TEMPORAL AND SPATIONAL VARIATION IN FRUIT PRODUCTION BY CALIFORNIA CHAPARRAL SHRUBS

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INTRODUCTION

Fires are a predictable feature of the California chaparral environment and on most sites the dominant shrubs recover readily by resprouts and/or seedlings. In the large genus Arctostaphylos some species lack the potential for laying down adventitous buds in the rootcrown and thus are incapable of resprouting. After fire, these obligate seeding species are present only as seedlings. Arctostaphylos species that resprout also may establish seedlings and thus are best referred to as facultative seeding species. In all Arctostaphylos species, as well as certain other taxa in chaparral, seedlings that establish after fire arise from seeds in the soil at the time of fire. As a consequence, the concentration of seeds in the soil at the time of fire may be critical to successful regeneration after fire.

The soil seed pool of Arctostaphylos species is quite dynamic. These shrubs arise from seeds that largely remain dormant until germination is stimulated by charcoal produced during fire (Keeley 1987a). One early study (Keeley 1977) suggested, however, that the accumulation of seeds in the soil was relatively slow. It was noted that for two species, an obligate seeding species and a facultative seeding species, both were capable of producing more seeds in one year than were found in the soil seed pool. This seed pool changed relatively little over the period of one decade (Keeley 1987b), despite the fact that > 10^6 seeds/m^2 were dispersed into the stand over that period of time. It is apparent that there are large influxes and outfluxes of seeds in natural stands and the magnitude of these fluxes could have important effects on postfire seedling reproduction.

The purpose of this study was to document the annual variation in fruit production in obligate seeding and facultative seeding species of Arctostaphylos. An additional focus was to evaluate what factors influence the magnitude of fruit production. One potentially important factor is the level of flowering inflorescence primordia (nascent inflorescences) differentiated in the year prior to flowering and fruiting. In Arctostaphylos, the flowering phenology patterns begins with the initiation of floral inflorescence primordia in late spring and summer. These nascent inflorescences remain dormant for 6-8 months, and if they survive the summer and fall drought and winter freezing, may develop into flowers in late winter or early spring of the following year. As fruits are nearing maturity in early summer, nascent inflorescences for the following year are initiated. In this study, production of both fruits and nascent inflorescences were measured each season for nine years. The correlation between the magnitude of annual fruit and inflorescence crops and monthly temperature and precipitation were analyzed.

SPECIES AND SITE SELECTION

As a general rule, obligate seeding species of <u>Arctostaphylos</u> tend to be distributed from low to mid-elevation and facultive seeding species from mid to high elevation. Populations along gradients from low to mid elevation in Southern California and the central Sierra Nevada Range of California were selected. In each population 15 shrubs were tagged and a map was drawn to facilitate relocating each shrub in subsequent years. For each shrub, height and length and width, of the canopy were measured.

Along the Sierra Nevada transect, eight populations were monitored: two low elevation (1000-1200 m) populations of the obligate seeding <u>Arctostaphylos viscida</u> ssp. <u>mariposa</u> (Dudley) Wells, two mid-elevation (1700-1800 m) populations of this species, each of which was existing sympatrically with a population of the facultative seeding <u>A</u>. <u>patula</u> Greene, and two high elevation (2000-2200 m) populations of <u>A</u>. <u>patula</u>. In Southern California, populations were selected across two elevational transects, one on the coastal and one on the desert side of the San Gabriel Mountains. On each transect there was a low elevation (1050-1100 m) population of the obligate seeding <u>A</u>. <u>glauca</u> Lindl, a mid-elevation (1500-1550 m) population of <u>A</u>. <u>glauca</u> sympatric with a population of the facultative seeding <u>A</u>. <u>glandulosa</u> Eastw., and a high elevation (1800-1850 m) population of <u>A</u>. <u>glandulosa</u>.

Sampling began in 1978 and was done each year in mid-summer, prior to fruit dispersal. A rigid circular loop of 0.25 m^2 area was randomly tossed onto the bush and all fruits and nascent inflorescences within the loop were counted.

Stepwise regressions were done for each site using number of fruits on an individual shrub in a particular year(t) as the dependent variable. Independent variables were number of nascent inflorescences in the previous year(t-1), precipitation and mean temperature each month from June of the previous year(t-1) through June of the year(t) of fruiting, total precipitation in the year from July(t-1) to June(t), and seasonal precipitation for summer(t-1), fall(t-1), winter(t) and spring(t), and a sum of monthly mean temperatures for each of these seasons. Stepwise regressions were also run with nascent inflorescences in year(t) as the dependent variable. Independent variables were number of fruits in year(t) and the same climatic parameters described in the previous sentence.

