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INTERACTION OF FIRE AND COMMUNITY DEVELOPMENT IN CHAPARRAL OF SOUTHERN CALIFORNIA[1]

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Abstract. Fire is an ecosystem property rather than an exogenous force in southern California chaparral, and it interacts with processes of drought-mediated canopy development, production, and mortality to affect stability of community composition. Where species that must reproduce from seed, such as *Ceanothus crassifolius* or *Ceanothus oliganthus,* are predominant, composition can be altered by a single fire with little or no recruitment after initial postfire establishment.

Water balance apparently regulates subsequent leaf area development; after 15–22 yr of postfire growth, foliage biomass in monospecific *C. crassifolius* stands in this study had approached a maximum that was unrelated to incident solar radiation and insensitive to initial population density over a 10-fold range. Thus, establishment success, above that required for canopy closure, should have little effect on the foliage biomass that sustains combustion. After canopy closure, total biomass accumulated at an accelerating rate through at least two decades with aboveground net primary production as great as 12–13 $Mg \cdot ha^{-1} \cdot yr^{-1}$. *C. crassifolius* mortality was substantially less than predicted from growth rates and the $-3/2$ power model of Yoda et al. (1963), and there was no approach to a common asymptotic density by stands of disparate initial density.

With low deadwood biomass and absence of ground fuels, *C. crassifolius* cannot sustain burning in the absence of wind, steep slopes, or exceptionally low live-fuel moisture. Increased *Ceanothus* abundance in multispecies communities with *Adenostoma fasciculatum* or *Salvia mellifera* alters biomass structure and could modify subsequent fire effects even if foliage area fully redevelops in concert with site water balance. Rare, low-intensity fires can devastate *Ceanothus* chaparral, that reproduces only from seed. *Salvia mellifera* and *Eriogonum fasciculatum* can occupy resulting openings in the canopy, and their abundant deadwood and compact biomass can readily spread low-intensity fires, thereby perpetuating the degraded community. Productive stands within a chaparral association are probably subject to especially severe fires that limit nutrient accumulation and may also limit subsequent productivity. Copious nitrogen volatilization during burning is promoted by high nitrogen concentrations in foliage and fine woody biomass of *Ceanothus* and heavy leaf litter of *Quercus dumosa* and *C. crassifolius.* The communities most prone to severe fires also accumulate and cycle nitrogen and phosphorus rapidly.

Key words: Ceanothus; *chaparral; fire; nitrogen cycling; phosphorus cycling; −3/2 power model; primary production;* Quercus; *stand structure; system properties.*

INTRODUCTION

The chaparral ecosystem in California consists of diverse plant associations subject to prolonged summer drought and catastrophic fires that typically recur every 15–100 yr, depending on species composition, environment, and the vagaries of weather and ignition (Philpot 1974). Where shrubs establish predominantly from seed, species composition can be recast by even a single fire depending on its severity, prefire stand conditions, and subsequent weather. If canopy continuity is lost, subshrubs that disperse from abundant seed, such as *Salvia mellifera* or *Eriogonum fasciculatum,* can expand within a community (Riggan and Dunn 1982). Few new shrubs are recruited as a community matures (Patric and Hanes 1964), so an altered postfire composition could persist throughout the fire-free period. If community-level primary production, foliage development, biomass structure, or mortality are substantially altered by a change in predominant species or population density, then so may the severity or likelihood of subsequent fires and thus persistence of the new community's composition. Alternatively, these community properties may be regulated by site water balance and may be insensitive to potential changes in composition.

Regulation of chaparral-community leaf area by site

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water balance has been inferred from the timing of physiological drought along geographical gradients. Summer water stress progresses from coastal and desert boundaries of the chaparral to inland sites, yet its development there is earlier than would be expected from local water balance (Poole and Miller 1981). Similarity in timing of soil drying and water stress between adjacent north- and south-facing aspects also belies their contrasting evaporative potentials (Poole and Miller 1975, Krause and Kummerow 1977). In both circumstances, the relative uniformity of plant water stress may be attributed to greater leaf area on more favorable sites, which hastens transpiration and soil drying. If so, then community leaf area should reach a maximum as an increment of foliage lengthens or deepens the drought stress with no net gain in carbon uptake. This condition should develop most rapidly where resprouting shrubs predominate, since their primary roots survive despite burning of aboveground vegetation. If drought stress controls canopy development, mortality induced by competition should commence in seedling-regenerated populations as the growth of dominant plants aggravates summer water stress. However, the competitive pressure may be weak since moisture is favorable for all during an extended period in winter and spring, species are adapted to water stress, and all shrubs must periodically endure drought regardless of competitive effects.

Persistence of an altered community composition may ultimately be affected by fire-associated losses of nitrogen and phosphorus, especially on geomorphically active landscapes. From 10 to 25% of the nitrogen in vegetation, litter, and surface soil can be volatilized during burning (DeBano and Conrad 1978, Riggan and Lopez 1982), and subsequent soil erosion, as great as 500 m^3/ha the 1st yr (Rowe et al. 1951), further depletes nutrients. Since volatilization and erosion may increase with fire severity, a change in composition that promotes severe fires—by increasing foliage mass, deadwood, or altering biomass structure—will deplete system nutrients unless there is a compensatory means of nutrient accumulation.

In this paper, we compare canopy development, flammability, and nutrient cycling in chaparral communities where *Ceanothus* is predominant, and consider the degree to which changes in *Ceanothus* abundance after fire may affect subsequent community properties, fire effects, and persistence of the altered composition. From a reconstructed history of population density and growth in *Ceanothus crassifolius* stands, we also test for development of a maximum leaf area and a rate of shrub mortality that departs from the $-3/2$ power model of Yoda et al. (1963).

Site Description

Community properties were measured at the San Dimas Experimental Forest (Fig. 1) in the San Gabriel Mountains of Los Angeles County, California (34°12′ N, 117°46′ W), and southern Laguna Mountain in San Diego County (32°47′30″ N, 116°27′30″ W). Mature chaparral at San Dimas had developed after successive wildfires in 1896, 1919, and 1960. Young *Ceanothus* stands were present within the perimeter of the 1975 Village Fire in San Dimas Canyon and in nearby Little Dalton Canyon, which last burned in 1968. At Kitchen Creek on Laguna Mountain, we examined adjacent 1-, 11-, and 35-yr-old stands of *Quercus dumosa* chaparral located along an east-facing slope of 45–60% gradient at an elevation of 1340–1580 m. The 1-yr-old *Q. dumosa* regenerated after a prescribed fire during November 1979 (Dougherty and Riggan 1982). The 11-yr-old stand developed after the Laguna Fire of 1970.

At San Dimas, *Ceanothus crassifolius* forms both monospecific and mixed stands with *Adenostoma fasciculatum,* generally on southerly aspects; *Ceanothus oliganthus* is dominant on steep north-facing slopes, with an occasional understory of *Quercus dumosa. Salvia mellifera* is common in mixed stands dominated by *A. fasciculatum* and *C. crassifolius.* Although *A. fasciculatum* is the most common shrub species in the San Gabriel Mountains (Hanes 1971), it rarely forms monospecific stands at San Dimas and predominates only on steep slopes on southerly aspects. Mixed-composition chaparral in the lower productivity environment of Laguna Mountain is dominated by either *Quercus dumosa,* with *Ceanothus leucodermis* and *Ceanothus greggii* var. *perplexans* as minor elements, or a *C. greggii* var. *perplexans–Adenostoma fasciculatum* association (nomenclature of taxa follows that of Munz 1974). Of the four *Ceanothus* species encountered, only *C. leucodermis* can sprout after fire.

Soils at San Dimas are most commonly Typic Xerorthents, Entic Haploxerolls, and Typic Xerochrepts (USDA Forest Service, Angeles National Forest, Soil Resource Inventory) developed from diorites, granodiorites, schists, and gneiss (Crawford 1962). Clay loam derived from andesite is present on Johnstone Peak. The terrain is dissected by steep-walled canyons; 86% of the hillslopes have a gradient exceeding 55% (Bentley 1961). At Kitchen Creek, soils have developed from quartz diorite and mica schist and are classified as a fine loamy, mixed, mesic, mollic Haploxeralf (Bowman 1973).

At Tanbark Flats field station on the San Dimas Experimental Forest, annual precipitation averages 696 mm (SD = 335 mm) (USDA Forest Service records, 1928–1929 through 1984–1985, Riverside, California), 95% of which falls from October through April (Rice 1974). Pan evaporation there is 1580 mm/yr (Reimann 1959*a*). Estimated mean annual precipitation is 700 mm at the Bluebird and Johnstone Peak sites, 850 mm in the Upper East Fork of San Dimas Canyon, and 750–800 mm at all other locations studied. The mean daily maximum temperatures during

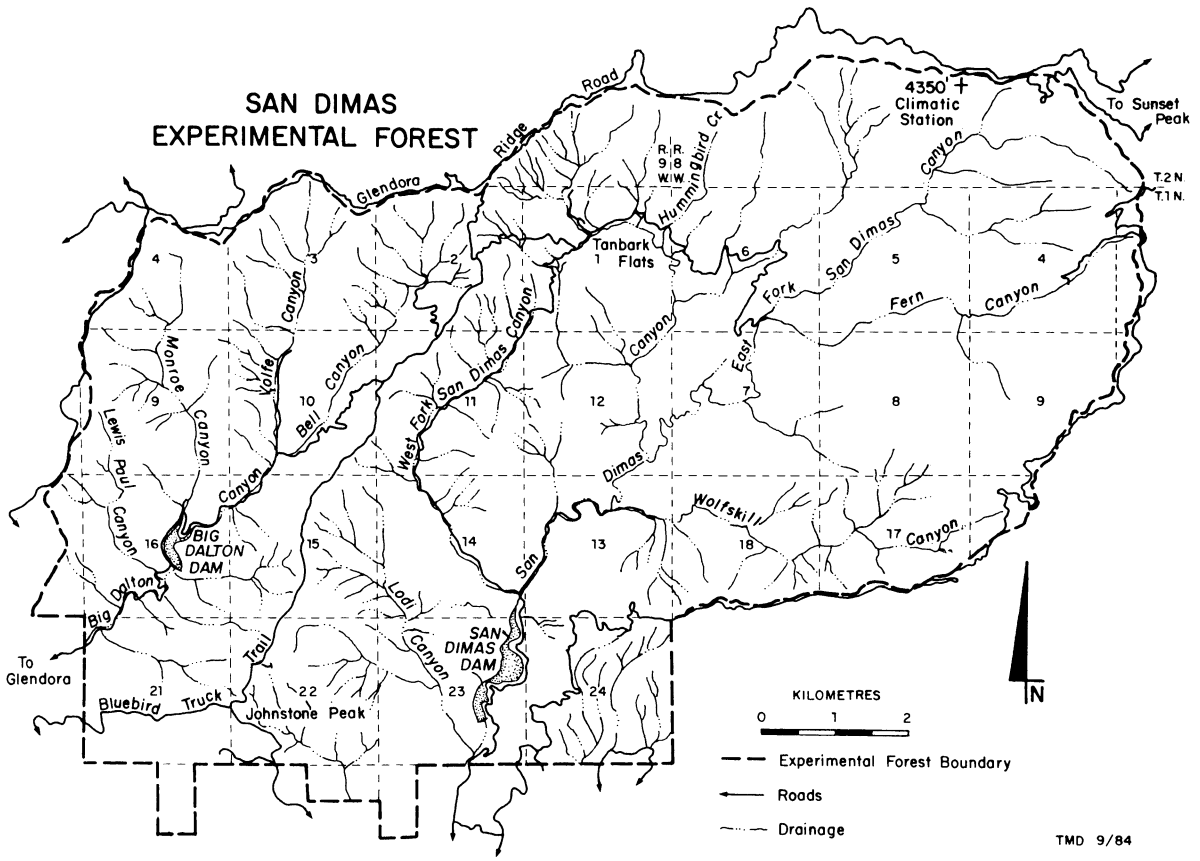

FIG. 1. The San Dimas Experimental Forest, Angeles National Forest.

January and July are 14.8° and 30.5°C; daily minima for the same months are 2.6° and 13.8° (measured from 1933 through 1958) (Reimann 1959*b*).

Average annual precipitation at Kitchen Creek, 890 mm, was estimated from a regression on elevation based on the Campo, Descanso, and Cuyamaca stations within this climatic zone (United States Department of Commerce 1981). Mean air temperature for 1981 was estimated to be 12.9°, based on a regression from five climatic stations.

METHODS

Community biomass was estimated by combining destructive analyses of individual shrubs with areal estimates of basal area distribution and population density.

For mature *Ceanothus* communities, shrub basal areas were calculated (assuming a circular cross-section) from measured stem circumferences or diameters (on stems of <8 cm circumference). On irregular small stems, maximum and minimum diameters were averaged. Plots encompassed 120 m^2 (6 × 20 m), with 11 in the *C. crassifolius* and 12 in the *C. oliganthus* communities. Plot size was 32 m^2 in more densely populated *A. fasciculatum,* young *Ceanothus,* and mixed-composition chaparral in Bell Canyon (Jacks 1984). *Eriogonum fasciculatum* biomass in three 20-m^2 plots was also harvested and weighed.

