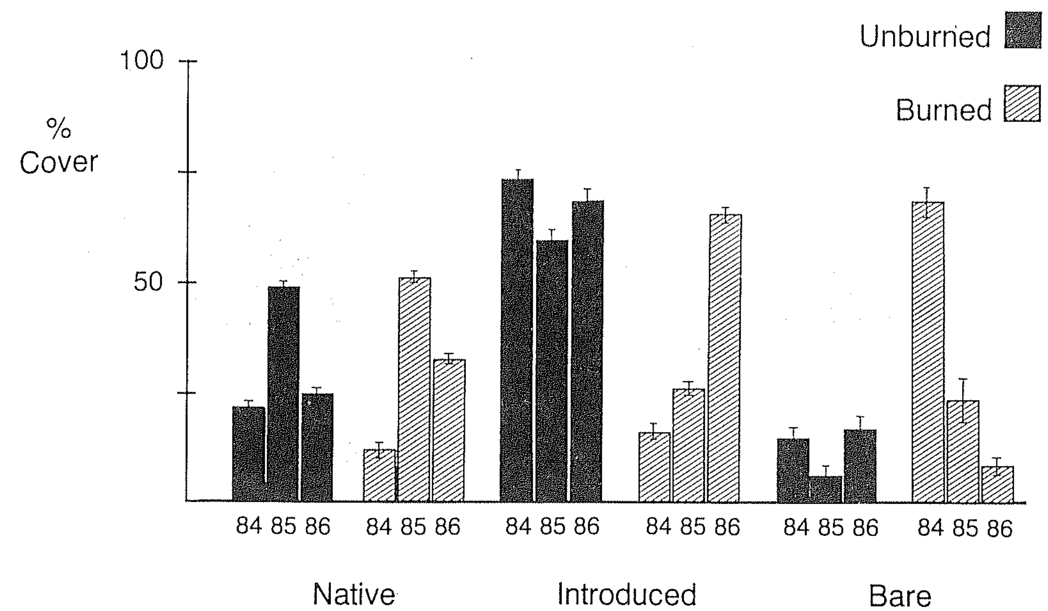

Figure 3. Comparative cover of native plants, introduced plants and bare ground in burned and unburned plots: White's Landing, Santa Catalina Island, 1984-1986.

Pebbly Beach (burned) - One year after fire the total cover on burned plots was less than 100% and was comprised of significant proportions of both native and introduced species (Fig. 2; Table 2). Species richness was much greater in burned than in unburned areas, with 38 species in burned quadrats versus only 11 in unburned ones (Table 3). More than twice as many native species were present as introduced species. This pattern of dominance by natives also is visible in a comparison of the total importance values for burned and unburned plots (Table 3). Resprouting shrubs, annual forbs and grasses form the primary post-fire vegetation at this site (Table 2) and of particular note is the increased importance of the invasive exotic shrub *Cytisus linifolius* (see Mastro 1993).

Conspicuously absent was *Quercus dumosa*, a shrub that was abundant in adjacent unburned chaparral. It is not known whether this species was specifically found in the burned area prior to fire. Mainland *Q. dumosa* resprouts readily after fire but only gradually recolonizes a burned area (Keeley & Keeley 1981). The island scrub oaks are thought to be hybrids between *Q. dumosa* and other white oaks, particularly *Q. douglasii* and *Q. lobata*; their fire tolerance is unknown, although many produce basal sprouts in the absence of fire. Also of interest, but with low importance values, were several species of annuals that, on the mainland, occur most abundantly after fires. These included *Antirrhinum nuttallianum*, *Eucrypta chrysanthemifolia* and *Emmenanthe penduliflora*.

White's Landing (unburned) - The total vegetative cover on unburned plots approached or exceeded 100% during each of the two years of our study (Fig. 3), but was comprised primarily of introduced species, particularly annual grasses (Fig. 4). The dominance by introduced grasses further is emphasized in comparisons of the importance values of the top ten species (Table 2). During both years species diversity was much greater at this unburned site than it was at the unburned, Pebbly Beach site (Table 3), due to greater representation by