RESULTS AND DISCUSSION

Sierra Nevada Range Transect

Mid-elevation populations of both the obligate seeding <u>Arctostaphylos viscida</u> and the facultative seeding <u>A</u>. <u>patula</u> were largely indistinguishable in pattern of annual fruit production (Fig. 1). These two taxa produce similar size fruits with the same number of seeds per fruit. Thus, it appears that at least over the period of this study at these sites, there was little difference in allocation of energy to reproduction, contrary to what has been predicted (Keeley and Keeley 1977). However, <u>Arctostaphylos patula</u> is distributed at higher elevations than <u>A</u>. <u>viscida</u> and at these sites annual fruit crops were consistently smaller than at lower elevations.
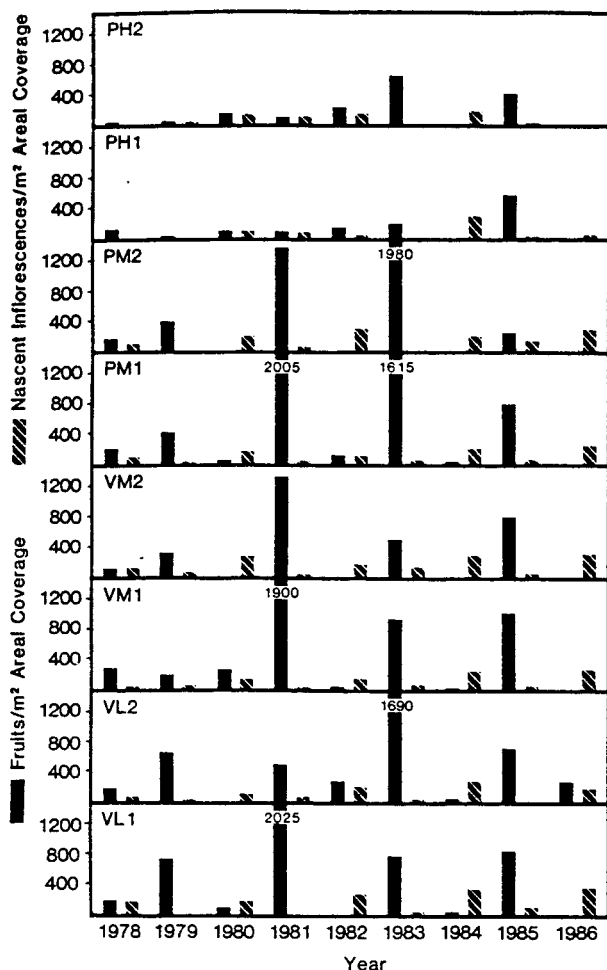
Fig. 1. Fruit and inflorescence crop size for Sierra Nevada populations of Arctostaphylos:
  VL1, VL2 = low elevation A. viscida;
  VM1, VM2 = mid-elevation A. viscida;
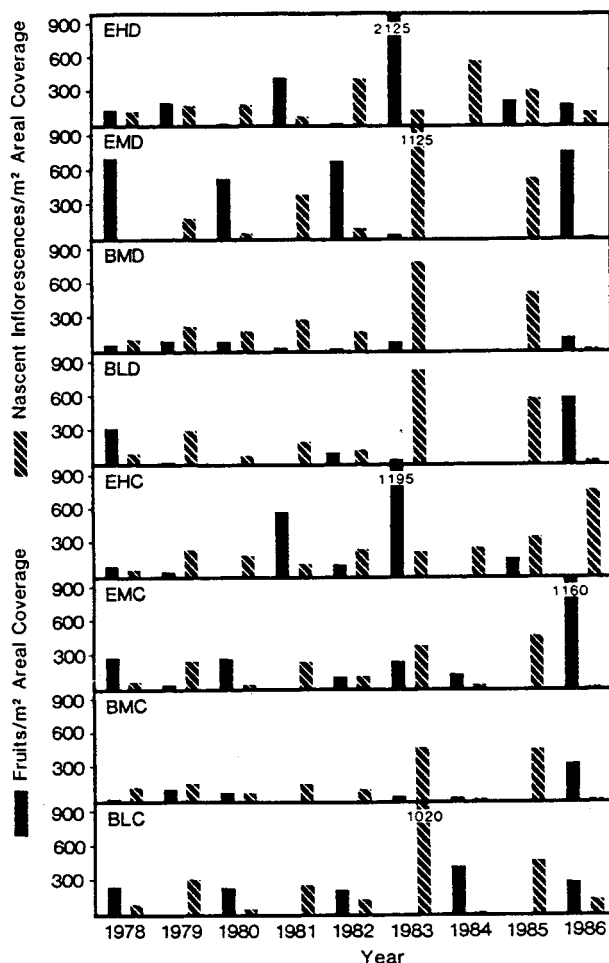 PM1, PM2 = mid-elevation A. patula;
  PH1, PH2 = high elevation A. patula