Basal area and population density were estimated in five 64-m^2 plots in 35-yr-old *Q. dumosa* at Kitchen Creek and in a nearby *A. fasciculatum–C. greggii* var. *perplexans* community at Fred Canyon, where stem diameters were measured in 15 6-m^2 plots within an area of 0.1 ha.

Regressions of biomass as a function of basal area, by species, age, and region, were computed separately for data collected in plots spanning the observed range in stand biomass and stature (Table 1, Fig. 2). By using the extra-sum-of-squares principle (Draper and Smith 1981), we compared regressions for 35-yr-old *Q. dumosa* at two sites on Laguna Mountain, 21-yr-old *C. oliganthus* at two sites at San Dimas, and 21-yr-old *C. crassifolius* at three sites. Biomass in the 1-yr-old *Q. dumosa* at Kitchen Creek was estimated from regressions developed using prefire basal area as the independent variable.

Harvested shrubs were measured for length of the longest branch and basal circumference, weighed fresh, then separated into deadwood, live stems, and foliage. Each fraction was weighed and subsampled to deter-

TABLE 1. Regressions of biomass (B) as a function of basal area (BA). A power function model with bias correction, $B = B_0(BA)^{(B_1)}e^{0.5\,s}$, where s is the residual mean square, was used unless otherwise indicated. Maximum values of dry biomass, *db*, and basal area that were used in the regressions are given.

Species	Stand age (yr)	Regression coefficients		Maximum values		r^2	Sample size	Notes
		$B_0 \cdot e^{0.5\,s}$	B_1	*db* (kg)	*BA* (cm²)			
Total shrub biomass								
San Dimas Experimental Forest								
Ccr[a]	6	0.063	1.13	0.8	9.5	0.87	35 shrubs	[b]
	7	0.105	0.98	5.0	42.	0.82	32 shrubs	[c]
	14, 21, 22	0.156	1.01	56.	230.	0.87	108 shrubs	[c,d]
Co	6	0.052	1.30	2.0	21.	0.97	30 shrubs	[e]
	21	0.143	1.22	202.	550.[f]	0.91	28 shrubs	
	21	8.1×10^{-5}	1.18[g]	202.	550.	0.96	30 shrubs	
Af	18	0.148	1.10	5.6	26.	0.91	42 stems	[h]
Qd	21	0.113	1.35	6.6	24.	0.92	15 shrubs	
Sm	22	0.162	0.84	9.4	4.1[f]	0.58	30 shrubs	[i]
	22	0.85	0.98[j]	9.4	(6. m²)	0.49	30 shrubs	[i]
Laguna Mountain								
Qd	11	0.060	1.41	1.4	10.5	0.90	30 stems	[k]
	35	0.076	1.30	2.7	13.5	0.95	34 stems	[k,l]
	35	0.072	1.32	1.4	6.2	0.86	16 stems	[k,m]
	37	0.101	1.12	8.1	47.	0.93	23 stems	[k]
	35–37	0.083	1.22	8.1	47.	0.97	57 stems	[k, n]
Af	35	0.069	1.17	1.0	9.5	0.89	95 stems	[o]
	35	−0.14	0.087[p]	2.3	28.	0.98	10 shrubs	
Cgp	35	0.175	1.01	8.2	3.6	0.92	7 shrubs	[q]
	35	0.132	1.05	8.2	4.3	0.85	7 shrubs	[r]
Cl	35	0.056	1.30	22.7	78.	0.88	9 shrubs	[k]
Foliage biomass								
San Dimas Experimental Forest								
Ccr	6	0.0145	1.43	0.28	9.5	0.95	10 shrubs	
	7	0.0199	1.10	1.2	42.	0.53	32 shrubs	
	14	0.0429	0.99	4.9	95.	0.86	38 shrubs	
	21	0.0120	1.12	7.7	230.	0.85	51 shrubs	
	22	0.0424	0.93	4.8	158.	0.72	16 shrubs	
Co	6	7.2×10^{-3}	1.26	0.3	21.	0.99	9 shrubs	
	21	5.6×10^{-3}	1.08	4.2	550.[f]	0.85	17 shrubs	
	21[g]	5.8×10^{-6}	1.07	4.2	550.	0.82	17 shrubs	
Af	18	0.015	0.07[s]	1.8	(17. kg)	0.98	13 shrubs	
Qd	21	8.5×10^{-3}	1.41	0.56	24.	0.83	15 shrubs	
Sm	22	0.093	0.83[j]	0.74	(6. m²)	0.49	30 shrubs	
Laguna Mountain								
Qd	11	2.1×10^{-3}	1.72	0.13	10.5	0.85	30 stems	
	35	0.120	0.015[p]	1.25	77.	0.95	5 shrubs	
	37	3.4×10^{-3}	1.36	0.54	33.	0.72	10 stems	
Af	35	3.4×10^{-3}	0.107[s]	0.27	(2.3 kg)	0.77	10 shrubs	
Cgp	35	0.040	0.158[s]	0.56	(3.1 kg)	0.75	9 shrubs	

[a] Species identification: *Af, Adenostoma fasciculatum*; *Ccr, Ceanothus crassifolius*; *Cgp, C. greggii* var. *perplexans*; *Cl, C. leucodermis*; *Co, C. oliganthus*; *Qd, Quercus dumosa*; *Sm, Salvia mellifera.*

[b] Shrub dry to fresh biomass ratio (*db*:*fb*) is 0.70.

[c] Shrub *db*:*fb* = 0.56.

[d] No significant differences were found among regressions for these three ages.

[e] Shrub *db*:*fb* = 0.65.

[f] Basal area (*BA*) measured at 30 cm.

[g] The product of *BA* and average stand height (cm³) was used as the independent variable; *BA* alone accounted for 0.91 of the variance.

[h] Shrub *db*:*fb* = 0.73.

[i] Live wood *db*:*fb* = 0.56, foliage *db*:*fb* = 0.32, deadwood *db*:*fb* = 0.8.

[j] Shrub cover (m²) was used as the independent variable.

[k] Shrub *db*:*fb* = 0.75.

[l] Sample collected at Kitchen Creek.

[m] Sample collected at Fred Canyon.

[n] No significant differences were found among the regressions for ages 35 and 37; coefficients determined from the pooled data are given here.

[o] Shrub *db*:*fb* = 0.72.

[p] A linear model was used.

[q] Shrub *db*:*fb* = 0.71. *BA* was measured by planimeter; the area estimated from stem diameter (BA_d) = 0.04 + 1.19(BA_{pl}).

[r] *BA* was estimated from maximum and minimum stem basal diameters.

[s] B_f was estimated as a linear function of B_t.

mine water content, after drying to constant mass in a forced-draft oven at 75°C. Woody tissue in a limited number of shrubs, selected from across the range of basal areas, was separated into diameter classes of 0–0.5, 0.5–1.0, 1.0–2.0, and >2.0 cm. Live wood and foliage in harvested *Ceanothus* and *Quercus* were separated by 1 m height increments in order to determine the vertical distribution of biomass. Ratio estimates, r, and their approximate variances, v, for the fraction of deadwood within live plants and the proportion of wood within each size class were computed from the formulae

$$r = \sum_i y_i / \sum_i x_i \quad (1)$$

and

$$v = \frac{1}{n\bar{x}} \sum_i (y_i - rx_i)^2/(n-1), \quad (2)$$

where the summations are made over measurements for different shrubs, $x = \sum_i \bar{x}_i/n$, y_i is the biomass of a shrub component, and x_i is the total mass considered (Cochran 1977).

In order to estimate relative differences in fire behavior among community types, we further assumed surface-area : volume ratios of 2400, 535, 265, and 90/m for the four wood size classes sampled (from smallest to largest). Leaf thickness reported for *C. greggii* (0.65 mm) and *Q. dumosa* (0.29 mm) (Krause and Kummerow 1977) were used to compute surface-area : volume ratios for relatively sclerophytic (3100/m) and mesophytic (6900/m) leaves. (The former value was assumed for *C. crassifolius*; the latter for *C. oliganthus* and *S. mellifera*.)

Stand total and foliage biomass, B, were estimated by

$$B = \sum_{j=1}^{n} a(BA_j)^b e^{0.5s}, \quad (3)$$

where regression coefficients were derived from harvest data, BA_j is shrub or stem basal area, and s is the residual mean square. The summation is taken over all individual shrubs within a plot. The approximate variance of an estimate, v, based on the mean and variance of a lognormal distribution, was computed as:

$$v = e^{s^2}(e^{s^2} - 1) \cdot \sum_{j=1}^{n} \{\exp[\ln(a) + b(\ln BA_j)]\}^2. \quad (4)$$

One-half the width of the estimated 95% confidence interval for *C. crassifolius* stands averaged 15.7% of the mean for foliage biomass and 8.7% for total aboveground biomass.

Trends in stand structure with age may be obscured by site differences and different historical patterns of establishment or environment when different-aged stands are compared. These difficulties can be avoided if trends can be measured or reconstructed for individual stands. We reconstructed the development of biomass, basal area, and population density for each of the 21-yr-old *C. crassifolius* stands by the following procedure. (1) Basal area at ages 7, 14, and 22 yr, estimated by planimeter for a sample of shrubs spanning the range of observed sizes, was related to basal area at age 21; age could be determined within 1 yr on live stems. A correction was made to relate stem outside-bark circumference to planimetered area. (2) Regressions of total and foliage biomass as functions

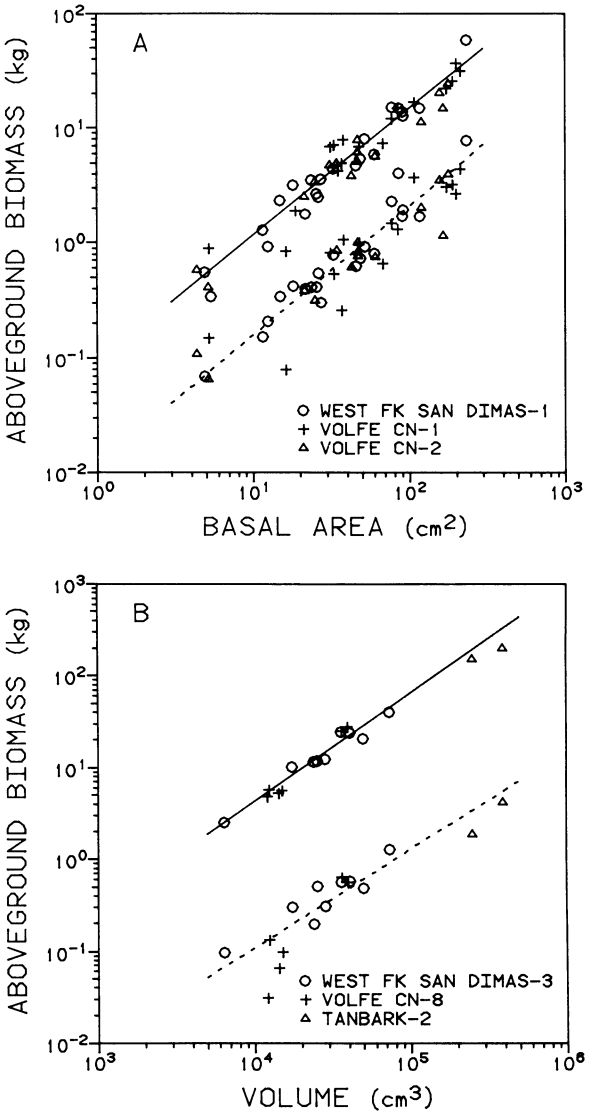

FIG. 2. Biomass of 21-yr-old shrubs at several different sites as a function of (A) shrub basal area for *Ceanothus crassifolius* and (B) the product of basal area and stand height (a measure of shrub volume) for *C. oliganthus*. In each figure, data and regressions for foliage (-----) and total biomass (——) are shown. The regressions did not differ significantly among sites of widely varying productivity.