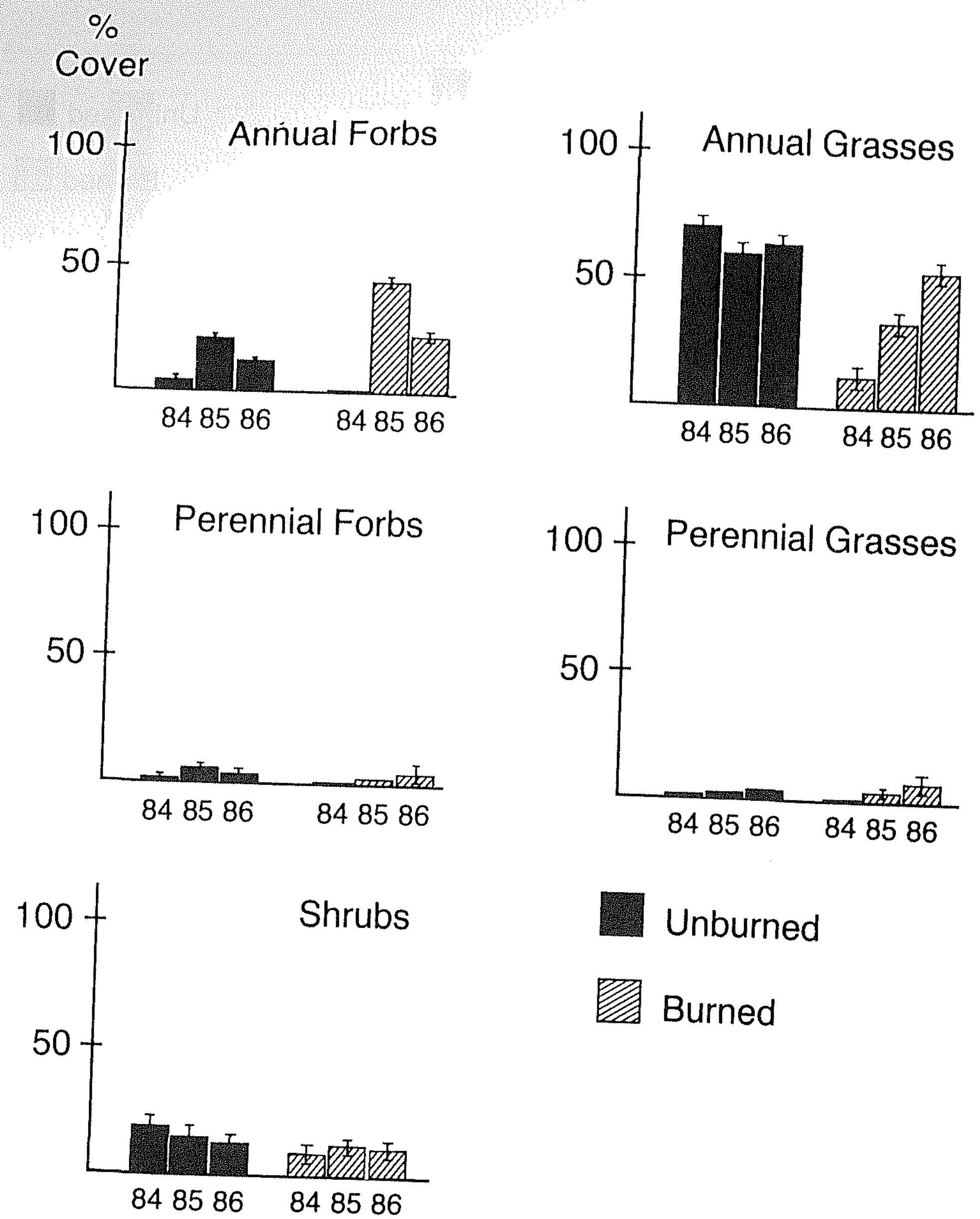

Figure 4. Comparative cover of forbs, grasses and shrubs in burned and unburned plots: White's Landing, Santa Catalina Island, 1984-1986.

weedy annual and perennial species. Although introduced species were significantly more important than native species, the number of native species greatly exceeded the number of introduced species. The total number of species present at the site was about the same during the two years, but the dominance of natives, represented by total importance values, changed greatly from one year to the next (Table 3). Native and introduced species were equally important in 1985, but introduced species achieved much greater dominance in 1986. The higher rainfall in 1985-1986 may have favored establishment of weedy annual grasses. The

Table 4. Comparative germination of selected chaparral species - no pretreatment vs. burning pretreatment. Mean percentage and SE (n = 8, 50 seeds per replicate).