Fig. 2. Fruit and inflorescence crop size for Southern California San Gabriel populations of Arctostaphylos 3-letter codes are:
  B = Bigberry Manzanita   A. glauca;
  E = Eastwood Manzanita A. glandulosa;
  L = low, M = mid, H = high elevation;
  C = coastal, D = desert face of San Gabriel Mountains

Stepwise multiple regression revealed that for all populations, nascent inflorescence production in the year prior to fruit production was the best predictor of fruit crop size (Table 1). Precipitation and temperature also were correlated but the parameter, and whether it had a positive or negative effect, varied with the population.

Table 1. Stepwise regressions for Sierra Nevada <u>Arctostaphylos</u> fruit crops

ARCTOSTAPHYLOS VISCIDA FRUIT CROPS

LOW ELEVATION				MID ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
NASCENT INFLORESCENCES	t-1	+	0.38	NASCENT INFLORESCENCES	t-1	+	0.58
PPT-MARCH	t	+	0.46	PPT-NOVEMBER	t-1	-	0.66
PPT-TOTAL	t-1/t	+	0.57	PPT-MAY	t	-	0.75
TEMP-SUMMER	t-1	-	0.61	TEMP-MAY	t	-	0.77
PPT-JANUARY	t	+	0.63	TEMP-JULY	t-1	-	0.78
F = 30.5 (5,234)		P<0.001		F = 74.7 (5,234)		P<0.001	

ARCTOSTAPHYLOS PATULA FRUIT CROPS

MID ELEVATION				HIGH ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
NASCENT INFLORESCENCES	t-1	+	0.45	NASCENT INFLORESCENCES	t-1	+	0.62
PPT-MARCH	t	+	0.53	TEMP-TOTAL	t-1/t	-	0.69
PPT-TOTAL	t-1/t	-	0.60	PPT-MARCH	t	-	0.70
TEMP-SUMMER	t-1	-	0.64	TEMP-JANUARY	t	+	0.71
TEMP-FALL	t-1	+	0.66				
F = 36.1 (5,234)		P<0.001		F = 58.9 (4,235)		P<0.001	

Inflorescence production at all but the highest elevation sites of <u>A. patula</u> was negatively correlated with fruit crop size that year (Table 2). Thus, in years of high fruit production there is low inflorescence production and that year is followed with a year of low fruit production and high nascent inflorescence production. This pattern of alternating years of high fruit production is readily seen at all but the highest elevation sites (Fig. 1).

Table 2. Stepwise regressions for Sierra Nevada <u>Arctostaphylos</u> inflorescence production

ARCTOSTAPHYLOS VISCIDA INFLORESCENCE PRODUCTION

LOW ELEVATION				MID ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
FRUIT CROP	t	-	0.41	FRUIT CROP	t	-	0.42
PPT-JANUARY	t	-	0.48	TEMP-AUGUST	t-1	-	0.56
PPT-WINTER	t-1/t	+	0.55	PPT-JUNE	t	+	0.61
PPT-SUMMER	t-1	-	0.62	TEMP-MARCH	t	+	0.68
TEMP-SPRING	t	-	0.64	TEMP-APRIL	t	+	0.69
TEMP-WINTER	t-1/t	+	0.66	TEMP-JANUARY	t	+	0.70
F = 32.9 (6,263)		P<0.001		F = 41.0 (6,263)		P<0.001	

ARCTOSTAPHYLOS PATULA INFLORESCENCE PRODUCTION

MID ELEVATION				HIGH ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
FRUIT CROP	t	-	0.43	PPT-MARCH	t	-	0.39
TEMP-FEBRUARY	t	+	0.52	PPT-AUGUST	t-1	+	0.52
PPT-JUNE	t-1	-	0.55	TEMP-FEBRUARY	t	+	0.57
PPT-FALL	t-1	+	0.59	PPT-JUNE	t-1	-	0.61
TEMP-APRIL	t	-	0.62	TEMP-APRIL	t	-	0.62
PPT-FEBRUARY	t	+	0.63				
F = 29.2 (6,263)		P<0.001		F = 35.5 (5,264)		P<0.001	

San Gabriel Mountains Transect

Overall it would appear that fruit production is more tenuous for these southern California populations than for the Sierra Nevada populations (Fig. 2). Although populations within the Sierra Nevada were largely synchronized in fruit production across much of the elevational gradient, there is no obvious synchrony between Southern California populations. Additionally, years of high fruit production in the Sierra Nevada were not high years in Southern California.

