

# FRUIT PRODUCTION PATTERNS IN THE CHAPARRAL SHRUB *CEANOTHUS CRASSIFOLIUS*

JON E. KEELEY  
Department of Biology, Occidental College,  
Los Angeles, CA 90041

## ABSTRACT

Annual fruit production patterns in *Ceanothus crassifolius* varied significantly over a period of six years and significant differences occurred between sites. Plants on southern exposures out-produced similar aged shrubs on northern exposures. Whether or not the causative factors are associated with aspect or differences in density of vegetative cover are unknown. Significant differences occurred among shrubs on the same slope. Some plants produced, on average, nearly an order of magnitude more fruits (per unit of areal coverage) than other plants. Fruit production patterns in *Ceanothus* species, particularly members of subg. *Cerastes*, are, in part, a function of conditions in the year prior to flowering and fruiting because flower buds are produced nearly 12 months prior to flowering. In years of heavy fruit production, internal competition for resources may limit flower bud production for the following year. This pattern is particularly likely if heavy fruit production occurs in a year of sub-normal precipitation. During the course of this study, rainfall levels were above normal in five of six years. In plants on south-facing slopes there were consecutive years of large fruit crops. Stepwise multiple regression analysis revealed that total fruit production per slope face was correlated significantly with high precipitation in February, just prior to flowering. Fruit production by individual shrubs, however, was correlated with different parameters on north-facing vs. south-facing slopes. On the former aspect, fruit production was higher in years with warmer March temperatures and on the latter aspect larger fruit crops were correlated positively with October temperature and December precipitation.

Chaparral vegetation dominates the drier slopes and foothills throughout cismontane California. Its fire-prone nature and ability to regenerate rapidly after such disturbance is well documented (Hanes 1977). Many of the dominant shrub species are capable of regeneration by vegetative sprouts from basal burls and rootcrowns, whereas others depend upon seedling establishment. Noteworthy among the latter type of shrub are the majority of species in *Ceanothus* and *Arctostaphylos*. These species have no adaptations for vegetative regeneration and are referred to commonly as obligate seeding shrubs (Wells 1969). The shrubs begin fruit production between five and 10 years of age and continue flowering and fruiting throughout their lifespan. Although seeds are dispersed soon after maturation, they remain dormant in the soil and duff until germination is stimulated by fire, or occasionally by other disturbances.

Previous studies of *Ceanothus* and *Arctostaphylos* have shown that the bulk of the seed crop is lost to predation soon after dispersal

(Keeley 1977, Davey 1982). Thus, the soil seed banks are relatively dynamic and have large fluxes in and out following dispersal of seed crops. Over long periods of time there may be relatively little increase in size of the seed banks (Keeley 1987). Consequently, postfire reproduction for obligate seeding shrubs may be tied intimately to seed production in the preceding years.

Flower and fruit production has been studied in some chaparral shrubs. In general, for both obligate and facultative seeding species of *Ceanothus* and *Arctostaphylos*, substantial fruit crops are not produced every year (Keeley 1977, Baker et al. 1982, Davey 1982, Schlesinger et al. 1982). The size and periodicity of fruit crops reported for various chaparral shrubs is highly variable and the causes for such variability are unknown. The purpose of the present study was to document fruit production patterns for one such species over a period of many years. Specific questions addressed were: 1) What is the extent of year to year variability? 2) Is this variability related to patterns of precipitation? 3) What effect does slope aspect have on fruit production patterns? 4) To what extent do individual plants vary in fruit production? and 5) Is there any relationship between the size of fruit crops in one year and the size the following year?

*Ceanothus crassifolius* (nomenclature for all species follows Munz 1974) was selected because it is an obligate seeding shrub and is restricted to chaparral vegetation. It is common throughout much of southern California and dominates slopes away from the immediate coast from northern San Diego Co. to San Bernardino and Santa Barbara cos. *Ceanothus crassifolius* is similar in life history to *C. megacarpus*, which was described in detail by Schlesinger et al. (1982). Seed germination and seedling establishment of *C. crassifolius* is restricted to the first spring after fire; thus, it normally forms even-aged stands. Flowering may begin as early as five years of age, although substantial flower and fruit production may not occur until 15 years of age or older. Flowering continues sporadically until the next wildfire, which typically occurs every 20–40 years in southern California.