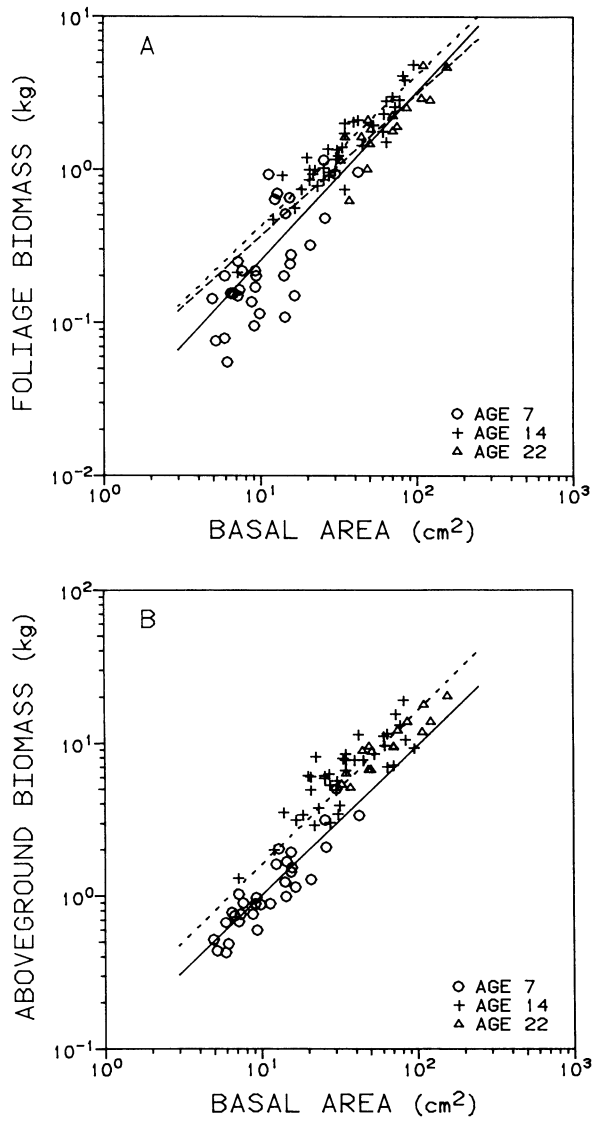

FIG. 3. Regressions of (A) foliage and (B) total biomass as a function of basal area for *Ceanothus crassifolius*. The three regressions for foliage biomass in 7- (——), 14- (-----), and 22-yr-old stands (– – –) were significantly different. The total biomass regression for the 7-yr-old stand (——) differed from that of the older ages combined (-----).

of basal area were estimated for 7-, 14-, and 22-yr-old stands prior to shoot expansion during early spring 1983 and compared by the extra-sum-of-squares principle (Draper and Smith 1981) and a Bonferroni a posteriori test. (3) For a sample of dead shrubs, final age and basal area were related by regression. (4) Then we computed, for the three ages and each stem measured at age 21 yr, its approximate basal area (from 1), live or dead state (from 3), and biomass (from 2).

Accumulated leaf litter was collected from each of four 0.25-m^2 quadrats in mature stands at San Dimas during the late summer of 1981. Samples from 35-yr-old *Q. dumosa* at Kitchen Creek were collected from two 0.5-m^2 quadrats in each of nine 64-m^2 plots located across the 8-ha site. Senescing foliage cast from mature *Ceanothus* at San Dimas was also collected, from mid-May through September 1982, by five 0.094-m^2 traps per plot. All samples were dried and weighed, with subsamples ground in a Wiley mill for chemical analysis.

Four composite soil samples containing 12 cores each were collected from a depth of 0–10 cm in all mature stands during late summer 1982. These were sieved through a 2-mm screen and subsampled to determine water content, total nitrogen and phosphorus, and mineralizable nitrogen.

Soil, plant tissue, and litter samples were digested using a modified micro-Kjeldahl procedure (Parkinson and Allen 1975). Soil mineralizable nitrogen was estimated using a 40°, 2-wk, anaerobic incubation followed by 1 mol/L KCl extraction and ammonium analysis (Keeney and Bremner 1967). Ammonium and Kjeldahl nitrogen and phosphorus were determined using a Technicon AutoAnalyzer II (Industrial Method Number 33474W/B revised March 1977).

RESULTS

Biomass regressions and harvest data

The two-stage sampling employed to estimate biomass is profitable only if the regressions of biomass components as a function of basal area are not different for stands of different environment and productivity. No significant differences were apparent among either total biomass or foliage biomass regressions (Table 1) developed for each of three 21-yr-old *Ceanothus crassifolius* stands that spanned the elevational and productivity range of the species at San Dimas. Similarly, total biomass regressions of 35-yr-old *Quercus dumosa* in mixed chaparral and pure stands at two sites 3 km distant at Laguna Mountain were virtually identical.

Regressions of total biomass as a function of basal area were significantly different between 7- and 14-yr-old *C. crassifolius*, but not between ages 14 and 22, primarily because of the rapid height growth between the first two ages measured. Foliage biomass regressions from each of the three ages differed significantly (Fig. 3).

Estimating stand properties

Basal area distributions.—The basal area frequency distributions for mature *C. crassifolius* and *C. oliganthus* showed a strong differentiation of the populations into dominant and suppressed shrubs with high rates of mortality in the smallest size classes (Fig. 4). The live *Adenostoma fasciculatum* population was similarly differentiated into size classes, but small dead shrubs were absent. By age 21 yr, mortality apparently had reduced the number of live *Ceanothus* shrubs by one-half, if it is assumed that the total density of live and

dead shrubs at maturity is equivalent to the live population established 3–5 yr after fire. A wide range in the apparent initial population density was observed: 0.65–5.9 *C. crassifolius*/m² and 0.12–2.6 *C. oliganthus*/m². Some smaller shrubs had died in each of the *Ceanothus* stands measured.

Stand biomass.—Smaller shrubs, although numerous, accounted for only a small proportion of either total or foliage biomass in *C. crassifolius*. Those with a basal area less than the 70th percentile in the population (60 cm²) made up only 35% of the foliage or total live-shrub biomass (Fig. 5).

For monospecific, 21-yr-old stands, the range of total biomass in *C. crassifolius* (42–95 Mg/ha) was comparable to that of *C. oliganthus* (43–115 Mg/ha) (Tables 2 and 3). *A. fasciculatum* had biomass in the range from one-half to the equivalent of the minimum observed in *Ceanothus* (Table 4). *Eriogonum fasciculatum*, measured where it had invaded a roadside fuelbreak after burning in 1960, had an average standing biomass of 26.5 Mg/ha (SE = 4.0 Mg/ha).

Early development in the resprouting species *Q. dumosa* was rapid at Kitchen Creek. Production in the 1st yr after burning was 2.8 Mg/ha, whereas the average annual biomass increment over 35 yr (including foliage production) was 3.2 Mg/ha. Foliage biomass after 1 yr of postfire growth was 1.1 Mg/ha, ≈40% of that in mature stands (Table 5).

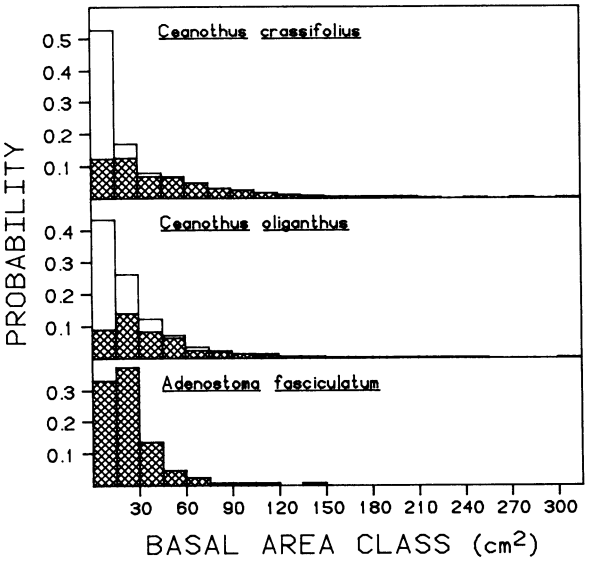

FIG. 4. Sample basal area distributions for 21-yr-old *Ceanothus crassifolius*, *C. oliganthus*, and *Adenostoma fasciculatum* at San Dimas. The ordinate represents the probability that a randomly chosen shrub will fall within a given basal area class. Live shrubs are indicated by the cross-hatched histograms; the sum of live and dead shrubs is given by the open histograms. Shrubs of basal area >300 cm² are indicated in the right-most class. Small dead shrubs are numerous in both *Ceanothus* populations, which form locally continuous stands. Shrubs of basal area >120 cm² are rare but important in the canopy; in *C. crassifolius*, they support 30% of stand foliage (cf. Fig. 5).

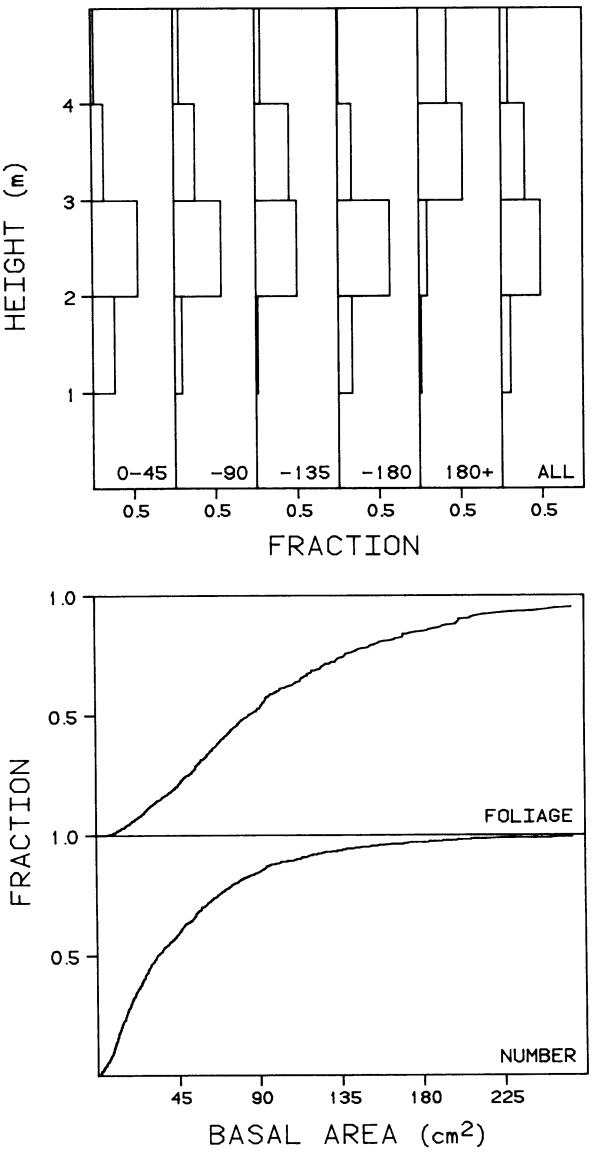

FIG. 5. Canopy height structure by shrub basal area class (top) and the cumulative frequency distributions of foliage biomass and shrub numbers (bottom) in 21-yr-old *Ceanothus crassifolius*. Live shrubs of basal area <45 cm² account for 60% of the population, yet account for only 20% of the foliage biomass (bottom). One-half of their foliage is found between heights of 2 and 3 m (top).

Relative productivity of the two regional locations studied is indicated by the biomass accumulation rate (total biomass divided by stand age) in *A. fasciculatum* stands, which was 0.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$ at Laguna Mountain and 1.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$ at San Dimas (Table 4).

Deadwood biomass.—Deadwood biomass varied widely among the mature chaparral communities examined. At San Dimas, the lower range of deadwood

TABLE 2. Foliage biomass (B_f), total aboveground biomass of live shrubs (live B_t), dead-shrub biomass (B_d), total stand biomass (stand B_t), population density, and annual aboveground net primary production (P_n) in stands dominated by *Ceanothus crassifolius*. The fraction of total biomass that is dead (F_d) is also given for the mature stands.

Site	Biomass (Mg/ha)					*Ccr* density (shrubs/m²)		
	*Ccr**			*Af** B_t	Stand B_t			
	B_f	Live B_t	B_d			Live	Dead	Total
A) Age 6 yr								
Upper San Dimas Canyon-1	3.5	8.9	3.4	1.5	14.	2.4	1.9	4.3
Upper San Dimas Canyon-2	3.1	7.8	4.1	2.8	15.	2.3	3.1	5.4
Upper San Dimas Canyon-3	3.1	7.9	0.5	3.9	12.	2.6	0.3	2.9
Upper San Dimas Canyon-4	1.1	3.4	0.1	7.8	11.	2.1	0.03	2.1
Upper San Dimas Canyon-5	2.6	6.9	1.1	8.1	16.	2.7	0.66	3.4
Upper San Dimas Canyon-6	2.8	6.8	0.1	5.3	12.	2.0	0.03	2.0
Mean	2.7	7.0	1.6	4.9	13.	2.4	1.0	3.4

Site	Biomass (Mg/ha)						Density (shrubs/m²)			P_n† (Mg·ha⁻¹·yr⁻¹)
	Live									
	B_f	B_t	½ CI‡	B_d	Stand B_t	F_d	Live	Dead	Total	
B) Age 21 yr										
Bell Canyon-1	5.1	37.	8.8	8.6	45.	0.30	0.58	1.31	1.9	5.2
Bell Canyon-2	10.5	76.	7.0	2.3	78.	0.16	1.44	0.48	1.9	10.6
Bell Canyon-3	12.7	90.	9.4	1.1	91.	0.13	0.53	0.12	0.65	12.8
Hummingbird Creek-1	7.5	54.	9.8	0.4	54.	0.13	0.57	0.07	0.64	7.6
Johnstone Peak-1	5.7	40.	14.3	5.2	46.	0.22	0.28	0.45	0.73	5.7
Johnstone Peak-2	8.9	65.	5.3	12.9	78.	0.29	2.0	3.9	5.9	8.9
Tanbark-1	12.3	88.	6.8	6.8	95.	0.19	1.01	0.68	1.7	12.5
Volfe-1	6.4	46.	8.9	3.1	49.	0.20	1.16	0.5	1.7	6.5
Volfe-2	12.7	91.	7.9	3.3	95.	0.16	0.91	0.25	1.16	12.9
Volfe-3	9.4	67.	9.5	0.5	68.	0.13	0.59	0.06	0.65	9.6
W. Fork San Dimas Creek-1	5.4	39.	8.2	2.4	42.	0.19	0.75	0.55	1.3	5.6
Mean	8.8	63.	8.7	4.2	67.	0.19	0.89	0.76	1.7	8.9

* Species identification: *Ccr, Ceanothus crassifolius*; *Af, Adenostoma fasciculatum.*

† Estimated from the average wood increment rate in live shrubs from 7 to 22 yr plus one-half of the average foliage biomass in 21- and 22-yr-old stands (assuming 2 yr of foliage retention).