	Mainland		Island	
	Control	Burn	Control	Burn
Ceanothus megacarpus	5.8 (± 1.2)	43.1^ (± 6.4)	30.5* (± 1.5)	52.0*^ (± 6.2)
Dendromecon rigida	0.8 (± 0.4)	0.8 (± 0.4)	5.0* (± 1.5)	7.5* (± 2.5)
Lotus scoparius	8.3 (± 0.1)	31.0^ (± 1.8)	16.8* (± 3.4)	20.3 (± 3.3)
Ceanothus arboreus	-	-	22.3 (± 2.8)	42.8^ (± 3.4)
Arctostaphylos insularis	-	-	9.3 (± 1.8)	15.3 (± 2.9)

* P<0.01 island vs. mainland for same treatment
^ P<0.01 burn vs. control for the same location

Mainland = Santa Ynez Mountains
Island = Santa Cruz Island

importance and numbers of non-native annual species at this site is probably a reflection of its grazing history .

White's Landing (burned) - Total vegetative cover steadily increased at this site during successive postfire years (Fig. 3). The 1984 measurements represent sampling in September 1984, three months after the fire and prior to the rainy season, which accounts for the high proportion of bare ground. During the two springs after the fire the majority of cover consisted of annual forbs, annual grasses and some shrubs (Fig. 4). Annual forbs were slightly more abundant in the first postfire year and annual grasses increased in cover during the second postfire year. Although greater numbers of species were observed in the burned plots, the increase in species diversity was not as great as at the Pebbly Beach site (Table 3). Species observed in the first postfire year that are common on mainland burns include *Eucrypta chrysanthemifolia*, *Apiastrum angustifolium*, *Clarkia epilobioides*, *Lotus salsuginosus*, *Pholistoma membranaceum* and *Stylomecon heterophylla*. Both *Eucrypta* and *Pholistoma* were among the top ten most important species present the first year after fire (Table 2).

Native species declined in importance from the first to second years after fire (Table 3), while introduced annuals, especially grasses, became more dominant. Two factors may be responsible. First, the greater rainfall in 1985-1986 may have favored establishment of grasses. Second, seeds of non-native grasses are more readily killed by fire than those of natives. As a result, fewer viable seeds may have been present onsite the first year after fire but seed quantities may have increased during the second season due to recolonization from nearby unburned sources. In both years shrubs in non-burned areas had greater importance values than respouting shrubs in nearby burned areas (Table 3).

Santa Cruz Island - We report here some unpublished data collected by Mr. R. Hoffmann, Mrs. D. Croftin-Atkins, and Mrs. D. Cooke from the aftermath of the September 1931 Pelican Bay fire on Santa Cruz Island. This human-caused fire burned approximately 4800 ha of pine forest and brushland along the island's north shore. Postfire seeding establishment was recorded within a single 1 m plot during a botanical collecting trip in the spring of 1932. The species and densities recorded were: *Antirrhinum nuttalianum* (1); *Calystegia macrostegia* (1); *Ceanothus arboreus* (2); *C. megacarpus* (1); *Dendromecon rigida* (1); *Helianthemum greenei* (130); *H. scoparium* (12); *Lotus grandiflorus* (26); *L. scoparius* (3) and *Pinus muricata/remorata*(2). *Silene multinervia* also was reported in the area (C. Smith, pers. comm.). These plants or their close relatives are common on mainland burn sites.

Table 5. Percentage of germination of *Emmenanthe penduliflora* in response to heat pretreatment and charate presence in medium. Mean percentage and SE ($n = 8$, 25 seeds per replicate).

	Mainland		Island	
	Control	Charate	Control	Charate
Control	1.7 (± 0.8)	7.4 (± 1.3)	0	25.1^ (± 7.8)
80°C (2 hrs)	0.6 (± 0.6)	27.4^ (± 3.4)	0	44.6*^ (± 5.6)
120°C (5 min)	0	7.4 (± 2.9)	0	13.1 (± 3.3)

* $P<0.05$ island vs. mainland for same treatment
^ $P>0.05$ charate vs. control for the same location and heat treatment
% $P<0.05$ heat vs. control for the same location and heat treatment

Mainland = Santa Monica Mountains
Island = Santa Catalina Island

Source	*F* value	
Location	11.6	$P<0.001$
Charate	119.0	$P<0.0001$
Temperature	17.2	$P<0.0001$
Charate*Temperature	14.5	$P<0.0003$
Location*Temperature	0.9	$P<0.4$
Location*Charate	17.1	$P<0.0001$
Location*Charate* Temperature	1.3	$P<0.27$