#### STUDY SITES AND METHODS

*Study sites.* This study was conducted in the San Dimas Experimental Forest maintained by the U.S. Forest Service on the coastal front of the San Gabriel Mountains in Los Angeles Co. Two populations on north-facing and two populations on south-facing slopes with inclinations of 15–20° were selected. The slopes were on opposite sides of two east–west running ridges adjacent to Dalton Canyon Road between elevations 725 and 750 m. These stands had burned in 1960 and, thus, the plants were 17 years old at the beginning of this study in 1978.

*Methods.* Vegetative cover on each slope was characterized by measuring shrub coverage on each slope with two 25 m line transects. Fifteen shrubs were selected randomly on each slope and tagged. A few tagged shrubs died during the study and were replaced with adjacent individuals, so that the sample size remained the same throughout the study. Height and diameter of the nearly circular canopy were recorded in the third year of the study and did not change appreciably through the remainder of the study.

Fruit production was measured on each shrub in late spring prior to seed dispersal. A 0.25 m<sup>2</sup> hoop was placed randomly on each shrub and all fruits within the hoop were counted. This was done for six consecutive years (all sites were destroyed by a controlled burn in 1983).

Precipitation and temperature data were derived from the NOAA (1977–1983). The nearest station at this elevation with complete precipitation data was Big Tujunga Dam (710 m), which is 40 km to the west of the study site. This site, however, lacked temperature data. The Mt. Wilson Station (1740 m) had complete temperature and precipitation data and was used in the stepwise regression analysis. Although this site is at a substantially higher elevation than Big Tujunga, the yearly variations in weather patterns are similar. For example, over the period 1977–1983 monthly precipitation was correlated significantly between Big Tujunga and Mt. Wilson ( $r = 0.96$ ,  $p < 0.001$ ,  $n = 84$ ).

A one-way ANOVA was used to test for differences in level of fruit production between years and among individuals on the same slope. Within a given year, a two-tailed t-test was used to test for differences between the different aspects on the same ridge and, for the same aspect, for differences between ridges. The Kendall coefficient of rank correlation analysis was used to test for a relationship between the size of the fruit crop on an individual shrub in a given year with the size of the fruit crop the following year. A stepwise multiple regression analysis was made between fruit crop size and monthly precipitation and mean temperature.

## RESULTS

*Cover.* Total shrub coverage of all species (percentage ground surface covered) was markedly greater on the two north-facing slopes; 120% and 130% for Ridges 1 and 2, respectively, vs. 70% and 90% on the southern exposures. *Ceanothus crassifolius* comprised nearly all of the cover on the south-facing slopes, but only approximately three-fourths of the cover on the north-facing slopes. The mean height of the *C. crassifolius* shrubs was slightly more than 2.5 m on all slope faces, but generally the shrubs on the south-facing exposures had larger canopies. The largest individual shrubs were on

TABLE 1. COMPARISON OF *Ceanothus crassifolius* INDIVIDUALS ON NORTH-FACING AND SOUTH-FACING SLOPES IN THE SAN GABRIEL MOUNTAINS. Fruit production was measured on 15 individuals on each of two north-facing and two south-facing slopes for six years (slope aspects were compared with a 2-tailed t-test, ns =  $p > 0.05$ , \*\* =  $p < 0.01$ ). Each fruit potentially can mature three seeds.

Slope aspect	Height (m)	Average areal cover	Annual fruit production
	$\bar{X} \pm$ s.d. (n)	(m <sup>2</sup> /shrub) $\bar{X} \pm$ s.d. (n)	(fruits/m <sup>2</sup> areal coverage) $\bar{X} \pm$ s.d. (n)
Ridge 1			
North	2.5 $\pm$ 0.3 (15) ns	3.0 $\pm$ 2.5 (15) **	284 $\pm$ 497 (90) **
South	2.6 $\pm$ 0.3 (15)	7.9 $\pm$ 3.4 (15)	576 $\pm$ 515 (90)
Ridge 2			
North	2.6 $\pm$ 0.6 (15) ns	2.2 $\pm$ 1.0 (15) ns	223 $\pm$ 515 (90) **
South	2.6 $\pm$ 0.3 (15)	3.2 $\pm$ 2.1 (15)	386 $\pm$ 405 (90)

the south face of Ridge 1, which was the most open of the four slope faces.

