Postfire Reproduction of *Croton californicus* (Euphorbiaceae) and Associated Perennials in Coastal Sage Scrub of Southern California

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Abstract

Postfire regeneration of *Croton californicus* and associated perennials in a coastal sage scrub community was studied at 1.5 and 2.5 years postburn. Reproduction and vegetative growth of *Lotus scoparius* and *C. californicus* were significantly stimulated in the burn area while the preburn dominants *Eriodictyon trichocalyx*, *Eriogonum fasciculatum*, *Senecio flaccidus*, and *Opuntia littoralis* were significantly reduced after fire. *Croton californicus* increased in density and cover approximately three times and eight times that of the control at 1.5 years and 2.5 years postburn respectively. The insignificant difference between burn and control crown diameters at 1.5 years postburn indicates that *Croton* resprouts following fire (resprouting was observed in another burn at 0.5 years postburn with a resprouting rate of 68.8%). A major portion of the postburn density was derived from first, second, and third season seedlings. There was significantly more new seedlings germinating in the burn area when compared to the control area during the third postburn season, with 57% of the burn seedlings occurring in rodent disturbed soils.

Postburn *C. californicus* population patterns of sex expression were not greatly affected by the fire. Female plants were more numerous than male plants in both the burn and control areas with a total male:female sex ratio of 0.90. Female biased sex ratios were slightly less pronounced in the burn area especially at 1.5 years postburn. Male plants were significantly larger than female plants for crown diameter regardless of postburn time. Both sexes in the burn area had exceeded the mean crown diameters of the control area by 2.5 years postburn.

Introduction

Croton californicus Muell. Arg. is a subshrub that inhabits sandy soils, dunes, and washes below 900 m in various plant communities of southwestern North America. It is reported to be a dioecious plant (Webster, 1993), although it appears to be in a diclinous condition other than dioecy proper due to the presence of monoecious morphs in several *C. californicus* populations of southern California (Martin, 1995). The range of *C. californicus* extends from the central and south coast of the California Floristic Province to the Desert Province of California, Arizona, and Baja California (Webster, 1993). Although *C. californicus* can be found in various desert communities of the southwest, it is a prominent component in several associations of coastal sage scrub throughout southern California (Howell, 1929; Kirkpatrick and Hutchinson, 1977; Westman et al., 1981; Zembal and Kramer, 1984; Wheeler, 1988; Martin, 1995).

Kirkpatrick and Hutchinson (1977) described *C. californicus* as a co-dominant of the

Lepidospartum squamatum - Eriodictyon crassifolium - Yucca whipplei association (association 2) in Riversidian coastal sage scrub. This association is confined to washes and gently sloping fans between 300 and 450 m above sea level in the basin bound by the Santa Ana, San Gabriel, San Bernardino, and San Jacinto Mountains (Kirkpatrick and Hutchinson, 1977, 1980). The dominance of the tallest stratum is highly variable, but usually consists of rounded evergreen shrubs more than two meters tall (i.e. *Rhus ovata* S. Watson, *Rhus integrifolia* (Nutt.) Brewer & S. Watson, *Malosma laurina* (Nutt.) Abrams, and *Juniperus californica*), while a variable proportion of the space between the tall shrubs is dominated by smaller shrubs (i.e. *Lepidospartum squamatum* (A. Gray) A. Gray, *Eriodictyon crassifolium* Benth., *Eriodictyon trichocalyx*, *Yucca whipplei*, *Eriogonum fasciculatum*, *Artemisia californica* Less., and *C. californicus*). *Croton californicus* had a 60% frequency in this association (Kirkpatrick and Hutchinson, 1977). Westman et al. (1981) reported *C. californicus* to be associated with *Encelia farinosa* Torrey & A. Gray, *Mirabilis californica*, *A. californica*, *E. fasciculatum*, *Opuntia parryi*, *Dudleya lanceolata*, *Keckiella antirrhinoides* (Benth.) Straw, *Malacothamnus fasciculatus* (Torrey & A. Gray) E. Greene, *Solanum parishii* A. A. Heller, and *Yucca schidigera* K. E. Ortgies in postburn Riversidian coastal sage scrub just south of Redlands, California. This was an *Encelia farinosa - Mirabilis californica* association (association 3), however, Kirkpatrick and Hutchinson (1977) did not find *C. californicus* in this association.