‡ One-half of the 95% confidence interval is given as a percentage of live-shrub biomass.

biomass, 0.13 of the total, was comparable in the two *Ceanothus* species (Tables 2 and 3). The greatest accumulations, 0.43 of total biomass in *C. oliganthus,* and 0.30 in *C. crassifolius,* reflected numerous small dead shrubs (Tables 2 and 3). Deadwood in *Adenostoma fasciculatum* constituted a greater proportion of stand biomass (0.41–0.53) than in *Ceanothus* even though few dead plants were present (cf. Tables 2, 3, and 4). Considering live shrubs only, deadwood ranged from 0.06 of total biomass in *C. oliganthus* to 0.53 in *A. fasciculatum* (Tables 4 and 6). Deadwood accounted for only 0.07 of the live *A. fasciculatum* at the lower productivity site at Fred Canyon, despite the older stand age. For none of the species examined was the proportion of deadwood related to shrub basal area.

Wood size classes.—Woody biomass of mature *Ceanothus* at San Dimas was dominated by larger branches; only 0.12–0.15 of the live wood was <0.5 cm diameter (Table 7). The largest fraction of live small-diameter woody biomass was measured in *Salvia mellifera,* where approximately one-half was <1 cm diameter. Deadwood within live plants, a result of natural self-pruning in the lower canopy, was typically of smaller diameter; one-half of that in *C. crassifolius* was within the 0–0.5 cm size class.

Foliage biomass.—After seasonal growth and senescence, foliage biomass of mature *C. crassifolius* ranged from 5.1 to 12.7 Mg/ha (Table 2). In comparison, foliage was less abundant in *C. oliganthus* (0.8–1.9 Mg/ha), *A. fasciculatum* (1.1–2.4 Mg/ha) (Tables 3 and 4), or *E. fasciculatum* (1.9 Mg/ha, SE = 0.28 Mg/ha). Despite the difference in biomass, leaf-area index during autumn and winter was comparable in the two *Ceanothus* species because of the wide disparity in specific leaf areas: 25 cm²/g for *C. crassifolius* (S. Hastings, *personal communication*) and 129 cm²/g (SE = 8.3 cm²/g) in *C. oliganthus* (Table 8).

Foliage was vertically stratified in the canopy of *C. crassifolius* and *C. oliganthus* stands, with the greatest mass located within the upper 2 m (Fig. 5). Small-diameter shrubs supported a significantly higher proportion of foliage in the lower reaches of this zone.

Stand height.—Stand height averaged 5.6 m (SD = 0.6) in mature *C. oliganthus* and 4.0 m (SD = 0.8) in *C. crassifolius* (Fig. 6). It was unrelated to total or foliage biomass or computed annual incident solar radiation. The range of observed *C. oliganthus* heights was relatively invariant, i.e., the tallest was only 40% greater than the least. By contrast, total biomass exhibited a 2.7-fold range.

TABLE 3. Foliage biomass (B_f), total aboveground biomass of live shrubs (live B_t), dead-shrub biomass (B_d), total stand biomass (stand B_t), and population density in stands dominated by *Ceanothus oliganthus*. The fraction of total biomass that is dead (F_d) is also given for the mature stands

Site	Biomass (Mg/ha)				Density (shrubs/m²)		
	B_f	Live B_t	B_d	Stand B_t	Live	Dead	Total
A) Age 6 yr							
Sunset Ridge-1	1.8	13.6	0.1	14.	3.9	0.03	3.9
Sunset Ridge-2	1.8	14.0	0.6	15.	5.3	0.88	6.2
Sunset Ridge-3	1.0	14.0	0.7	15.	7.8	1.7	9.5
Glendora Ridge-1	3.2	7.8	<0.1	8.	2.2	0.06	2.3
Glendora Ridge-2	1.4	24.3	0.5	24.	9.8	1.2	11.0
Mean	1.8	14.7	0.4	15.	5.8	0.8	6.6

Site	Biomass (Mg/ha)						*Co* density (shrubs/m²)		
	*Co**			*Qd**					
	B_f	Live B_t	B_d	B_t	Stand B_t	F_d	Live	Dead	Total
B) Age 21 yr									
Volfe-4	0.86	34.	6.7	38.	79.	0.16	0.48	0.25	0.73
Volfe-5	1.13	48.	9.7	2.6	60.	0.24	0.72	0.65	1.37
Volfe-6	1.56	76.	34.	0.3	110.	0.35	0.78	1.84	2.62
Volfe-7	1.76	86.	4.4	2.2	92.	0.12	0.11	0.01	0.12
Volfe-8	1.22	48.	13.9	26.	88.	0.43	0.74	0.87	1.61
Tanbark	1.45	63.	10.7	41.	115.	0.26	0.28	0.24	0.52
Bluebird	1.69	71.	32.7	0.	103.	0.36	0.43	0.91	1.34
W. Fork San Dimas Creek-2	0.8	29.	13.2	0.	43.	0.35	1.18	1.11	2.29
W. Fork San Dimas Creek-3	1.19	49.	9.7	0.	58.	0.22	0.46	0.25	0.71
Wolfskill Canyon-1	1.90	84.	22.4	0.	107.	0.26	0.30	0.17	0.47
Wolfskill Canyon-2	0.92	38.	23.0	0.	61.	0.41	0.28	0.54	0.82
Hummingbird Creek-2	1.47	61.	12.3	8.0	81.	0.20	0.45	0.23	0.68
Mean	1.33	57.	16.1	9.8	83.	0.28	0.52	0.59	1.11

* Species identificaton: *Co, Ceanothus oliganthus*; *Qd, Quercus dumosa.*

Reconstructed trends of biomass and population density in Ceanothus crassifolius.—Shrub basal area, as determined from stem cross-sections, showed an early exponential rise that became linear in larger shrubs after ages between 5 and 10 yr. This growth rate did not decline in shrubs with a basal area >80 cm² at age 21. Basal area at ages after 5–7 yr was linearly related to basal area at age 21, with $BA_{14} = 0.55(BA_{21})$ ($r^2 = 0.99$, $n = 19$).

The age of mortality, A_m (years), was positively related to dead shrub basal area, BA_m (centimetres), as given by the regression $A_m = 6.2 + 0.4\ (BA_m)$ ($r^2 = 0.4$). The large variance around the regression was due to difficulty in counting annual rings in dead stems and the propensity of *Ceanothus* to survive many years in a severely suppressed state; annual rings may be produced along a small ribbon of wood even though the cambium has died around three-fourths of the stem circumference.

The approximate pattern of growth for plants that died prior to 21 yr of age was reconstructed with a generalized growth model and the above regression of $A_m = f(BA_m)$. A modified Chapman-Richards function (Pienaar and Turnbull 1973) was used to describe growth in basal area, with the assumption, consistent with observations from small live shrubs, that the inflection in the growth curve occurred when basal area, BA_t, was one-half of that at mortality;

$$BA_t = BA_m[1 + e^{-k(t-A_m/2)}]^{-1}. \quad (5)$$

As a shrub approaches mortality,

$$\lim BA_t/BA_m = [1 + e^{-k(A_m/2)}]^{-1} \quad (6)$$

and

$$\lim k = \frac{-2 \ln(BA_m/BA_t - 1)}{A_m}. \quad (7)$$

Given a value of BA_t/BA_m close to 1.0 (say 0.99), a value for k can be calculated and used with the $A_m = f(BA_m)$ regression and Eq. 5 to estimate the growth pattern of a shrub of given final size.

The reconstructed trends in *C. crassifolius* population density showed a large decline in the more dense stands between ages of ≈7 yr and 14 yr (Fig. 7). Most stands had a slow decline from approximately ages 5 to 21, with a slightly more rapid response during earlier years. There was no asymptotic approach to a common limiting density.

Ceanothus crassifolius foliage biomass apparently increased rapidly between ages 7 and 14 yr and approached a maximum after age 20 (Fig. 8). This pattern was apparent in all stands measured, including one with a density of live shrubs as low as 0.3/m² at age 21. The period of most rapid increase corresponded with the period of greatest stand mortality, whereas slow early accumulation of foliage suggests a period of

TABLE 4. Stand foliage biomass (B_f), total biomass (B_t), the fraction of *Adenostoma fasciculatum* biomass that is dead (F_d), and population density in stands dominated by *A. fasciculatum*.

Site	Biomass (Mg/ha)					
	*Af**					
	B_f	B_t	Dead stems†	*Ceanothus** B_t	F_d‡	*Af* density (shrubs/m²)
San Dimas *A. fasciculatum* stands (age 21 yr)						
Hummingbird Creek-5	1.8	30.	5.0	0.	0.44	0.63
Hummingbird Creek-6	2.4	39.	6.0	0.	0.42	0.78
W. Fork San Dimas Creek-4	1.8	29.	3.7	2.9	0.41	0.53
W. Fork San Dimas Creek-5	1.1	22.	6.8	0.	0.53	1.00
Mean	1.8	30.	5.4	0.7	0.45	0.74
San Dimas mixed composition plots§						
	0.57	12.	4.	21.	0.48	0.089
Laguna Mountain mixed composition plots (age 35 yr)‖						
	1.3	12.	0.	18.	0.07	1.4

* Species identification: *Ceanothus* at San Dimas is *C. crassifolius*; at Laguna Mountain it is *C. greggii* var. *perplexans*. *Af*, *Adenostoma fasciculatum*.

† Biomass of entirely dead stems within live plants.

‡ Fraction dead computed from sum of dead-stem biomass and the fraction of deadwood within live stems (see Table 6).

§ Mean values are given for six of 12 32-m² plots, from a systematic sample that contained substantial amounts of *A. fasciculatum* (Jacks 1984).

‖ Mean values from 13 6-m² plots containing *A. fasciculatum* and *C. greggii* var. *perplexans* are given.

establishment lasting 5–7 yr. Shrubs that died had contributed little to stand biomass or the pattern of canopy development.

Between ages 7 and 22, the biomass of live shrubs rose at a slowly accelerating rate ranging from 2.2 to 5.7 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 9). Aboveground primary production during this period, estimated as average wood increment plus one-half the average foliage biomass for ages 21 and 22, averaged 8.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$. Production by the three most productive stands ranged from 12.5 to 12.9 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Table 2).

These estimates are insensitive to the assumptions used in modeling the growth of shrubs that died prior to age 21, as demonstrated by varying from 0.4 to 0.6 the value of BA_f/BA_m where the inflection occurs in the incorporated growth model. For age 7, where effects were greatest, a 50% increase in this parameter yielded a 15% increase in the total biomass estimate, excluding data from the Johnstone Peak-2 and Bell Canyon-1 plots. These latter plots had an especially high rate of mortality and number of small plants; biomass estimates for them were more sensitive to the value assumed: a 50% increase in the inflection value of BA_f/BA_m produced a similar increase in the total biomass estimate for age 7. These differences, however, did little to alter the predicted average trends. At age 14, the estimate was insensitive to such variation in the value of BA_f/BA_m at the inflection, even for the high-density stand (33.7 vs. 35.2 Mg/ha).

Confidence in the reconstructed stand development patterns was strengthened by the similarity of means and ranges for live-shrub biomass estimated in the 6-yr-old *C. crassifolius* ($\bar{X}$ = 7.0 Mg/ha; range: 3.4–8.9 Mg/ha) with those of the now mature stands when they were 7 yr old (7.8 Mg/ha, 4.7–10.9 Mg/ha).

Litter accumulation and litterfall.—Litter accumulation in mature stands ranged threefold among species, with *A. fasciculatum* < *C. oliganthus* < *C. crassifolius* < *Q. dumosa* (Table 9). Litter accumulation was relatively uniform among stands of the same species: no clear relation with stand foliage biomass or slope was apparent.

Foliage senescence and litterfall in *C. crassifolius* (3.7 Mg/ha) and *C. oliganthus* (3.8 Mg/ha) reflected similar rates of foliage production despite different patterns of foliage retention. Litterfall in *C. crassifolius* was 0.42 of the dormant season foliage biomass, corresponding with the annual retention of approximately two age classes of foliage. In contrast, *C. oliganthus* is appar-

TABLE 5. Total biomass (B_t), foliage biomass (B_f), and shrub population density in 35-yr-old and regenerating *Quercus dumosa* at Kitchen Creek in San Diego County. Foliage of this species is retained for a single year. In the absence of herbivory, late-summer foliage biomass is equivalent to foliage production.