*Fruit production.* Due to the different sizes of shrubs on these slopes, fruit production is expressed on an areal coverage basis. Averaged over the six years of this study, the number of fruits produced per m<sup>2</sup> of areal coverage was significantly greater on south-facing exposures than on north-facing exposures (Table 1). Level of fruit production was similar between the two north-facing slopes, but the south face of Ridge 1 had significantly greater annual fruit production than that exposure on Ridge 2 ( $p < 0.01$ ). Because there was much plant to plant variation and yearly variation in size of fruit crops, the variance in fruit production was generally high on all slopes (Table 1).

Annual patterns of fruit production are illustrated in Fig. 1. For all exposures there was a significant difference in fruit production between years. For all slopes, 1978 was a year of high fruit production and, for the south-facing exposures, this was followed by another year of high fruit production. The shrubs on the southern exposures significantly ( $p < 0.01$ ) out-produced shrubs on the northern exposures in all years except 1978 on Ridge 1 and 1979, 1982, and 1983 on Ridge 2. In all years, fruit production between the two north-facing slopes was not significantly different ( $p < 0.05$ ). In 1980 and 1981, production on the south-facing slope on Ridge 1 was significantly higher than the same exposure on Ridge 2 ( $p < 0.01$ ).

Within a given year the variation in fruit production between plants on a single slope was high; the coefficient of variation usually

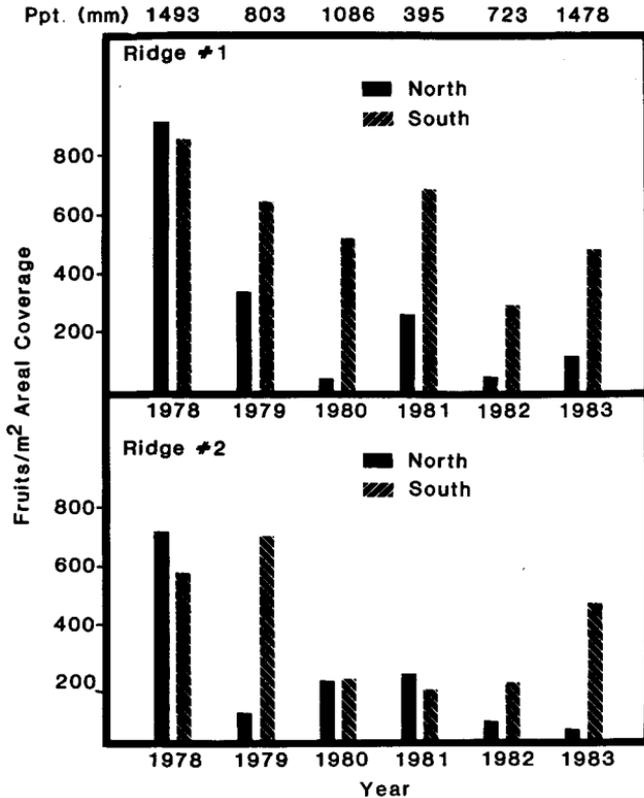


FIG. 1. Annual fruit production for years 1978–1983 for *Ceanothus crassifolius* on north- and south-facing exposures in Dalton Canyon in the San Gabriel Mountains of southern California ( $n = 15$  shrubs per slope). Statistical analyses are given in the text. Precipitation data is for the period July–June and is from Big Tujunga Dam; average = 660 mm per year.

exceeded 80% and often was above 100%. During the period of this study there was a significant difference between individuals on the south face of Ridge 1 ( $p < 0.01$ ). On this slope, over the six-year period, one shrub averaged  $1140 \pm 747$  fruits  $m^{-2}$  areal coverage per year whereas another produced nearly an order of magnitude fewer ( $173 \pm 80$  fruits  $m^{-2}$  areal coverage). On the other slopes, there was much variation in size of fruit crops, but across all six years there was no significant difference among shrubs.

An analysis of the size of the fruit crop on an individual shrub in a given year with the size in the following year showed that there was a significant positive relationship in fruit production between 1978 and 1979, and between 1980 and 1981 ( $p < 0.01$ ). Thus, for

those years, shrubs on south-facing slopes that produced the largest fruit crops in 1978 and 1980 produced the largest crops in the succeeding year. Shrubs on the northern exposure showed no significant correlation between any years.