Several authors have listed *C. californicus* as a dominant species in the Santa Ana River floodplain of Orange, Riverside, and San Bernardino Counties (Howell, 1929; Zembal and Kramer, 1984; Wheeler, 1988; Martin, 1995). Zembal and Kramer (1984) and Wheeler (1988) concluded that *C. californicus* has habitat requirements similar to the endangered *Eriastrum densifolium* ssp. *sanctorum* (Milliken) H. Mason as well as *L. squamatum*, *Eriodictyon trichocalyx*, *Eriogonum fasciculatum*, and *Ericameria pinifolia* in the Santa Ana River floodplain of San Bernardino County. *Juniperus californica*, *Y. whipplei*, *O. parryi*, *M. californica*, *E. farinosa*, *R. ovata*, *Lotus scoparius*, *Gutierrezia californica* (DC.) Torrey & A. Gray, *Opuntia littoralis*, *Senecio flaccidus*, *Solanum xanti*, and *Rhamnus crocea* were also associated with *C. californicus* in these areas (Zembal and Kramer, 1984; Wheeler, 1988). A similar floodplain association in a Redlands location of the Santa Ana River floodplain was reported by Martin (1995). The above dominants of the Santa Ana River floodplain correlate highly with the species composition of Kirkpatrick and Hutchinson's (1977) Riversidian coastal sage scrub and Thorne's (1976) inland sage scrub. Floodplains and washes are often occupied by coastal sage scrub because actively eroding surfaces give the easily dispersed subligneous shrubs a distinct advantage over both perennial grasses and chaparral shrubs (Kirkpatrick and Hutchinson, 1980).

The ability of coastal sage scrub to regenerate after fi re has been reported widely. Previously, coastal sage scrub shrubs were thought to resprout poorly from root crowns after fire (Horton and Kraebel, 1955; Hanes, 1971; Kirkpatrick and Hutchinson, 1980) with most postfire regeneration produced from seedlings (Hanes, 1971). Most studies now indicate that coastal sage scrub shrubs are vigorous sprouters after fire (Wells, 1962; Mooney, 1977; Westman, 1981; Westman et al., 1981; Malanson and O'Leary, 1982; Keeley and Keeley, 1984; Martin, 1984) and that the percentage of topkilled shrubs that resprout varies with fire intensity (Westman, 1981; Westman et al., 1981) and slope aspect (Martin, 1984). It is now known that coastal sage scrub dominants typically produce basal sprouts continually in the absence of fire (Malanson and Westman, 1985).

Coastal sage scrub historically occupied approximately 2.5% of the area in the state of California and only 10-15% of this original area remained in 1981 due to rapid urbanization (Westman, 1981). It is important that we continue to study this endangered ecosystem in order to conserve and manage the small remaining areas that coastal sage scrub now occupies. Little has been published on the ability of *C. californicus* to regenerate following fire. Westman et al. (1981) reported an increase of *C. californicus* in one postburn study site. It is suspected that *C. californicus* is fire-adapted and will respond favorably to fire disturbance in coastal sage scrub. This study reports the response of *C. californicus* and its associated species to wildfire in a coastal sage scrub community of a southern Californian floodplain. This paper also presents the postfire patterns of sex expression in *Croton* to observe how fire affects reproduction in a diclinous species.

Methods

Approximately 16 ha of Riversidian coastal sage scrub association 2 in the Santa Ana River floodplain of East Highlands, California burned as the result of a wildfire in late summer of 1992. This burn area is located immediately south of where Weaver Street intersects Greenspot Road. Postburn measurements of *Croton californicus* were performed on 29 April 1994. Plot sampling, using 25 m^2 quadrats, was performed in the burn and control areas to determine population density, cover, and frequency for all perennial species as well as to record sexual condition for *C. californicus*. Cover was calculated from plant crown diameters and sexual condition was determined by examining all of the flowers on a plant and by the presence or absence of fruits. Monoecious morphs were determined to be plants that bore both pistillate and staminate flowers. Twenty quadrats were randomly sampled in the burn area and twenty quadrats were randomly sampled in approximately 6 ha of an adjacent unburned control area. The control area was a continuation of the flood plain immediately west of the burn area which contained a similar topography and slope aspect.

A second set of postburn measurements were taken on 30 April 1995 in the East Highlands burn. Plot sampling, using 1 m^2 quadrats, was performed to determine presence and frequency of all perennial species as well as density, cover, and sexual condition for *C. californicus*. Cover was calculated from plant crown diameters. Newly germinated seedlings were recorded and noted if occurring in rodent disturbed soils. Two hundred 1 m^2 quadrats were randomly sampled in each of the burn and control areas.

Approximately 3 ha of Riversidian coastal sage scrub association 3 (Kirkpatrick and Hutchinson, 1977) in the Santa Ana River floodplain near the mouth of the Santa Ana Canyon, California burned as the result of a wildfire in late summer of 1994. This burn area is located immediately southwest of where Santa Ana Canyon Road intersects Greenspot Road. This association was dominated by resprouting *Encelia farinosa* and *Mirabilis californica*. Postburn measurements and observations were performed on 19 May 1995 to document *C. californicus* resprouting from basal root crowns during the first postfire season.