Plot no.	Stand biomass (Mg/ha)				Density (shrubs/m²)
	Age 1 yr		Age 35 yr		
	B_t	B_f	B_t	B_f	
5	3.5	1.4	18.6	3.3	0.77
6	3.3	1.2	22.7	3.1	0.31
13	2.4	0.91	15.8	2.3	0.33
15	2.7	1.0	19.5	2.6	0.27
17	2.3	0.84	15.9	2.0	0.20
Mean	2.8	1.1	18.5	2.7	0.38
SE	0.24	0.10	1.3	0.24	0.10

TABLE 6. Biomass of deadwood within live shrubs as a fraction of their total aboveground biomass (f_d).

Species*	Age (yr)	f_d	Sample size	Species	Age (yr)	f_d	Sample size
	San Dimas				Kitchen Creek		
Ccr	6	<0.01	35 shrubs	*Cgp*	35	0.037	9 shrubs
	21	0.12	54 shrubs	*Cl*	35	0.22	9 shrubs
Co	6	<0.01	30 shrubs	*Qd*	11	<0.01	30 stems
	21	0.061	28 shrubs		35	0.107	34 stems
Sm	21	0.34	30 shrubs		37	0.106	23 stems
Qd	21	0.085	15 shrubs	*Af*	35	0.072	10 shrubs
Af	18	0.32	13 shrubs				

* Species identification: *Af, Adenostoma fasciculatum*; *Ccr, Ceanothus crassifolius*; *Cgp, C. greggii* var. *perplexans*; *Cl, C. leucodermis*; *Co, C. oliganthus*; *Qd, Quercus dumosa*; *Sm, Salvia mellifera.*

ently semideciduous, since its litter production was 2.9 times the foliage biomass measured during autumn.

We also analyzed the annual variation, from 1935 to 1953, in *C. crassifolius* litterfall as reported by Kittredge (1955). Litterfall, L (megagrams per hectare), measured from May through the following April, may be best described ($R^2 = 0.80$) by the regression

$$L = 0.061 + 0.0018(P_{t-2}) + 0.0010(P_{t-3}) + 0.0011(P_{t-4}), \quad (8)$$

where the independent variables are annual precipitation (in millimetres) during years of foliage expansion (P_{t-2}) and bud set (P_{t-3}), and prior to bud set (P_{t-4}), considering the retention during winter of two annual age classes of foliage.

Nitrogen and phosphorus distributions.—Foliage nitrogen concentrations at both San Dimas and Kitchen Creek were high in the three *Ceanothus* species relative to other species measured, ranking *A. fasciculatum* < *E. fasciculatum* = *Q. dumosa* < *C. crassifolius* = *C. leucodermis* < *C. oliganthus* (Table 10). There were no significant differences in foliar nitrogen concentration between 6- and 21-yr-old shrubs of either *C. crassifolius* or *C. oliganthus* or among 11-, 35-, and 37-yr-old *Q. dumosa.*

Wood nitrogen concentrations were greatest in branches <0.5 cm in diameter (Table 10); fine deadwood had lower concentrations than comparably sized live stems. Average wood nitrogen concentrations were greater in mature *C. oliganthus* than in *Q. dumosa* or *C. crassifolius,* and showed no consistent differences between immature and mature shrubs (Table 10).

Foliage phosphorus concentrations were similar among *C. crassifolius, C. oliganthus, E. fasciculatum,* and *Q. dumosa*; no trends with age were apparent. As with nitrogen, *Ceanothus* wood phosphorus concentrations were greatest in small-diameter branches, both live and dead, and greater in live wood than in deadwood.

No differences were discernible in leaf-litter nitrogen

TABLE 7. Distribution of live and dead woody biomass by diameter class, expressed as a fraction of the total wood in each category. Standard errors of the estimates for the smallest class are also given.

Species*	Age (yr)	Size class (cm) <0.5	0.5–1	1–2	>2	Sample size (kg)
		Live wood				
San Dimas						
Ccr	21	0.15 ± 0.045	0.13	0.18	0.54	220.
Co	21	0.12 ± 0.020	0.08	0.10	0.70	57.
Sm	22	0.34 ± 0.029	0.17	0.23	0.26	27.
Qd	22	0.29 ± 0.027	0.09	0.11	0.51	17.
Kitchen Creek						
Qd	11	0.37 ± 0.001	0.14	0.22	0.27	4.
	37	0.19 ± 0.010	0.15	0.11	0.56	12.
		Deadwood				
San Dimas						
Ccr	21	0.50 ± 0.087	0.26	0.15	0.10	20.
Co	21	0.30 ± 0.068	0.36	0.27	0.07	4.
Sm	22	0.48†		0.52		21.
Qd	22	0.64 ± 0.056	0.26	0.09	0.	1.
Kitchen Creek						
Qd	37	0.43 ± 0.034	0.31	0.20	0.07	2.

* Species identification: *Af, Adenostoma fasciculatum*; *Ccr, Ceanothus crassifolius*; *Cgp, C. greggii* var. *perplexans*; *Cl, C. leucodermis*; *Co, C. oliganthus*; *Qd, Quercus dumosa*; *Sm, Salvia mellifera.*

† Size classes for *Salvia mellifera* are ≤1 and >1 cm.

TABLE 8. Foliage biomass, leaf area index (the ratio of leaf area to projected ground surface), and environment in *Ceanothus crassifolius* and *C. oliganthus* stands. Variability estimates are ± SE.

	C. oliganthus	*C. crassifolius*
Foliage biomass (Mg/ha)		
Dormant season	1.3 ± 0.11	8.8 ± 0.90
Leaf area index		
Peak season*	6.6	3.1
Dormant season	1.7	2.2
Specific leaf area (cm^2/g)	129.	25.
Solar radiation		
Annual average ($MJ \cdot m^{-2} \cdot yr^{-1}$)	5410. ± 333.	8180. ± 357.
December ($MJ \cdot m^{-2} \cdot d^{-1}$)	5.1 ± 0.8	14.5 ± 1.7
June ($MJ \cdot m^{-2} \cdot d^{-1}$)	26.2 ± 0.4	28.0 ± 0.3
Air temperature (°C)†	21.8	17.1
Soil moisture (percent)‡	12.	7.5

* Computed from the sum of litterfall and dormant season foliage biomass.

† Mean annual temperatures, 1936–1938, at 1050 m elevation on adjacent north- and south-facing aspects (from Miller 1947).

‡ Annual average at 1050 m elevation (from Miller 1947).

FIG. 6. Interior view of live stands of (top) *Ceanothus oliganthus* and (bottom) *C. crassifolius* at the San Dimas Experimental Forest. Both species form highly productive communities, accumulating standing biomass as great as 95–115 Mg/ha at 21 yr of age. Stand heights averaged 5.6 m in *C. oliganthus* and 4.0 m in *C. crassifolius*. Edge length of the black scale triangle in lower photo is 30 cm.

concentration among *C. crassifolius, C. oliganthus,* and *Q. dumosa,* or in the litter phosphorus concentrations for the two *Ceanothus* species (Table 9). Litterfall nitrogen and phosphorus concentrations were significantly greater in *C. oliganthus* than in *C. crassifolius.*

Soil nitrogen concentrations formed a significant progression among communities at San Dimas with *C. oliganthus* > *C. crassifolius* > *A. fasciculatum* (Table 10). Soil nitrogen in the *Q. dumosa* community at Kitchen Creek was enriched with respect to the soils at San Dimas. Soil phosphorus concentrations were significantly different among the three chaparral communities at San Dimas. Within each community, variations in soil nitrogen and stand productivity were apparently unrelated. Soil available nitrogen in *C. crassifolius, C. oliganthus,* and *A. fasciculatum* communities, assessed by anaerobic incubations, was well correlated ($r^2 = 0.75$) with Kjeldahl nitrogen (Fig. 10).

DISCUSSION

Biomass and primary production

Maximum stand biomass and primary production estimates for 21-yr-old *C. oliganthus* and *C. crassifolius* at the San Dimas Experimental Forest establish record-high values for the chaparral ecosystem. The most productive chaparral measured previously, comparably aged *Ceanothus megacarpus* in coastal Santa Barbara County, grows at rates two-thirds of the maximum reported here (Schlesinger and Gill 1980), although average values for the three species are similar. *Ceanothus* production is two to three times that of chaparral dominated by *A. fasciculatum* or *Q. dumosa* in San Diego County (Table 11). Average biomass accumulation is three to four times as great as that previously reported for 18-yr-old *A. fasciculatum* chaparral on south-facing aspects at San Dimas (Specht 1969). Biomass varies widely among monospecific *Ceanothus* stands, 2.7-fold in the *C. oliganthus,* and 2.3-fold in *C. crassifolius,* in contrast with trends previously reported for uniform, south-facing aspects (Specht 1969, Schlesinger and Gill 1980).

Production by *Ceanothus* is comparable to that reported for similarly aged, low-site-quality *Pseudotsuga*

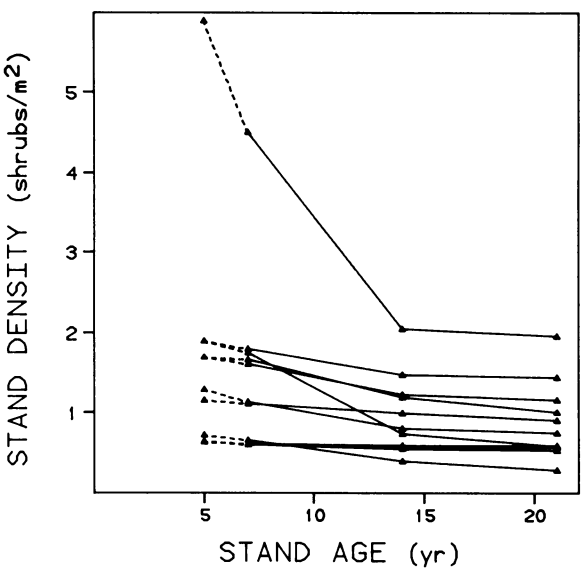

FIG. 7. Population density trends estimated for 11 stands of *Ceanothus crassifolius.* The number of dead and live plants present at age 21 was assumed to represent the density of established seedlings at an age of ≈5 yr. The intermediate values (ages 7 and 14 yr) were estimated from the dead shrub basal area distributions and a relation of shrub size to the age of mortality.

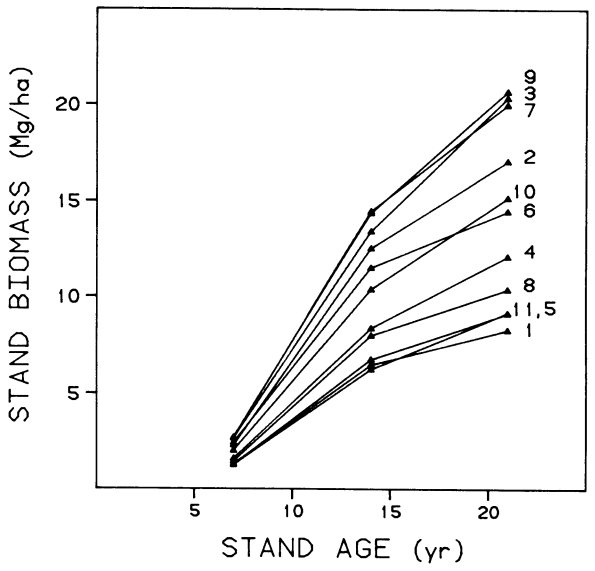

FIG. 8. Reconstructed temporal trends in *Ceanothus crassifolius* foliage biomass, showing maximum canopy development only at extended stand ages. The numbers at the right refer to the sequence of plots indicated in Table 2B.

menziesii (Douglas-fir) in western Washington, the Mediterranean *Quercus ilex* in France, and deciduous forests in the eastern United States (Table 11). Average foliage biomass in *C. crassifolius* is greater than that reported for Douglas-fir or red alder (*Alnus rubra*) in the northwestern United States or mediterranean oak woodlands, and twice that of the eastern deciduous forests (Table 11), partly because of high specific leaf masses. The standing biomass of the most productive *Ceanothus* stands, 95–115 Mg/ha (Tables 2 and 3), is 0.7–1.2 times as great as the reported overstory biomass (biomass of shrubs or herbaceous cover, where present, is excluded) of eastern deciduous forests. It is remarkable that *C. crassifolius* and *C. oliganthus,* with xeric environments and stand heights averaging 4.0 and 5.6 m, can develop within 21 yr a standing biomass approaching that achieved at ages exceeding 100 yr by humid deciduous forests with heights of 17–25 m. Clearly, small stature does not limit biomass accretion in this mediterranean environment.