*Precipitation and temperature patterns.* During the course of this study, five of the years had above average precipitation levels (Fig. 1). The year of highest fruit production, 1978, was also the year of highest precipitation (the 1977–1978 rainfall season had more than double the average). There also was much greater than average rainfall during the 1982–1983 season, yet fruit production, particularly on north-facing exposures, was not high in 1983. In three years of this study the summer drought was interrupted by measurable precipitation resulting from unusual subtropical storms; >30 mm precipitation was recorded in either August or September of 1977, 1978, and 1982. On south-facing slopes these were followed by years of high fruit production.

A stepwise multiple regression analysis was made between annual fruit crop size and precipitation and mean temperature for all months from March of the previous year through June of the year of the fruit crop, and including annual precipitation total as well as summer, fall, winter, and spring precipitation totals. There was a highly significant positive correlation between the mean fruit crop size per slope and February precipitation ( $r = 0.61$ ,  $p < 0.005$ ,  $n = 24$ ). However, this relationship did not hold up if slopes were compared separately. Using fruit crop size for each shrub on the two north-facing slopes revealed that only March temperature was positively correlated with fruit crop size ( $r = 0.52$ ,  $p < 0.001$ ,  $n = 180$ ). On the south-facing slopes, the stepwise regression included both October temperature and December precipitation ( $r = 0.35$ ,  $p < 0.001$ ,  $n = 180$ ), both of which were positively correlated with fruit crop size.

## DISCUSSION

Annual variation in fruit production by chaparral shrubs is likely dependent upon environmental conditions during the season of flowering and fruiting. Flower production by species of *Ceanothus* (subg. *Cerastes*) also may be dependent upon conditions during the previous growing season. This is because flower buds are produced at the end of the previous year's growing season, and as a consequence, flowering is on old growth branchlets (Keeley 1977, Kummerow et al. 1981; found in all species of subg. *Cerastes*, although not easily recognized, cf. Baker et al. 1982).

I propose a model in which fruit production is a function of the number of nascent flower bud primordia produced at the end of the previous growing season, flowering success, and the level of pho-

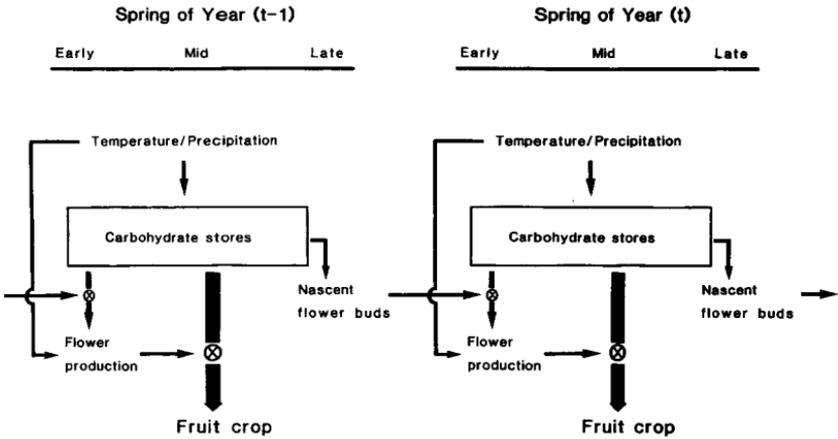


FIG. 2. Schematic model of factors influencing the size of fruit crops in *Ceanothus* species. Fruit production in year (t) will be a function of the number of nascent flower buds produced the previous year (t - 1), flowering success, and the level of carbohydrates available during fruit maturation.

tosynthates available during fruit maturation (Fig. 2). This model may be useful for interpreting annual fruit production patterns in other chaparral shrubs that produce floral primordia in the year prior to fruiting [viz., all species of *Arctostaphylos*, *Garrya*, and *Rhus*, excluding *R. (Malosma) laurina*, Keeley unpubl. data].

In the model, nascent flower bud production is a function of the level of carbohydrate stores available at the end of the growing season and carbohydrates are a function of photosynthate production and demands by carbohydrate sinks. Photosynthate production by chaparral shrubs is insensitive to annual variations in temperature relative to the role of soil moisture (Oechel et al. 1981). Thus, in years of high precipitation, carbohydrate production should be higher than in years of low precipitation. Carbohydrate sinks include growth and maintenance as well as fruit production. The latter represents a substantial, and annually variable, carbohydrate drain. Because *Ceanothus* flower buds arise from axillary meristems in the nodes of leaves, nascent flower bud production also would be an indirect function of the extent of terminal branch and leaf production during that growing season.