Chi-square contingency analysis was used to compare the differences between the burn and control densities for *C. californicus* and the other dominant perennials. Community coefficients of similarity, percent similarity indices, and dominance and diversity indices were calculated for comparisons between the burn and control areas (Brower and Zar, 1984). Comparisons were made between sexual morphs and crown diameters for *C. californicus* in the burn and control areas using one-way ANOVA.

Results

Reproduction of *Lotus scoparius* and *Croton californicus* was greatly stimulated by the fire indicated by a significant increase ($p < 0.001$) in density in the burn area at 1.5 years postburn (Table 1). These two species were the number one and two dominant postburn species with importance values (*IV*) of 145.3% and 96.1% respectively. Preburn dominants *Eriodictyon trichocalyx* (*IV* = 85.1%), *Eriogonum fasciculatum* (*IV* = 81.8%), *Senecio flaccidus* (*IV* = 22.3%), and *Opuntia littoralis* (*IV* = 22.1%) were significantly reduced ($p < 0.001$) in density after fire. Total density for all species was higher in the burn area, while total cover and frequency were lower when compared to the control area at 1.5 years postburn. Total frequency for all species in the burn area was higher than the control area at 2.5 years postburn (Table 2). *Eriodictyon trichocalyx*, *Senecio flaccidus*, *Artemisia dracunculus*, and *Rhamnus crocea* were not encountered at 1.5 years postburn but were observed at 2.5 years postburn indicating some postfire recovery. Unique species to the burn area were *Mirabilis californica* and *Solanum xanti* while unique species to the control area were *Ericameria pinifolia* and *Lupinus albifrons*.

Coefficients of community similarity and percent similarity were relatively low at 1.5 years postburn (Table 3). These coefficients increased considerably by 2.5 years postburn. Species dominance was higher in the burn area with a Simpson's index of dominance of 0.43 and 0.28 for the burn and control areas respectively at 1.5 years postburn. Species diversity was higher in the control area with a Shannon diversity index of 0.44 and 0.80 for the burn and control areas respectively at 1.5 years postburn. Species diversity could not be calculated with the 2.5 years postburn data, however, species richness for the burn area indicated that these values should have been higher at 2.5 years postburn. There were 8 species measured in the burn area out of 16 possible species at 1.5 years postburn (Table 1), while 14 species were encountered in the burn area out of 16 possible species at 2.5 years postburn (Table 2).

Importance values for *C. californicus* increased in the burn area three fold when compared to the control area at 1.5 years postburn (Table 4). *Croton* significantly increased ($p < 0.001$) in density and cover approximately three times and eight times that of the control at 1.5 years and 2.5 years postburn respectively. There was an increase from 3200 to 6350 individuals/ha and 3.4 to 6.9% cover in the burn area during the third postburn year. Mean crown diameter for the burn area was slightly smaller than control area at 1.5 years postburn and was larger than the control area at 2.5 years postburn (Table 4). The large size of postfire plants and the insignificant difference between burn and control crown diameters at 1.5 years postburn indicates that a considerable number of these plants could not have originated from seed and must have resprouted. Resprouting was observed in the Santa Ana Canyon burn at 0.5 years postburn with a postfire sprouting rate of 68.8% ($n = 11$ resprouts out of 16 topkilled plants) and a mean crown diameter of 69.5 ± 15.2 cm. Most of the resprouts exhibited large charred basal stems.

If 100% of the East Highlands preburn plants resprouted following fire, then approximately 66% of 1.5 years postburn density was derived from first and second season seedlings, while approximately 50% of the 2.5 years postburn density was produced from second and third season seedlings. A higher proportion of small plants was observed in the burn area when compared to

Table 1. Dominance of *Croton californicus* and associated perennials in burn and control areas of coastal sage scrub in East Highlands, California at 1.5 years postburn. Ad = *Artemisia dracunculus*; Cc = *Croton californicus*; Dl = *Dudleya lanceolata*; Ep = *Ericameria pinifolia*; Et = *Eriodictyon trichocalyx*; Ef = *Eriogonum fasciculatum*; Jc = *Juniperus californica*; Ls = *Lotus scoparius*; La = *Lupinus albifrons*; Mc = *Mirabilis californica*; Ol = *Opuntia littoralis*; Op = *O. parryi*; Rc = *Rhamnus crocea*; Sf = *Senecio flaccidus*; Yw = *Yucca whipplei*. *** = $p < 0.001$.