Canopy development

Foliage biomass of *C. crassifolius* communities does indeed approach a maximum as shrubs mature, but only after 15–20 yr. It is dominated by larger shrubs, with little effect of competition-induced thinning. Foliage develops more rapidly in *C. oliganthus* on northerly aspects. The 6-yr-old stands we measured there actually averaged 35% more foliage biomass than stands that were age 21 yr. In contrast, young *C. crassifolius* had developed only one-third as much foliage as mature stands. A linear increase in foliage biomass through age 22 has been reported for *C. megacarpus* (Schlesinger and Gill 1980). However, these estimates were made using a single regression developed from different-aged stands, which may have obscured a change with age in the relation of shrub foliage mass to basal area.

The primary production and leaf area of *C. crassifolius* stands are apparently insensitive to changes in initial population density above that required for canopy closure (in accordance with the law of constant final yield proposed by Hozumi et al. 1956). Indeed, stand biomass of over 80 Mg/ha at age 21 yr was achieved from initial densities ranging from 0.6 to 5.9 shrubs/m^2 (Table 2, Fig. 11).

As a community matures, the expanding foliage area of dominant shrubs may advance seasonal soil drying and the onset of drought stress even as it reduces subsurface flow and water evaporation from the soil surface. Community leaf area is maximized, presumably, when the effects of extended drought are no longer compensated by enhanced early-season carbon uptake or competition for water with smaller plants. In *C. crassifolius,* the effect is probably manifest by a peak in the number of growing shoots, since foliage expansion is completed well before strong drought stress occurs. Changes with age in the seasonal initiation of drought stress, probably a primary control of *Ceanothus* stand structure, have apparently not been measured.

Stand leaf area responds annually to precipitation in addition to the long-term trend with age. *Ceanothus crassifolius* foliage was 14% of total biomass after 376 mm of rain in 1981 and 19% of the total after 826 mm in 1982. As shown by our analysis of a 19-yr record

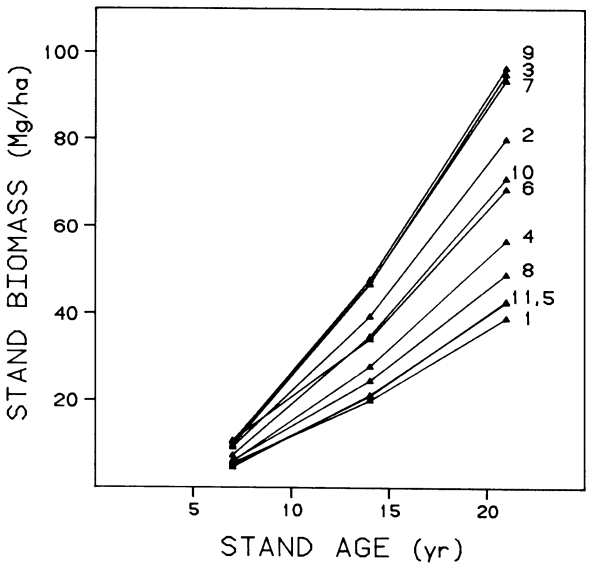

FIG. 9. Reconstructed temporal trends in the total biomass of live *Ceanothus crassifolius.* After an initial establishment period of ≈7 yr, biomass accumulated quickly with no decline in growth rate as stands matured.

TABLE 9. Biomass and concentrations of nitrogen and phosphorus in accumulated litter ($\bar{X} \pm$ SE) and litterfall ($\bar{X} \pm$ SD) from mature chaparral. n = number of plots.

Species†	Litter				Litterfall*			
	Biomass (Mg/ha)	[N] (%)	[P] (%)	n‡	Biomass (Mg/ha)	[N] (%)	[P] (%)	n‡
			San Dimas Experimental Forest					
Ccr	45.5 ± 5.8	.69 ± .16	.068 ± .027	10	3.7 ± .51	0.76 ± .12	.047 ± .013	11
Co	28.7 ± 2.0	.75 ± .07	.087 ± .023	12	3.8 ± .65	1.10 ± .11	.075 ± .009	12
Af	20.5 ± 2.6			6				
			Kitchen Creek					
Qd	54.3 ± 7.8	.73 ± .12		9				

* Litterfall was measured during the period of foliage senescence, mid-May through September 1982.
† Species identification: *Ccr, Ceanothus crassifolius*; *Co, C. oliganthus*; *Af, Adenostoma fasciculatum*; *Qd, Quercus dumosa.*
‡ Plot areas are 32 m^2 in *A. fasciculatum*, 120 m^2 in *C. crassifolius* and *C. oliganthus*, and 100 m^2 in *Q. dumosa.*

(Kittredge 1955), *C. crassifolius* litterfall is unrelated to rain during the previous winter; hence, the number of foliage age classes retained does not vary with drought severity. Foliage biomass must be buffered against annual variation, as litterfall does respond to precipitation in years of leaf expansion and bud set, and immediately prior to bud set. In fact, we estimate that 95% of the annual variation in foliage biomass is within 50% of the long-term mean.

In contrast to *C. crassifolius*, foliage of resprouting *Q. dumosa* grows rapidly. Aboveground production during the year after burning at Kitchen Creek was

TABLE 10. Nitrogen and phosphorus concentrations (% dry mass) in woody biomass, foliage, and soil. Data are means ± SD, with sample sizes in parentheses.

Age (yr)	Woody biomass			
	<0.5 cm	0.5–1 cm	>1 cm	Combined
Percent nitrogen				
		San Dimas Experimental Forest		
Ceanothus crassifolius				
6				0.73 ± 0.10 (9)
21				
Live	0.70 ± 0.09	0.44 ± 0.12	0.27 ± 0.07	0.36 ± 0.04 (14)
Dead	0.58 ± 0.11	0.46 ± 0.11	0.29 ± 0.09	0.48 ± 0.11 (15)
Ceanothus oliganthus				
6				0.73 ± 0.18 (9)
21				
Live	0.94 ± 0.14	0.76 ± 0.15	0.63 ± 0.14	0.69 ± 0.12 (6)
Dead	0.80 ± 0.13	0.60 ± 0.21	0.57 ± 0.06	0.65 ± 0.09 (6)
Adenostoma fasciculatum				
Eriogonum fasciculatum				
		Kitchen Creek		
Quercus dumosa				0.29 ± 0.05 (18)
Ceanothus leucodermis				
Adenostoma fasciculatum				
Percent phosphorus				
		San Dimas Experimental Forest		
Ceanothus crassifolius				
6				0.072 ± 0.022 (9)
21				
Live	0.035 ± 0.008	0.024 ± 0.006	0.02 ± 0.004	0.023 ± 0.003 (14)
Dead	0.023 ± 0.007	0.021 ± 0.006	0.018 ± 0.006	0.021 ± 0.007 (15)
Ceanothus oliganthus				
6				0.041 ± 0.010 (9)
21				
Live	0.056 ± 0.009	0.046 ± 0.004	0.041 ± 0.008	0.044 ± 0.007 (6)
Dead	0.034 ± 0.005	0.025 ± 0.009	0.022 ± 0.001	0.027 ± 0.004 (6)
Adenostoma fasciculatum				
Eriogonum fasciculatum				
		Kitchen Creek		
Quercus dumosa				0.047 ± 0.019 (10)

comparable to that in mature stands. The canopy attained heights greater than 1 m as foliage biomass reached 40% of that in mature stands.

Foliage dynamics of the two *Ceanothus* species reflect adaptation to contrasting slope aspects. Their leaf areas are equivalent during winter, increasing threefold during the growing season in *C. oliganthus* on north aspects and 0.4-fold in *C. crassifolius* on south aspects (Table 8). During June, computed solar radiation incident upon *C. crassifolius* is only 7% greater than on *C. oliganthus*, yet there is a threefold difference during December (Table 8). With its semideciduous foliage and high specific leaf area (leaf area per unit biomass), *C. oliganthus* maintains the same winter leaf area as *C. crassifolius* with a fraction of the foliage biomass and, presumably, respiratory cost. Senescence and abscission of foliage by *C. oliganthus* during late summer reduces respiration at a time when water stress prohibits appreciable carbon uptake and should improve carbon balance during the low irradiance and air temperatures of winter. Lower transpiration during mesic conditions should reduce soil moisture depletion so that its relatively mesophytic leaf can survive and function during early summer: in fact, average annual soil moisture has been reported to be 60% greater in north-aspect *C. oliganthus* than in adjacent south-aspect *C. crassifolius* stands at San Dimas (Miller 1947).

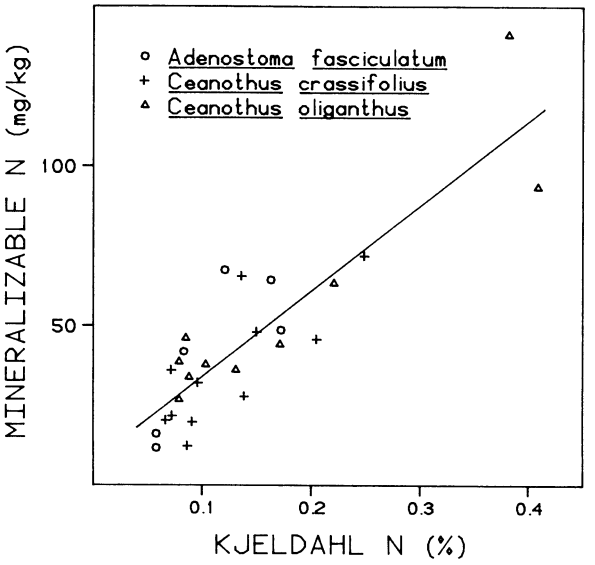

FIG. 10. Nitrogen mineralized during anaerobic incubation as a function of Kjeldahl nitrogen in the soils from stands of *Ceanothus crassifolius*, *C. oliganthus*, and *Adenostoma fasciculatum*. The relative soil nitrogen availability as assayed is apparently related to nitrogen capital only; no differences could be discerned among soils from the different communities.

TABLE 10. Continued.

Foliage	Soil
San Dimas Experimental Forest	
1.44 ± 0.18 (33) 1.48 ± 0.20 (41)	0.125 ± 0.06 (11)
1.69 ± 0.23 (28) 1.66 ± 0.16 (16)	0.175 ± 0.125 (10)
1.02 ± 0.26 (10)	0.109 ± 0.051 (6)
Kitchen Creek	
1.08 ± 0.12 (50) 1.50 ± 0.12 (9) 0.89 ± 0.07 (8)	0.209 ± 0.033 (11)
San Dimas Experimental Forest	
0.098 ± 0.020 (33) 0.083 ± 0.017 (42)	0.063 ± 0.025 (11)
0.086 ± 0.019 (28) 0.108 ± 0.013 (16)	0.107 ± 0.036 (10)
0.092 ± 0.021 (10)	0.069 ± 0.048 (6)
Kitchen Creek	
0.089 ± 0.021 (35)	

Mortality

The pattern of mortality in *C. crassifolius* chaparral is a notable exception to that described by the $-3/2$ power model of intraspecific competition. As first demonstrated with herbaceous species, survival curves arising from different initial densities commonly converge toward an asymptote that is dependent on the stage of development (Yoda et al. 1963). In monolayer canopies where mortality is driven by an increasing area of shade cast by larger plants, the course along which growth in average individual plant mass ($\bar{m}$) diminishes the density of live plants (ρ) is expected to follow a limiting relation of the form $\bar{m} = C(\rho)\exp(-3/2)$ (Yoda et al. 1963). In 63 of 75 field studies surveyed by Weller (1987), the exponent ranged from -1.2 to -2.2 with one instance as low as -4.8. Mortality in *C. crassifolius* produced no approach to a common asymptotic density (Fig. 7). Although mortality was evident in all mature stands (Table 2), it approached the theoretical rate only in the most dense stand encountered, with an initial density >5.9 m^{-2}.

Schlesinger and Gill (1978) examined growth and mortality in *C. megacarpus* and developed for two different age classes an overall relation of average plant

TABLE 11. Total biomass (B_t), foliage biomass (B_f), and net aboveground primary production (P_n) in selected chaparral and forest ecosystems.

Species†	Location	B_t (Mg/ha)	B_f (Mg/ha)	P_n* (Mg·ha^{-1}·yr^{-1})	Age (yr)	Reference‡
	Mediterranean ecosystem					
Ccr	San Dimas, Los Angeles Co., CA	67	8.8	7.2	21	(1)
Co	San Dimas	73§	1.3	7.2	21	(1)
Cm	Santa Monica Mts., Los Angeles Co., CA	77	5.5	8.7	22	(3)
Cm	Santa Barbara Co., CA	63	4.7	7.5	21	(4)
Qd	Laguna Mt., San Diego Co., CA	19	2.7	3.2	35	(1)
Af-Cg	Boulder Creek, San Diego Co., CA	23	4.2	3.0	23	(5)
Af-Ccr	San Dimas	20			18	(2)
		49			37	
Qi	Rouquet, France	269	7.0	6.4	150	(6)
	Western forest					
Pm	Landsberg, WA (SI‖:27m)	135	5.0	8.8	22	(6)
Pm	North Bend, WA (SI:45m)	28	8.2	16.9	7	(7)
Ar	Landsberg, WA	151	4.1	12.8	30	(6)
	Eastern deciduous forest					
Acru-Qp	Coweeta, NC	132	3.5	8.8	60–200	(8)
Carya, Quercus	Walker Branch, TN	123	4.2	7.8	30–80	(8)
Acer, Betula, Fagus	Hubbard Brook, NH	101	3.2	9.6	110	(8)

* P_n was calculated here as the average wood biomass increment plus foliage production derived from average litterfall estimates.