Flower production should be a function of the number of nascent flower buds produced the previous year and the available carbohydrate stores present at the time of flowering. Because flowering takes place in early spring, temperature, through its effect on pollinators, presumably plays a role in determining success.

Although I recognize that other factors are involved, I suggest that this model is conceptually useful in understanding annual variation

in size of fruit crops observed for species of *Ceanothus*. For example, in a study of *C. greggii* in San Diego Co. massive fruit crops were reported for 1974 (Keeley 1977), a year with a 60% precipitation deficit (all references to annual precipitation are for the rainfall season, in this instance 1 Jul 1973 to 30 Jun 1974, most of which falls in winter and spring). The considerations discussed above would predict that 1) the 1973 season should have had high precipitation (requisite for flower bud production), and 2) poor fruit production in 1975 (due to limited flower bud production in 1974, a consequence of high fruit production combined with limited precipitation in 1974); both of these predictions were true. A four-year study of *C. megacarpus* in Santa Barbara Co. reported that the highest fruit production occurred in 1978, which was a year of very high rainfall (Schlesinger et al. 1982). Although it followed a year of subnormal precipitation, massive flower bud production in 1977 apparently was possible as a result of a lack of fruit production that year. This pattern was seen also for *C. crassifolius* in the present study, where the year of highest fruit production (1978) was preceded by a year of subnormal precipitation, but also one in which fruit production was low (reported by Davey in 1982 for a nearby site).

It is also apparent that on different slope faces fruit production may be sensitive to different environmental factors. Higher March temperatures are correlated with higher fruit production on north-facing slopes. March is the peak month for flowering and, thus, warmer temperatures may be critical to pollinator success on these cooler north-facing slopes. On south-facing sites, higher fruit production is correlated with higher December precipitation and October temperatures. These factors may affect seasonal carbon gain and, thus, overall carbohydrate stores on these south-facing slopes.

One implicit factor in the model (Fig. 2) is the effect of summer and fall drought on nascent flower bud survival. Baker et al. (1982) suggested this to be an important factor controlling fruit production in *Arctostaphylos*. Bud survival might be affected by total seasonal precipitation and also by atypical summer thunderstorms. As noted here, significant summer precipitation occurred in 1977, 1978, and 1982, and these years were followed by high fruit production on south-facing slopes.

An understanding of the factors responsible for temporal variation in fruit production is complicated in that there is significant spacial variation (Fig. 1). Throughout this investigation, the shrubs on southern exposures out-produced those on northern exposures. The regression analysis suggests that cooler temperatures during flowering may play a role in controlling fruit production on north-facing slopes. Soil moisture levels, however, may play a role because results from other studies would predict higher soil moisture levels for the sparsely vegetated south-facing slopes (Poole et al. 1981).

Elevational differences also may affect level of fruit production. Davey (1982) documented *C. crassifolius* seed production on a south-facing slope (last burned in 1960) within 1 km of my sites, but at approximately 200 m higher elevation. For the years 1978–1980, she reported seed fall of 6000–8000 seeds  $m^{-2}$  ground surface, which for her sites translates into 4000–5500 seeds  $m^{-2}$  areal coverage. Assuming each fruit dispersed the maximum number of seeds possible (i.e., three), the highest seed fall observed at my sites during those same years would have been 1500–2500 seeds  $m^{-2}$  areal coverage.

Even within a site there is much interplant variation. On the south-facing exposures studied here, some shrubs out-produced (by an order of magnitude) others that were only meters away. That some shrubs consistently produced larger fruit crops than others nearby suggests either inherent genetic differences in shrubs, or important microhabitat differences. Small scale differences in soil depth could produce different soil moisture regimes (Miller and Hajek 1981); however, nothing is known about the subsoil conditions at these sites.

More and longer term studies of fruit production will be needed before we can elucidate all factors responsible for the annual variation in magnitude of fruit crops in these chaparral shrubs. Future studies will need to consider microhabitat characteristics and other environmental parameters in order to fully account for fruit production patterns in these species.

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