	Dominance													
	Density (no./ha)		Relative density (%)		Cover (%)		Relative cover (%)		Frequency (%)		Relative frequency (%)		Importance value (%)	
Species	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control	Burn	Control
Ad	0	80	-----	1.4	-----	1.0	-----	5.5	-----	15.0	-----	4.7	-----	11.6
Cc	*** 3200	*** 960	46.4	17.3	3.4	1.2	24.7	6.8	55.0	25.0	25.0	7.8	96.1	31.9
Dl	0	60	-----	1.1	-----	<0.1	-----	0.1	-----	15.0	-----	4.7	-----	5.9
Ep	0	60	-----	1.1	-----	0.8	-----	4.5	-----	10.0	-----	3.1	-----	8.7
Et	*** 0	*** 2560	-----	46.0	-----	3.7	-----	20.3	-----	60.0	-----	18.8	-----	85.1
Ef	*** 300	*** 980	4.4	17.6	0.2	7.1	1.2	39.2	40.0	80.0	18.2	25.0	23.8	81.8
Jc	20	20	0.3	0.4	<0.1	1.0	0.2	5.5	5.0	5.0	2.3	1.6	2.8	7.5
Ls	*** 3180	*** 20	46.1	0.4	8.6	<0.1	62.8	0.2	80.0	5.0	36.4	1.6	145.3	2.2
La	0	20	-----	0.4	-----	0.7	-----	3.6	-----	5.0	-----	1.6	-----	5.6
Mc	40	0	0.6	-----	<0.1	-----	0.2	-----	10.0	-----	4.6	-----	5.4	-----
Ol	*** 100	*** 300	1.5	5.4	0.1	0.9	0.8	4.8	20.0	35.0	9.1	10.9	11.4	21.1
Op	20	60	0.3	1.1	0.4	0.1	3.1	0.5	5.0	15.0	2.3	4.7	5.7	6.3
Rc	0	20	-----	0.4	-----	0.2	-----	0.8	-----	5.0	-----	1.6	-----	2.8
Sf	*** 0	*** 300	-----	5.4	-----	1.4	-----	7.5	-----	30.0	-----	9.4	-----	22.3
Yw	40	120	0.6	2.2	1.0	0.2	6.9	0.8	5.0	15.0	2.3	4.7	9.8	7.7
Total =	6900	5560	100	100	13.7	18.2	100	100	220.0	320.0	100	100	300	300

Table 2. Frequency (%) and relative frequency (%) of *Croton californicus* and associated perennials in burn and control areas of coastal sage scrub in East Highlands, California at 2.5 years postburn. Two hundred $1m^2$ quadrats were measured in the burn and control areas each. * = species found only in the control area. ** = species new to burn area (not encountered at 1.5 year postburn). *** = species found only in the burn area.

	Frequency (%)		Relative frequency (%)	
Species	Burn	Control	Burn	Control
Artemisia dracunculus L. **	0.5	0.5	0.7	0.8
Croton californicus Muell. Arg.	33.0	5.5	43.4	8.6
Dudleya lanceolata (Nutt) Britton & Rose **	1.0	1.5	1.3	2.3
Ericameria pinifolia (A. Gray) H. M. Hall *	-----	1.0	-----	1.6
Eriodictyon trichocalyx A. A. Heller **	2.5	25.0	3.3	39.1
Eriogonum fasciculatum Benth.	7.5	23.0	9.9	35.9
Juniperus californicus Carriere	0.5	0.5	0.7	0.8
Lotus scoparius (Nutt.) Ottley	25.0	0.5	32.9	0.8
Lupinus albifrons Benth. *	-----	1.0	-----	1.6
Mirabilis californica A. Gray ***	0.5	-----	0.7	-----
Opuntia littoralis (Engelm.) Cockerell	1.5	2.0	2.0	3.1
O. parryi Engelm.	1.5	1.5	2.0	2.3
Rhamnus crocea Nutt. **	0.5	0.5	0.7	0.8
Senecio flaccidus Less. **	0.5	1.0	0.7	1.6
Solanum xanti A. Gray ***	1.0	-----	1.3	-----
Yucca whipplei Torrey	0.5	0.5	0.7	0.8
Total =	76.0	64.0	100	100

Table 3. Coefficients of community similarity for perennials in burn and control areas of coastal sage scrub in East Highlands, Calfornia. Jaccard's coefficient (CC_j), Sorensen's coefficient (CC_s) were analyzed using species presence. Percent similarity was analyzed using relative density (PS_d) and relative cover (PS_c). A coefficient of appoximately 70% is considered an indication that the two communities (areas) are virtually identical (Whittaker, 1975).