Seed Germination Experiments: All of the mainland and island shrubs and subshrubs had seeds that exhibited equal or greater germination when given the burning treatment compared with controls (Table 4). Significantly greater germination was observed for burn-treated seeds of mainland *Ceanothus megacarpus* and *Lotus scoparius* when compared with controls; seeds of mainland *Dendromecon rigida* showed negligible germination regardless of treatment. Seeds of burn-treated island *C. megacarpus*, *D. rigida* and *L. scoparius* exhibited equal to greater germination than mainland seeds that also were given burn treatments; clearly there is no decrease or loss of response to burn treatments by island seeds. Furthermore, the island endemic shrubs *Arctostaphylos insularis* and *C. arboreus* also produce seeds that respond vigorously to burning treatments. Unlike mainland seeds, however, a significant portion of seeds of island shrubs and subshrubs also germinate without any treatment.

Seeds of both mainland and island *Emmenanathe penduliflora* responded significantly to the treatment of charred wood plus preheating at 80°C for 2 hr (Table 5). Although seeds collected from the mainland exhibited greater germination in the presence of charred wood for all temperature pre-treatments, significantly enhanced germination resulted only for the temperature pretreatment of 80°C for 2 hr. Charred wood significantly stimulated germination of island seeds for all temperature pretreatments, and no germination was recorded in the absence of charred wood.

Discussion

We have established that natural fires on the California Islands are infrequent at the present time, with only three recorded during the past 140 yr. In contrast, human-caused wildfires have been relatively common, especially on those islands with a lot of human activity. Surprisingly, two islands, Anacapa and San Nicolas, have had no wildfires at all. The following questions are raised. Has the natural fire frequency on these islands been similarly low in the past? What was the relationship of aboriginal burning to wildfire frequency on the islands? What role did fire play in vegetated areas?

Wildfire frequency depends upon ignition source frequency and fuel conditions. During prehistoric times the primary sources of ignition were volcanic activity, lightning and in the last several thousand years, aboriginal burning. Volcanic activity and resultant fires may have played a role during significant portions of California's prehistory (Axelrod 1976), but their effects upon present vegetation on the islands or in southern California is beyond the scope of this paper. Volcanism is unlikely to have been relevant and historically it has not been a factor in this area. Paleoclimatic information for the Southern California Bight is not adequate to analyze prehistoric lightning frequency. However, paleobotanical studies reveal that during parts of the Pleistocene, cooler and wetter climates existed over this area than at present (Axelrod, 1983). This may have increased the potential for lightning storms but an analysis of these prehistoric conditions remains speculative.

Lightning has remained an important ignition source on the mainland (Kozlowski & Ahlgren 1974; Keeley 1982; Pyne 1982). Over 40 lightning-ignited fires have occurred in the mountainous areas of the Santa Barbara and Ojai Ranger Districts during the past 75 yr (Los Padres National Forest, unpub. data), often burning vast acreage. Only four lightning-ignited fires were reported for the coastal Santa Ynez range during the same period, which is similar to the frequency reported for the islands (three known lightning-ignited fires in 140 yr, all between 1967-1988). The lower incidence of lightning-ignited fires in coastal regions has been discussed by Keeley (1982); he reports an inverse relationship between frequency and proximity to the coast. Nonetheless, six lightning strikes were documented on Santa Cruz Island during the four year period, 1983-1987 (T. Greene, pers. comm.; P. Schuyler, pers. comm.).

Another difference between island and mainland conditions is that fires ignited in interior mainland areas of high ignition potential can spread into coastal areas overland or via aerial fire debris. Since the nearest landmass to a given island is often another island and the mainland is 21-100 km away (Philbrick 1967), only under extraordinary circumstances could a mainland fire now spread out to any of the islands via aerial fire debris. On the mainland such debris have ignited fires up to 19 km from an original burn source, although distances of 1-2 km are much more typical (Pyne 1982). The potential to for wildfire to spread to the islands by this mechanism may have been somewhat greater in prehistoric times when geographic conditions were different. As recently as about 17,000 years ago the northern Channel Islands were merged into one large landmass with boundaries extending much closer to the mainland. At the same time mainland shorelines extended farther towards the island. The resulting water gap was only about 6-8 km (Vedder & Howell 1980).