† Species identification: *Acru, Acer rubrum*; *Ar, Alnus rubra*; *Af, Adenostoma fasciculatum*; *Ccr, Ceanothus crassifolius*; *Cg, C. greggii*; *Cm, C. megacarpus*; *Co, C. oliganthus*; Pm, *Pseudotsuga menziesii*; *Qd, Quercus dumosa*; *Qi, Q. ilex*; *Qp, Q. prinus*.

‡ References: (1) this study, (2) Specht 1969, (3) Gray 1982, (4) Schlesinger et al. 1982, (5) Mooney et al. 1977, (6) Cole and Rapp 1981, (7) Riggan 1979, (8) DeAngelis et al. 1981.

§ Values are for the overstory *C. oliganthus* only (cf. Table 3). The dormant season foliage biomass is reported here.

‖ 50-yr site index: the average height (m) of dominant trees at this age.

size to population density. Assuming the model $\bar{m} = C\rho^b\epsilon$, where $\ln(\epsilon)$ is normally distributed, the 95% confidence limits for the exponent they estimated are -1.44 and -1.00. By definition, average shrub biomass in stands of equivalent total biomass, B, is given by $\bar{m} = B(\rho)^{-1}$, so this interval is bounded at one extreme by a value representing the relation among stands of uniform biomass and approaches the limiting law at the other. Thus, their approach did not produce an unequivocal result or test the theory.

The pattern of *C. crassifolius* mortality probably derives from an only marginally greater stress that growth of dominant plants produces in shrubs that are partially shaded or have less developed roots. In a companion study at San Dimas, water stress during summer drought was shown to be no greater in suppressed *C. crassifolius* than in large shrubs (W. C. Oechel and S. J. Hastings, *personal communication*). However, although Schlesinger et al. (1982) reported that water potential did not alter with shrub size in young *C. megacarpus* measured in mid-June, it ranged from -9 to -11 MPa across large- to small-diameter shrubs in late August when the entire community was physiologically inactive. The ecological significance of this difference is not apparent, since all shrubs suffered severe water stress.

Smaller shrubs certainly experience favorable water relations for an extended period during winter and spring and account for only a small proportion of stand leaf area. Thus, they are eliminated only by protracted competition and their demise has little effect on the water status of larger shrubs. An expanding stand leaf area apparently is the driving force for this shrub mortality in *C. crassifolius*, since the thinning ceased as maximum leaf area developed. Thinning also ceased at a comparable age in *C. megacarpus* (Schlesinger and Gill 1978).

Nutrient distributions and cycling

Copious amounts of nitrogen may volatilize during burning because of high concentrations of this element in foliage and fine woody biomass of *Ceanothus* and heavy leaf litter of *Q. dumosa* and *C. crassifolius*. Of the nitrogen in litter and foliage of these species alone, ≈435 kg/ha is subject to high fire temperatures and gaseous loss (Table 12). One-quarter of the nitrogen in aboveground biomass and surface soil (572 kg/ha) was volatilized during fires at Kitchen Creek that consumed 60% of the *Q. dumosa* biomass (Riggan and Lopez 1982); fires that consumed a comparable fraction of fuel volatilized 10% of the nitrogen in *A. fasciculatum–A. sparsifolium* chaparral (DeBano and Conrad 1978). Less nitrogen volatilization should be expected from *C. oliganthus* stands, since only 237 kg/ha are present in the readily consumed litter and foliage, and the fuel arrangement is not conducive to fire propagation or intense soil heating except under the most severe burning conditions.

Ceanothus foliage nitrogen concentrations, which

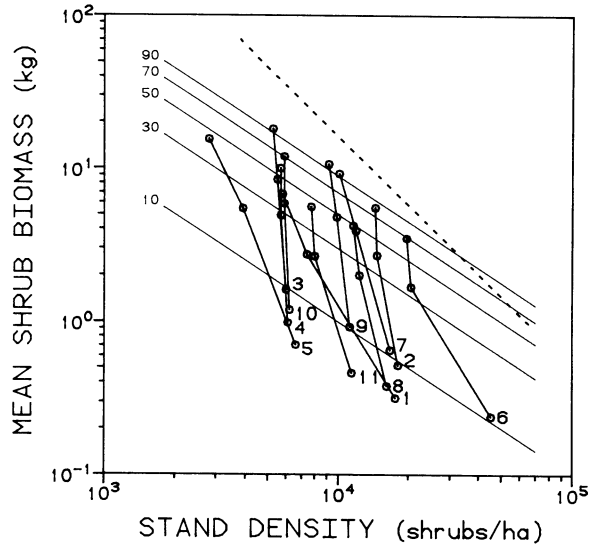

FIG. 11. Trends in average shrub biomass and population density in *Ceanothus crassifolius*. Solid lines with circles indicate the progressive changes in population density and size of live shrubs in 11 stands between ages 7, 14, and 22 yr (from lower right to upper left on each numbered line). Line annotations refer to the sequence of plots in Table 2B. Isopleths of total stand biomass (Mg/ha) are indicated as a measure of productivity. The slope of the −3/2 power thinning model of Yoda et al. (1963) is shown for comparison (dashed line); the intercept of the function is arbitrarily located. According to this model, stands where mortality is active should show a common trend in plant growth and density that parallels the slope of this relation.

were 55% greater than those of *A. fasciculatum, E. fasciculatum,* and *Q. dumosa* (Table 10), may reflect active symbiotic N_2 fixation. Large nodule masses and high rates of acetylene reduction by excised nodules have been observed in *C. crassifolius* at San Dimas (Poth 1982; S. Williams, *personal communication*). Accumulated nitrogen at San Dimas, regardless of the plant community, is partially determined by atmospheric deposition of nitrates, ammonium, and nitrogen oxides from the chronic pollution of the adjacent South Coast Air Basin. Nitrogen flux through the *C. crassifolius* canopy, 23 kg·ha^{-1}·yr^{-1}, reflects a record level of deposition nationally (Riggan et al. 1985).

Community differences in nitrogen accretion parallel those reported after 13 yr of growth in unreplicated containment lysimeters at San Dimas (Zinke 1969). From initially uniform soil, individual lysimeters accumulated 49 kg·ha^{-1}·yr^{-1} of N when planted with *C. crassifolius,* 38 kg·ha^{-1}·yr^{-1} with *Q. dumosa,* and 32 kg·ha^{-1}·yr^{-1} with *E. fasciculatum.* An unvegetated lysimeter lost 26 kg·ha^{-1}·yr^{-1} of N by an unknown mechanism, possibly denitrification or soil leaching; one containing *A. fasciculatum* lost 24 kg·ha^{-1}·yr^{-1}. Denitrification may be likely since the lysimeters prevent unsaturated water flow through the soil profile and may artificially impound some soil water.

The average nitrogen content of vegetation and litter in stands of *C. oliganthus* (726 kg/ha) and *C. crassifolius* (669 kg/ha) is comparable to that reported for *C. megacarpus* (686 kg/ha) in the Santa Monica Mountains of western Los Angeles County (Schlesinger et al. 1982). Nitrogen in the aboveground vegetation of these *Ceanothus* communities is three times that reported for *Adenostoma* chaparral in San Diego (135 kg/ha) and Santa Barbara (134 kg/ha) counties (DeBano and Conrad 1978, Mooney and Rundel 1979) and four to five times that of the older *Q. dumosa* at Kitchen Creek (Table 12). The *Ceanothus* contains 1.5–2.3 times as much nitrogen in standing vegetation alone as does 30-yr-old *Alnus rubra* (red alder) in the Pacific Northwest (240 kg/ha) (Cole and Rapp 1981). When litter is included in the comparison, the *Ceanothus* communities sequester 60% as much nitrogen aboveground. These accretion rates are remarkable considering the xeric environment and recurrent, fire-associated losses.

Nitrogen transfers within the plant, litter dynamics, and soil nitrogen reflect a greater availability of this element in *C. oliganthus* communities than in *C. crassifolius* (Table 13). Nitrogen incorporation in wood and foliage was greater and translocation prior to foliage abscission was lower in *C. oliganthus.* The larger nitrogen influx via litterfall and reduced nitrogen accumulation in the litter layer of *C. oliganthus* (Table 12) implicate more rapid mineralization there. Furthermore, soil mineralizable nitrogen, a measure of nitrogen availability, was proportional to the Kjeldahl nitrogen concentration, which was 40% greater under *C.*

TABLE 12. Nitrogen and phosphorus distribution (kg/ha) in mature stands of *Ceanothus crassifolius, C. oliganthus,* and *Quercus dumosa* chaparral. Data are means ± 1 SE.

Component	*C. crassifolius*	*C. oliganthus*	*Q. dumosa*
	Nitrogen		
Live shrubs	335. ± 24.	407. ± 40.	77. ± 5.
Foliage	130. ± 14.	22. ± 2.	31. ± 3.
Live stems	165. ± 18.	362. ± 40.	46.* ± 4.
Deadwood	40. ± 5.	23. ± 3.	
Dead shrubs	20. ± 6.	104. ± 19.	0.
Litter	314. ± 47.	215. ± 19.	394. ± 64.
Total aboveground	669. ± 53.	726. ± 48.	471. ± 64.
Soil (0–10 cm)	1500. ± 217.	2100. ± 474.	1700. ± 65.
Total	2170. ± 223.	2830. ± 478.	2170. ± 92.
	Phosphorus		
Live shrubs	19.6 ± 1.5	25.5 ± 2.5	
Foliage	7.3 ± 0.9	1.4 ± 0.1	
Live stems	10.6 ± 1.2	23.1 ± 2.5	
Deadwood	1.7 ± 0.2	1.0 ± 0.1	
Dead shrubs	0.9 ± 0.3	4.3 ± 0.8	
Litter	31. ± 5.5	25. ± 2.6	
Total aboveground	52. ± 5.7	55. ± 3.7	
Soil (0–10 cm)	756. ± 90.	1280. ± 137.	
Total	808. ± 90.	1335. ± 137.	

* Value includes live and dead stems.

TABLE 13. Nitrogen and phosphorus transfers in mature *Ceanothus crassifolius, C. oliganthus,* and *Quercus dumosa* chaparral. Data are means ± 1 SE.

Component	*C. crassifolius*	*C. oliganthus*	*Q. dumosa*
	Nitrogen		
Incorporation			
Wood* (net increment)	9.8 ± 0.88	18.3 ± 1.9	1.3 ± 0.15
Foliage†	55. ± 7.9	63. ± 10.7	31. ± 3.0
Redistribution‡	27. ± 4.5	21. ± 4.3	
Uptake§	38. ± 4.3	60. ± 7.5	
Litterfall	28. ± 4.2	42. ± 7.1	
	Phosphorus		
Incorporation			
Wood* (net increment)	0.59 ± 0.06	1.15 ± 0.12	
Foliage†	3.1 ± 0.47	4.1 ± 0.70	
Redistribution‡	1.3 ± 0.30	1.2 ± 0.29	
Uptake§	2.3 ± 0.28	4.1 ± 0.50	
Litterfall	1.7 ± 0.27	2.9 ± 0.50	

* Estimated as the sum of live plus deadwood nutrient contents (of live shrubs) divided by stand age.

† Foliage biomass increment approximated by litterfall rate; values calculated using the nutrient concentrations in the standing crop.

‡ Translocation prior to leaf abscission (or redistribution) calculated as the difference between the nutrient contents of the foliage biomass increment and litterfall.

§ Total uptake defined as the sum of litterfall loss and incorporation in wood.

oliganthus. Thus, nitrogen cycling and availability apparently increase along the gradient of declining water stress represented by monospecific stands of *A. fasciculatum, Q. dumosa, C. crassifolius,* and *C. oliganthus*.

Patterns of soil phosphorus and uptake in *Ceanothus* communities parallel those for nitrogen, with greater rates of accumulation and cycling in the more mesic *C. oliganthus* (Tables 12 and 13). The differential rate of cycling is best demonstrated by litterfall phosphorus transfers, which are 70% greater in *C. oliganthus* than in *C. crassifolius*. Phosphorus also accumulates at the same concentrations, but in greater quantity, in the more massive litter layer of *C. crassifolius* (Tables 9 and 12). Community phosphorus content, including the upper soil, litter, and vegetation, is similarly 65% greater in *C. oliganthus,* probably because of reduced postfire soil erosion or greater rates of phosphorus dissolution and uptake in the lower soil profile with subsequent cycling and sequestering in the organic matter of surface soils.

Community fuel and fire properties

The foliage and small-diameter stems that propagate chaparral fires are vertically stratified and comprise a range of specific surface areas, mixtures of dead and live tissue, and volatile organic compounds. The effect of this complexity on firespread has not been quantified, so fuel properties of different communities can be only partially compared via Rothermel's (1972) firespread model for homogeneous fuels, with which the contributions of fuel size, packing, and mass can be integrated.