	Coefficient of community similarity			
Postburn time	CC_j (%)	CC_s (%)	PS_d (%)	PS_c (%)
1.5 years	46.7	63.6	8.9	10.5
2.5 years	75.0	85.7	-----	-----

the control area (Figure 1). If second year seedlings were considered to be < 12 cm in diameter (a conservative maximum size) at 1.5 years postburn, there were significantly more ($p < 0.001$) seedlings in the burn area versus the control area. There was significantly more ($p < 0.001$) new seedlings germinating in the burn area when compared to the control area during the third postburn season, with 57% of the burn seedlings occurring in rodent disturbed soils. When third season seedlings are entered in the calculations, mean crown diameter for the burn and control areas at 2.5 years postburn were 30.1±22.1 and 32.2±21.9 cm respectively. The recruitment of small seedlings to the burn area decreases the mean crown diameter when compared to 1.5 years postburn mean crown diameter (31.8±18.5 cm) even though cover has increased.

Postburn *C. californicus* population patterns of sex expression were not greatly affected by the fire. Monoecious morphs of *Croton* were observed in both the burn and control areas (Table 5). Relative abundance of monoecious morphs was low with a total relative abundance of 1.0% and values for the burn and control being 0.8% and 1.8% respectively. Females were more numerous than males in both the burn and control areas. Male:female sex ratios were 0.92 for the burn and 0.80 for the control with a total male:female ratio of 0.90. Female biased sex ratios were slightly less pronounced in the burn area especially at 1.5 years postburn.

Male plants of *C. californicus* were larger than female plants (Table 6). Male crown diameter was significantly larger ($p < 0.05$ or $p < 0.001$) in both burn and control areas regardless of

Table 4. Dominance and crown diameters (mean ± SD) of *Croton californicus* in burn and control areas of coastal sage scrub in East Highlands, California. *IV* = importance value. K = number of 25 m^2 quadrats measured at 1.5 years postburn and 1 m^2 quadrats measured at 2.5 years postburn. *** = $p < 0.001$ between burn and control areas. Crown diameters at 2.5 years postburn were calculated without third season seedlings.

			Dominance							
Postburn time	Area	K	Density (no./ha)	Relative density (%)	Cover (%)	Relative cover (%)	Frequency (%)	Relative frequency (%)	*IV* (%)	Crown diameter (cm)
1.5 years	Burn	20	*** 3200	46.4	3.4	24.7	55.0	25.0	96.1	31.8±18.5
	Control	20	*** 960	17.3	1.2	6.8	25.0	7.8	31.9	34.9±21.0
2.5 years	Burn	200	*** 6350	-----	6.9	-----	33.0	43.4	-----	37.8±18.8
	Control	200	*** 750	-----	0.9	-----	5.5	8.6	-----	34.1±21.3