Aboriginal burning also was a likely source of fire ignition during human prehistoric times. Timbrook & co-authors (1985) present ample evidence of vegetation modification due to fires set purposefully by Chumash Indians on the mainland. Human occupation of the islands dates back to 9,000 B.P. (Orr 1968), with cultural practices being similar between island and coastal mainland populations (J. Timbrook & J. Johnson, pers. comm.). Also, wildfires could have started accidentally from campfires. The first known written record of fire on the islands is of these Chumash campfires. Cermeno, an early Spanish explorer, sailing near the northern Channel Islands wrote in his journal on 13 December 1595: "That night fire appeared on these islands...."(Johnson 1982). Archaeological investigations to date provide no information to further this analysis.

Evidence does exist on the islands for fires that predate European settlement. Much undated charcoal is scattered over several of the islands. Charcoal collected from Santa Cruz Island has been dated 350 and 395 years B.P. (Brumbaugh 1980) and from San Miguel at 7,000 to over 40,000 years B.P. (Johnson 1972).

Given an ignition source, several features have been identified that increase the likelihood and magnitude of a fire. These include favorable weather, low fuel moisture, fine fuel reservoirs with a high surface to volume ratio and high vegetation density (Mutch 1970; Countryman & Philpot 1970; Vogl 1977; Rundel 1981). Of particular interest is the lower probability of ignition and spread in grazed areas due to inefficient heat transfer and lack of fuel biomass (Vogl 1977; Rundel 1981). All of the islands containing chaparral and pine forests have been heavily grazed by non-native herbivores such as cattle, sheep, goats or deer, which has resulted in significant reductions in shrub and tree densities (Hobbs 1980; Hochberg 1980; Hochberg *et al.* 1980; Minnich 1980, 1982). Many of the ridges where lightning might strike are bare. In addition, the presence of browse lines interferes with the transfer of fire within and between plants (L. Loehrer, pers. comm.). Grazing has been associated with site degradation and decreased fire frequencies in many Mediterranean-climate ecosystems (Vogl 1977) and has even been used for the creation and maintenance of fuelbreaks (Green *et al.* 1978).

We contend that, in the absence of grazing, lightning-caused wildfires would be more frequent in island vegetation; lightning does occur with sufficient frequency, but fuel has been limiting for ignition. We would expect that the fire-frequency on the islands would be less than that of the mainland, since the lack of contiguous fire-prone land areas precludes the spread of fire onto the islands under ordinary conditions. Nonetheless, the data from the Santa Catalina Island burn sites suggest that California's insular floras have evolved in the presence of periodic fires and that they respond similarly to vegetation studied in mainland areas (Sampson 1944; Horton & Kraebel 1955; Minnich 1983; Keeley & Keeley 1981; Keeley *et al.* 1981).

On Santa Catalina Island during the first two post-fire years, many native shrubs resprouted from subterranean root crowns. At the relatively undisturbed Pebbly Beach site, there was a dramatic increase in species richness the spring following fire. The rise in species diversity after fire was less obvious at the White's Landing site, since both burned and unburned areas were dominated by introduced annual grasses and forbs as a result of heavy grazing. However, cover by natives exceeded that by introduced species the first spring after fire. The data from a burned site on Santa Cruz Island in 1932 also indicated vigorous seedling establishment by native trees, shrubs and annuals. Thus several island burn sites included annual and perennial species known to germinate primarily under post-fire conditions on the mainland.

Germination studies of seeds of both mainland and island chaparral shrubs revealed significant responses to fire-related treatments, which could suggest on-site selection of fire-adapted traits or, in the island populations, retention of traits inherited from mainland ancestors. The fact that significant numbers of island seeds exhibited higher germination under control conditions than their mainland counterparts may reflect greater intervals between fires in presettlement times than on the mainland. Under such conditions fire would continue to be an important selective force, but between-fire seedling establishment also would be advantageous. This pattern of post-fire and between-fire seedling establishment also has been described in mainland habitats where fire is an infrequent but regular component (Perry & Lotan 1979; McMaster & Zedler 1981). Isolation also may favor gene pools comprised of mixed or plastic dormancy mechanisms; such plasticity of characteristics expressed in island populations has been well documented (Carlquist 1974; Philbrick 1980).