Potential velocity of combustion (reaction velocity), defined as the fraction of biomass consumed within the flaming zone divided by the time required for the fire to spread a distance equivalent to its depth, is reduced by poor heat transfer in either very loosely or densely packed fuel. As empirically computed, it varies in the progression *Q. dumosa* > *C. oliganthus* > *C. crassifolius* > *A. fasciculatum* and *S. mellifera* (Table 14). In each case, fine fuels are loosely packed; the proportion of the canopy volume occupied by biomass ranges from 0.07 to 0.36 of the optimum for firespread.

Energy release in the fire front (or reaction intensity), as determined by surface-area weighted fuel loadings and reaction velocity (for equivalent moisture, specific heat, and mineral contents), follows a different progression with *C. oliganthus* > *C. crassifolius* > *Q. du-*

TABLE 14. Summary of stand fuel properties and expected components of fire behavior: total stand biomass (B_t), the fraction of live wood or deadwood biomass in the 0–1 cm diameter class, total deadwood biomass (B_d), the ratio of deadwood to total biomass in live plants (f_d), stand height, potential reaction velocity (Γ'), relative packing ratio (β/β_{op}), and the contribution to reaction intensity by Γ' and surface area weighted fuel mass [$\Gamma' \sum (f_i B_i)$].

Species*	Age	B_t (Mg/ha)	Fine fuel fraction		B_d (Mg/ha)	f_d	Stand height (m)	Γ' (min^{-1})	β/β_{op}†	$\Gamma' \sum (f_i B_i)$ (relative values)
			Live	Dead						
					San Dimas Experimental Forest					
Ccr	21	67.	0.28	0.76	11.8	0.12	4.0	7.6	0.26	0.75
Co	21	83.	0.20	0.66	20.3	0.06	5.6	10.2	0.36	1.00
Af	21	30.	0.30	0.50‡	14.9	0.32	3.1	3.8	0.09	0.14
Sm	21	8.4	0.51	0.48	2.9	0.34	1.3	3.7	0.07	0.05
					Laguna Mountain					
Qd	35	19.	0.34	0.74	2.1	0.11	1.9	13.0	0.36	0.43

* Species identification: *Af, Adenostoma fasciculatum*; *Ccr, Ceanothus crassifolius*; *Co, C. oliganthus*; *Qd, Quercus dumosa*; *Sm, Salvia mellifera.*

† β_{op} is the proportion of canopy volume occupied by biomass at which fire spread is optimized.

‡ For *A. fasciculatum* the fractions of live wood and deadwood biomass in the 0–1 cm diameter class were computed from data in Countryman and Philpot (1970).

mosa > *A. fasciculatum* > *S. mellifera* (Table 14). This ranking probably is valid only in fires sustained by extremes of low fuel moisture and humidity or strong winds because of the vertical arrangement of fine fuel.

Since mature, monospecific *Ceanothus* stands contain virtually no ground fuels, they sustain only crown fires of relatively high intensity. These primarily consume foliage that is restricted to the upper 2 m of the tall canopy (Fig. 6). In marked constrast, *S. mellifera* and *E. fasciculatum* have a more compact, uniform arrangement of fine biomass and substantial deadwood accumulation, are more readily ignited, and can spread fire rapidly under a wide range of moderate weather. In fact, they are often used to spread prescribed fires into heavier chaparral.

Low live-fuel moisture and winds consistently in excess of 8–12 km/h are apparently required to spread fire in *Q. dumosa,* largely because of a paucity of deadwood (Dougherty and Riggan 1982). Nonetheless, at Kitchen Creek prescribed fires with energy release just sufficient to achieve steady spread rates produced flame lengths reaching 6–10 m. Apparently, the damping effect of live-fuel moisture on the propagating heat flux is overridden at higher windspeeds by increasing efficiency of heat transfer to unburned fuel. Thus, an interaction of wind and live-fuel moisture establishes a threshold for fire propagation in communities with little deadwood such as the *Ceanothus* or *Q. dumosa.* The greater the proportion of dead biomass the more readily the community may be burned under moderate conditions, an important consideration given the modern experience with frequent arson and accidental ignitions.

Returning to our original scenario, how might a change in initial population density affect the likelihood or behavior of subsequent fires? For mature *Ceanothus crassifolius,* the number and biomass of dead shrubs were proportional to initial density (Figs. 12 and 13). (Deadwood accumulation in *C. oliganthus* was unpredictable because of random mortality of large shrubs.) However, since competition-driven mortality ceases at an early age, dead shrubs in mature stands are small compared with the dominant live plants and present a very dispersed fuel accumulation. They probably add little to the propensity to carry fire under moderate conditions, but contribute to the total heat released when a stand does burn. Furthermore, community leaf area is apparently insensitive to establishment success above that required for canopy closure, so the course by which more flammable fuels develop remains largely unaltered by a change in initial density.

If *Ceanothus* abundance were to increase within a multispecies community with *A. fasciculatum* or *Q. dumosa,* community leaf area would probably approach its prefire levels during stand development. Subsequent fires at a comparable stand age would propagate through live fuel of similar surface area, although its mass and spatial distribution could be altered. Where

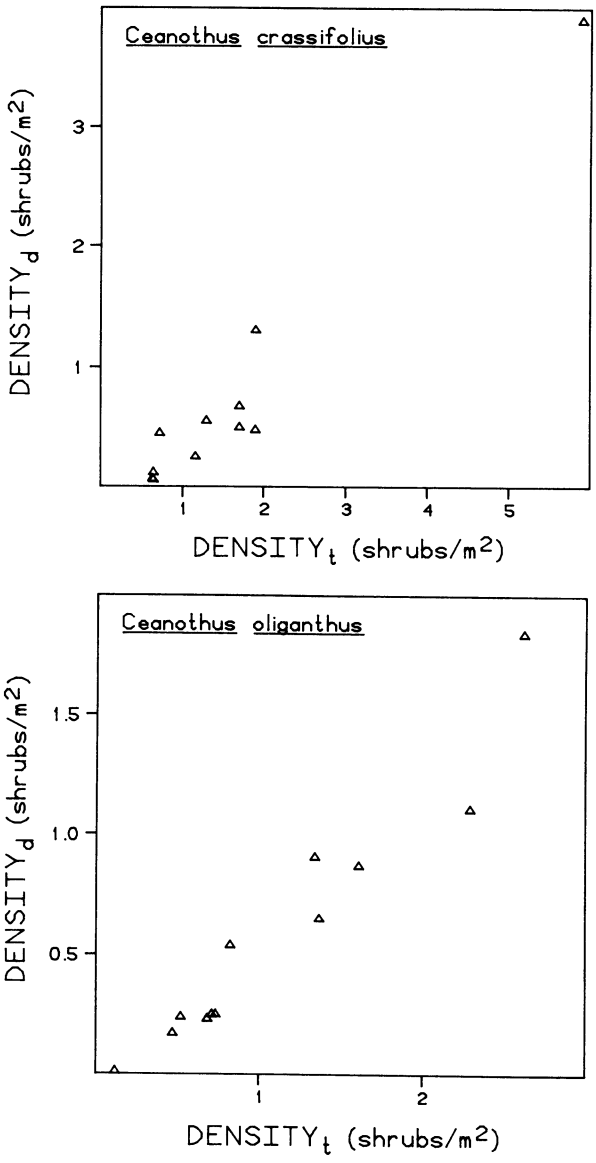

FIG. 12. Dead shrub density (DENSITY$_d$) as a function of total stand density (DENSITY$_t$) in 21-yr-old *Ceanothus crassifolius* and *C. oliganthus.*

the taller *Ceanothus* shades either *A. fasciculatum* or *Salvia,* the resulting accumulation of deadwood biomass could substantially increase the chances for severe fire.

Productive stands within a chaparral association probably sustain greater energy release when burned than do less productive stands, and can spread fire under a wider range of conditions. The fraction of deadwood within the productive *A. fasciculatum* at San Dimas is six times as great as that in the slow-growing chaparral at Laguna Mountain (Table 4), presumably because of greater height growth and self-shading. Given comparable terrain, the greater mass of readily com-

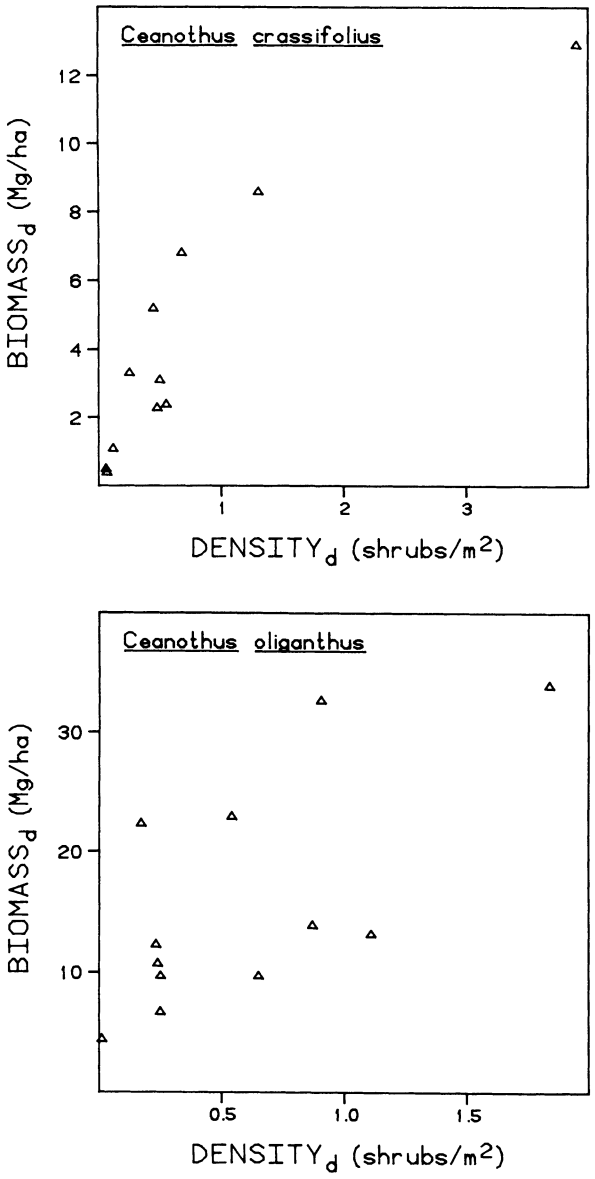

FIG. 13. The relation of biomass density to stand density for dead shrubs in 21-yr-old *C. crassifolius* and *Ceanothus oliganthus*. Rare death of large shrubs makes this component of stand structure relatively unpredictable in the *C. oliganthus*.

bustible material (foliage and deadwood) at San Dimas could allow the mixed chaparral there to burn during a wider range of weather and fuel moisture and release at least twice as much energy when it does burn. For *C. crassifolius*, the 2.7-fold range in foliage mass across sites should cause a range in fire intensity that is at least as great.

If fire-associated nutrient losses reduce primary production, then subsequent biomass accumulation, branch or stem mortality, fire severity, and nutrient loss could be reduced as well. Indeed, nitrogen or phosphorus has been shown to limit the growth of some chaparral communities (Hellmers et al. 1955, McMaster et al. 1982). These system feedbacks among fire and ecosystem processes may limit the divergence of community growth and structure along gradients of water balance. If *C. crassifolius* and *C. oliganthus* are most subject to severe fires, they may survive only by superior ability to accumulate nitrogen and phosphorus in their environments.

Since community leaf area is apparently controlled by site water balance, we expect that seed production, and thereby seedling establishment after a subsequent fire, are also independent of population density above a threshold required for canopy closure. Despite this independence, low-intensity fires or fires burning over moist soil can severely limit *Ceanothus* seedling establishment. We have seen failed regeneration where small prescribed fires consumed only the lightest fuel. Seedlings were abundant after fire consumed all woody biomass in adjacent areas of felled shrubs. Low-intensity fires are unlikely in the absence of concerted effort during prescribed burning, occurring naturally only after ignitions during severe weather in a young postfire community or in senescent stands with high fuel moisture. Poor germination could result where there is insufficient heating to break seed dormancy. Fire-generated steam in moist soils may also kill seeds (Westermeier 1978, Dunn and Poth 1979), although the moist soils may simply prevent the necessary heating of buried seed.

Salvia mellifera readily occupies gaps within a *Ceanothus* canopy. Because it is intolerant of shade (McPherson and Muller 1967), it accumulates fine deadwood in a flammable ladder-fuel arrangement where it is overtopped. Thus, a severely reduced *Ceanothus* population density may ultimately allow fire-spread at younger ages, higher fuel moistures, or lower windspeeds. A second low-intensity fire, especially at young ages, could prevent reestablishment of *Ceanothus* and perpetuate the degraded composition. Despite possible interactions of nutrient loss, canopy development, productivity, and fire severity that tend to stabilize these processes, such a rare event could for decades or centuries alter the structure of the ecosystem.

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