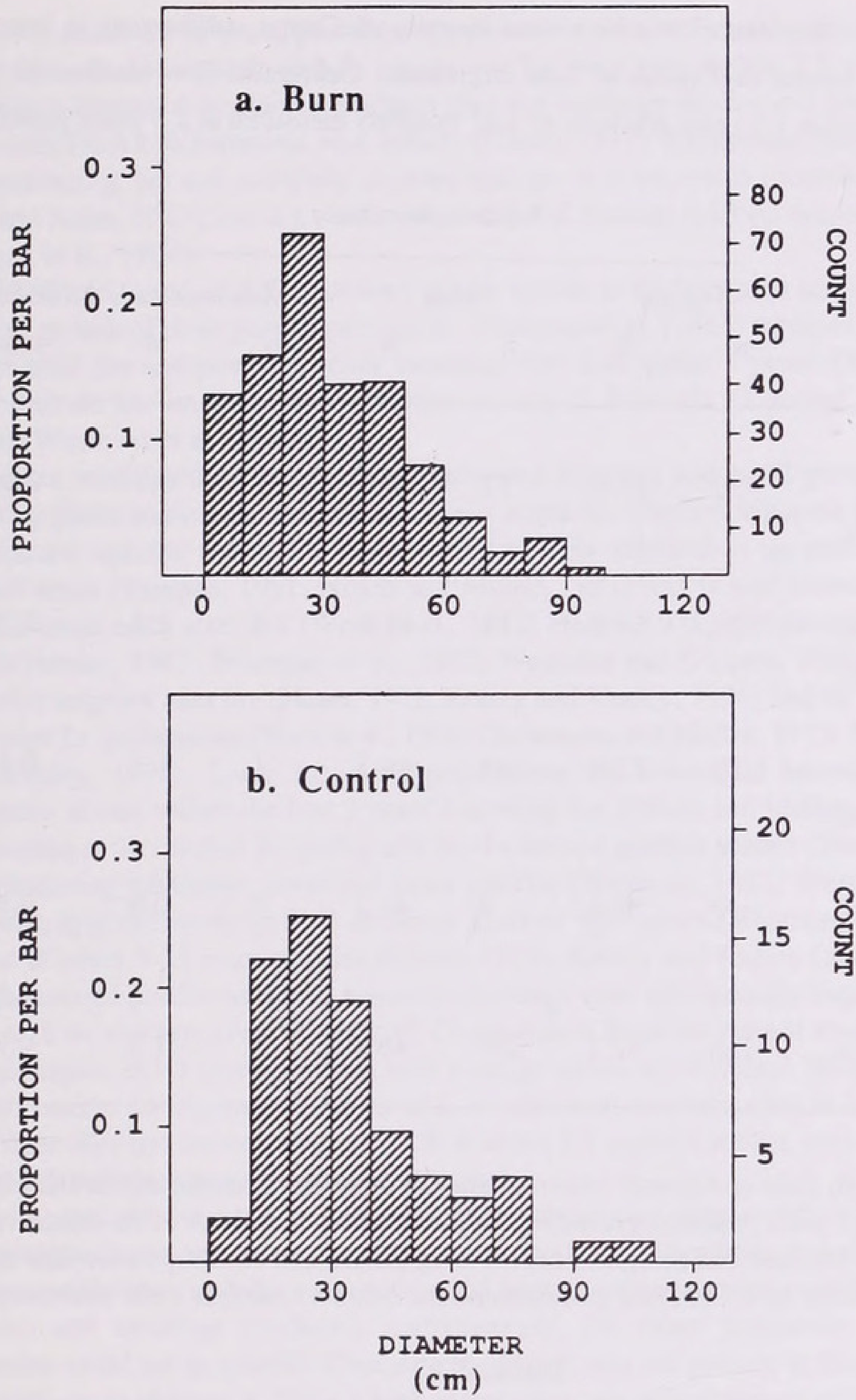

Figure 1. Proportion of *Croton californicus* by size class for burn (a.) and control (b.) areas in East Highlands, California at 1.5 years and 2.5 years postburn. Diameter is in cm. Proportion of 1.0 = 100%. Count = number of individuals.

Table 5. Relative abundance (%) for sexual morphs of *Croton californicus* in burn and control areas of coastal sage scrub of East Highlands, California. K = number of $25m^2$ quadrats measured at 1.5 years postburn or $1m^2$ quadrats measured at 2.5 years postburn.

Postburn time	Area	Female n	Female %	Male n	Male %	Monoecious n	Monoecious %	Male:Female ratio
1.5 years	Burn (K=20)	76	51.0	72	48.3	1	0.7	0.95
	Control (K=20)	23	54.8	18	42.9	1	2.4	0.78
2.5 years	Burn (K=200)	50	52.6	44	46.3	1	1.1	0.88
	Control (K=200)	7	53.8	6	46.2	0	0.0	0.86
	Total =	156	52.2	140	46.8	3	1.0	0.90

postburn time. Both male and female crown diameters increased considerably in the burn area from 1.5 years to 2.5 years postburn, exceeding the mean crown diameters of the control area by 2.5 years postburn. Monoecious morphs, nonflowering plants, and seedlings were also found to be significantly different ($p < 0.001$) for crown diameters, however, sample sizes were very small.

Discussion

Croton californicus is a dominant species in Riversidian coastal sage scrub and is associated with a wide array of perennials reported by Howell (1929), Kirkpatrick and Hutchinson (1977), Westman et al. (1981), Zembal and Kramer (1984), and Wheeler (1988). The association 2, observed in this study, is considered to have structural complexity and species diversity unrivalled among the rest of the coastal sage scrub associations (Kirkpatrick and Hutchinson, 1977). Many of the dominants of this community appear to recover quickly from or to even be stimulated by fire. This is observed by the appearance of preburn dominants *E. trichocalyx*, *S. flaccidus*, *A. dracunculus*, *D. lanceolata*, and *R. crocea* in the burn area within 2.5 years. *Eriodictyon trichocalyx* is known to recolonize postburn sites via seedlings (Hanes and Jones, 1967) as well as resprouts from a rhizomatous root system (Hanes, 1971). *Eriogonum fasciculatum* appears to be recovering, but not as rapidly as other species. It is known to increase in postburn sites (Hanes and Jones, 1967), but is a weak resprouter and initially exhibits decreased reproduction (Westman et al., 1981).