Of special interest to us was the response of island-collected *Emmenanthe penduliflora* to a variety of heat and charred wood treatments, as outlined by Jones & Schlesinger (1980), Keeley & Keeley (1981) and Keeley & Nitzberg (1986). Jones & Schlesinger (1980) obtained significant germination of chaparral-collected *Emmenanthe* seeds placed in the presence of charred stems compared with negligible germination under control conditions. These results contrasted with those obtained from desert-collected *Emmenanthe* seeds, which did not respond significantly to the presence of charred stems. Both populations, however, exhibited high germination rates upon scarification. Keeley & Keeley (1981) and Keeley & Nitzberg (1986) reported similar results for chaparral-collected seeds but did not test desert seeds. The ecotypic difference in response between seeds collected in chaparral and desert populations suggested to Jones & Schlesinger (1980) that in desert areas fire might be less important as a germination mechanism than other factors, such as scarification.

The clear response of island seeds to the presence of charred wood indicates that, as in mainland chaparral populations, fire continues to be an important germination mechanism for *Emmenanthe* on the islands. Although only rarely collected in unburned habitats, it has been reported on three island burns in sizeable numbers (M. Carroll, unpub. data). These results are of special interest since they occur in a species that has exhibited plasticity in the fire-response trait, depending on whether the population was exposed to regular or rare, random fire events.

In conclusion, we find that our data suggest that fire has been an important selective agent on the California Islands in chaparral and pine forest habitats, even though the intervals between fires may have been longer than on the mainland. The consistency of response across many species seems to preclude the simple explanation of retention of fire-adapted traits, and may indicate that the current fire-free period is either temporary or a result of human influence.

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Hybridization between *Malacothrix polycephala* and *M. incana* (Asteraceae) on San Nicolas Island, California

W.S. Davis[1] and Steven A. Junak[2]
[1]Department of Biology, University of Louisville, Louisville, KY 40292
[2]Santa Barbara Botanic Garden, Santa Barbara, CA 93105

Abstract – Natural hybridization between *Malacothrix polycephala* W. Davis (ined.), an annual, and *M. incana* (Nutt.) Torrey & A. Gray, a perennial, on San Nicolas Island, California was examined using herbarium studies, studies in the field, and studies of plants grown in growth chambers. *Malacothrix incana* has apparently been on San Nicolas Island for less than 25 yr, but *M. polycephala* is a long-time resident. The two species differ morphologically, physiologically, and in their banding patterns for the enzyme aspartatate aminotransferase. No strong isolating mechanisms have been found between the two species and extensive hybridization is occurring on San Nicolas Island. Studies of growth chamber progenies indicate that natural hybridization has produced many combinations of the morphological and physiological features of the parental species. The evolutionary potential of hybridization between *M. polycephala* and *M. incana* appears to be considerable.

Introduction

For the last 6 yr we have been studying natural hybridization between *Malacothrix incana* (Nutt.) Torrey & A. Gray, and *M. polycephala* W. Davis (ined.) on San Nicolas Island, California. Natural hybridization between *M. incana* and *M. polycephala* is of special evolutionary and systematic interest for several reasons. First, *M. incana* is a perennial species and *M. polycephala* is an annual species; published studies of natural hybridization between annual and perennial taxa are few. Second, both species are self-compatible. Evidence from a detailed study of the nature and extent of natural hybridization between *M. incana* and *M. polycephala* can be used to assess the efficiency of autogamy in its role as an isolating mechanism (*e.g.*, see Levin 1978). Third, it is likely that hybridization between *M. incana* and *M. polycephala* has been going on for less than 20 yr; evidence from a multifaceted study can be used to assess the rate at which variation can be generated by hybridization. Finally, the findings from a study of hybridization between *M. incana* and *M. polycephala* may be of help in understanding the evolution of other taxonomically confusing annual species of *Malacothrix*, endemic to the California Islands (Munz 1974:207), that appear to be closely related to *M. incana* and *M. polycephala* (Davis 1980).

Malacothrix polycephala is a small annual species endemic to San Nicolas Island. It is most closely related to *M. foliosa* A. Gray, and early collections were generally referred to that species or to another insular endemic, *M. indecora* E.Greene. The first documented collection of *M. polycephala* from San Nicolas Island was that of Blanche Trask in 1897 who noted that the species covered large areas on ridges (Eastwood 1898). Since that time, *M. polycephala* has regularly been collected by other visitors to the island. A historical summary of botanical exploration on San Nicolas Island is to be found in Foreman (1967).

Malacothrix incana is a sand dune endemic that occurs on mainland California in Santa Barbara and San Luis Obispo Counties, and on four of the Southern California Islands. The holotype of *M. incana* was collected in the 1800's at San Diego, California, but it has not been found in that area since then.

The first documented collection of *Malacothrix incana* from San Nicolas Island is