Mirabiliscalifornica and *S. xanti* were unique species to the burn area and indicated that fire stimulated growth of these pioneer perennials. Westman et al. (1981) reported *M. californica* to resprout after fire and postburn cover increased two fold within 3 years. Other current study species that are known to resprout after fire include *O. littoralis*, *O. parryi*, *R. crocea*, and *Y. whipplei* (Westman et al., 1981).

Species stimulated by fire exhibited increased densities and rapid growth in cover from resprouting plants and/or seed germination. *Lotus scoparius* displays vigorous growth, becoming the dominant species within 1.5 years postburn. This subshrub is an excellent colonizer of disturbed areas (Steppan, 1991; Nilsen and Muller, 1981) and is well known for its ability to dominate areas early after fire (Went et al., 1952; Hanes, 1971; Kirkpatrick and Hutchinson, 1977; Westman, 1981; Westman et al., 1981; Westman and O'Leary, 1986). It has not been observed to resprout after fire (Hanes, 1971; Keeley and Keeley, 1984) and its seeds require heat scarification for germination (Went et al., 1952; Christensen and Muller, 1975; Nilsen and Muller, 1981; Keeley, 1991). *Lotus scoparius* populations are even-aged because 100% of seed germination occurs within the first 2 years following fire (Nilsen and Muller, 1981).

Lotusscoparius reaches flowering size by the second postfire season (Horton and Kraebel, 1955) producing maximum cover 2-4 years postfire (Westman, 1981; Westman and O'Leary, 1986) with approximately an 80% decrease in cover by 7 years (Westman, 1981) and a 95% decrease in cover 9-21 years postfire (Hanes, 1971). Keeley and Keeley (1984) reported at the end of the second postfire season *L. scoparius* seedlings were substantially larger than most other species with an average cover of 466 cm^2. Cover values from the current study were more than five times higher at 1.5 years postburn with average values of 2709 cm^2. Westman et al. (1981) reported considerable increases in cover of *L. scoparius* at two burn sites at 2-3 years postburn. One of these sites had cover values of 7.2% at about 2.5 years postburn, very close to the 8.6% cover at 1.5 years postburn reported in this study.

The second most vigorous colonizer of the postburn area of this study was *C. californicus*. It appears that *Croton* was tremendously stimulated by fire and postburn sites for at least 3 years. Postfire reproduction includes resprouting and seed germination with considerable numbers of resprouts and seedlings produced. Unfortunately, the exact proportion of each type of propagation could not be quantified because the author was not present at East Highlands at 0.5 years postburn to observe it. Since a high resprouting rate was observed at Santa Ana Canyon, it is possible that resprouting could be higher than 68% if fire intensity is lower (Westman et al., 1981). If 100% of the East Highlands *Croton* resprouted, there still would be a tremendous amount of seedlings produced the first, second, and third seasons postfire. Many coastal sage scrub dominants exhibit decreased seedling establishment the first postfire season with the appearance of numerous seedlings the second season from seeds produced by resprouts (Westman et al., 1981; Malanson and O'Leary, 1982; Keeley and Keeley, 1984).

Table 6. Crown diameters (mean ± SD) for sexual morphs *Croton californicus* in burn and control areas of coastal sage scrub of East Highlands, California. All units are in cm. Sample sizes are numbers in parentheses (n). K = number of $25m^2$ quadrats measured at 1.5 years postburn or $1m^2$ quadrats measured at 2.5 years postburn. * = $p < 0.05$ between morphs. *** = $p < 0.001$ between morphs.

Postburn time	Area	K	Crown diameter: Female	Male	Monoecious	Nonflowering	Seedling
1.5 years	Burn	20	31.2±17.6***	35.2±18.6***	60.0***	11.0±5.0***	-----
			(76)	(72)	(1)	(11)	-----
	Control	20	34.1±17.8*	41.2±23.9*	60.0*	14.8±4.9*	-----
			(23)	(18)	(1)	(6)	-----
2.5 years	Burn	200	35.7±16.2***	41.0±19.1***	96.0***	15.0±2.2***	2.8±1.2***
			(50)	(44)	(1)	(4)	(28)
	Control	200	32.9±19.2	39.7±24.1	-----	10.0	5.0
			(7)	(6)	-----	(1)	(1)
		Total =	33.1±17.2***	38.0±19.7***	72.0±20.8***	12.7±4.7***	2.8±1.2***
			(156)	(140)	(3)	(22)	(29)

Although it appears that fire initially stimulates seed germination of *Croton*, seeds continue to germinate up to the third postburn season. Emery (1995) states that *C. californicus* does not require any special treatments for germination. The author of the current study has made numerous attempts and treatments to facilitate seed germination in the lab and has observed 0% germination. It appears that *C. californicus* has very complex seed germination requirements. Scarification appears to be one component of these requirements. It may be possible that rodents consume the seed and chemically scarify the seed coat. Over 57% of the third postburn season seedlings occurred in rodent disturbed areas Seedlings (n = 28) had a frequency of 7.5% with as many as 7 seedlings in one 1 m^2 quadrat. Seedling aggregation in rodent disturbed areas may be due to rodent activity and/or scarification. Pocket gophers become common in postburn chaparral within the second season after fire (Christensen and Muller, 1975) and coastal sage scrub exhibits higher rodent density, diversity, and activity when compared to chaparral (Bradbury, 1978). Rodent activity might explain why germination in the burn area continued to be higher than the more woody, chaparral-like control area during the second and third postburn seasons.

Density and cover values of *C. californicus* in this study were similar to those found by Zembal and Kramer (1984) and Martin (1995). The high density (6350 plants/ha) and cover (6.9%) in the burn area at 2.5 years postburn of the current study are close to the density (6550 plants/ha) and cover (5.48%) in an undisturbed San Bernardino population reported by Martin (1995). This demonstrates that fire stimulates growth and reproduction of *Croton* to optimal densities and cover within 2-3 years after fire.

Croton californicus and *L. scoparius* share many morphological characteristics and ecological strategies in common. First, both species are subshrubs (Hellmers et al., 1955; Webster, 1993). Second, both species were significantly stimulated by fire and dominated the postburn areas of this study. Third, it appears that both species have seeds that require scarification with fire being one mode of scarification (Went et al., 1952; Christensen and Muller, 1975; Nilsen and Muller, 1981). Fourth, unlike the fibrous roots that most coastal sage scrub subshrubs have (Hellmers et al., 1955), both species have clearly defined taproots. Hellmers et al. (1955) reports that *L. scoparius* has a clearly defined taproot. *Croton californicus* also has a clearly defined taproot with mature plants possessing taproots greater than 1 m deep (Martin, field observations). Fifth, both species are drought-deciduous (Nilsen and Muller, 1981; Martin, field observations). Sixth, both species exhibit continual basal sprouting in the absence of fire (Malanson and Westman, 1985; Webster, 1993). These features appear to allow both subshrubs to rapidly colonize and dominate disturbed areas of xeric, fire-adapted ecosystems.

Croton californicus and *L. scoparius* differ from each other in two ways. First, *Croton* resprouts following fire while *Lotus* does not. Second, seed germination of *C. californicus* is stimulated for at least 3 years postfire while 100% of seed germination for *L. scoparius* occurs within the first 2 years postfire. Both species are pioneer plants in succession and in many situations will eventually be displaced by more woody shrub species. The increased sprouting vigor and continual seed germination may allow *C. californicus* to persist longer in the succession of coastal sage scrub communities. Most perennial coastal sage scrub species continually sprout and produce non-dormant, non-fire resistant seeds that are constantly recruited between fires (Malanson and O'Leary, 1982). *Croton* differs from this in that its seeds appear to be somewhat dormant and fire-resistant. The hardseededness and relatively large size of *C. californicus* seeds probably reflect some fire-adaptations that differ from the typical light, non-fire resistant seeds produced by most coastal sage scrub perennials (Kirkpatrick and Hutchinson, 1980; Malanson and O'Leary, 1982).

Postburn *C. californicus* population patterns of sex expression were not greatly affected by the fire and very similar to those reported by Martin (1995). Again, size appears to be a secondary sex character in which males are larger than females. Most secondary sex characters of plants are subtle and usually are expressed in terms of growth, resource allocation, and timing or longevity (Richards, 1986). Female biased sex ratios, as observed in this study, are rarer in nature than male biased sex ratios (Willson, 1983; Richards, 1986). The sex ratio in plant populations may not be equal due to microhabitat segregation by the different sexes (Handel, 1983). There is some evidence in subdioecious species that females are relatively constant in their sex expression and it is the polleniferous plants which are variable (Heslop-Harrison, 1957; Charlesworth and Charlesworth, 1978). This may be true with *C. californicus* because when male and monoecious plants are added together, the male:female ratio is closer to 1.00.

The frequency of monoecious morphs observed in this study was low as has been previously observed (Martin, 1995). Although monoecious individuals compose only a small fraction of a given population, their presence suggests that *C. californicus* may have an unusual breeding system. The author will be publishing results of a flowering phenology study that monitored individual plants for the 1994 season by quantifying the number of pistillate and/or staminate flowers through time to reveal the constancy for sex expression of each individual plant. These plants are to be observed for two more seasons to discover if *Croton* is genetically and/or environmentally subdioecious or if sex reversal is occurring.

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