Comparing the magnitude of fruit production is less straight forward since the obligate seeding <u>A. glauca</u> produces fruits that have 3.4 times greater biomass than the facultative seeding <u>A. glandulosa</u>. Even so, taking this 3.4 fold

difference into account, there is no indication that the obligate seeding species has larger fruit crops than the facultative seeding species. In general there was a tendency for A. glauca to produce larger fruit crops on the coastal side of the mountains and A. glandulosa to produce larger crops on the desert face.

Stepwise multiple regression revealed that only one population (the low elevation, coastal, A. glauca population) had a significant correlation between fruit crops and nascent inflorescence production in the previous year (Table 3). This population also showed a very marked biennial pattern of fruit crops (Fig. 2), similar to what was observed for most Sierra Nevada populations. Why this population should behave so distinctly different from the other Southern California populations is unknown. One potential factor is that this site was cleared of other brush in the year following initiation of this study and in subsequent years total cover was maintained at approximately 30 % compared to close to 100% at most other sites. Knipe (1985, personal communication, P. Rundel) has shown how manipulations of reducing chaparral cover can have marked influences on reducing summer water stress in remaining shrubs. One possible conclusion is that if summer water stress is reduced, then the magnitude of fruit crops is largely driven by the size of the previous year's inflorescence crop.

Table 3. Stepwise regressions for Southern California Arctostaphylos fruit crops

ARCTOSTAPHYLOS GLAUCA (COAST) FRUIT CROPS

LOW ELEVATION				MID ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
NASCENT INFLORESCENCES	t-1	+	0.60	TEMP-SEPTEMBER	t-1	-	0.41
TEMP-JUNE	t-1	-	0.64	PPT-APRIL	t	-	0.52
TEMP-MARCH	t	+	0.67	TEMP-APRIL	t	-	0.66
PPT-DECEMBER	t-1	-	0.69	TEMP-SPRING	t	-	0.67
F = 25.5 (4,115) P<0.001				F = 22.5 (4,115) P<0.001			

ARCTOSTAPHYLOS GLANDULOSA (COAST) FRUIT CROPS

MID ELEVATION				HIGH ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
TEMP-SEPTEMBER	t-1	-	0.61	PPT-JUNE	t-1	+	0.57
PPT-FEBRUARY	t	+	0.74	TEMP-NOVEMBER	t-1	+	0.63
PPT-JUNE	t-1	-	0.80	NASCENT INFLORESCENCES	t-1	+	0.66
PPT-NOVEMBER	t-1	+	0.81	TEMP-FALL	t-1	+	0.68
F = 55.7 (4,115) P<0.001				F = 24.2 (4,115) P<0.001			

ARCTOSTAPHYLOS GLAUCA (DESERT) FRUIT CROPS

LOW ELEVATION				MID ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
TEMP-SEPTEMBER	t-1	-	0.61	TEMP-FEBRUARY	t	-	0.30
PPT-JUNE	t-1	-	0.71	PPT-NOVEMBER	t-1	-	0.39
PPT-TOTAL	t-1/t	+	0.78				
F = 61.0 (3,116) P<0.001				F = 10.8 (2,117) P<0.001			

ARCTOSTAPHYLOS GLANDULOSA (DESERT) FRUIT CROPS

MID ELEVATION				HIGH ELEVATION			
PARAMETER	YEAR	+	r	PARAMETER	YEAR	+	r
PPT-DECEMBER	t-1	-	0.52	PPT-JUNE	t-1	+	0.77
TEMP-OCTOBER	t-1	-	0.64	NASCENT INFLORESCENCES	t-1	+	0.78
TEMP-WINTER	t-1/t	-	0.69				
PPT-NOVEMBER	t-1	-	0.73				
TEMP-MARCH	t	+	0.76				
F = 30.4 (5,114) P<0.001				F = 93.8 (2,117) P<0.001			

For two other populations of A. glauca, temperature in September prior to fruiting was negatively correlated with fruit crop size (Table 3). High

September temperature may exacerbate the drought conditions, thus reducing survival of inflorescences. For A. glandulosa, both of the high elevation sites showed positive correlations between fruit crop size and precipitation in June prior to fruiting.

Inflorescence production by all populations of A glauca and one A. glandulosa population was most strongly correlated with precipitation in June of the previous year (Table 4). Whether there is a cause and effect relationship here and what it would be is unknown.

Table 4. Stepwise regressions for Southern California Arctostaphylos inflorescence production

ARCTOSTAPHYLOS GLAUCA (COAST) INFLORESCENCE PRODUCTION

LOW ELEVATION

PARAMETER	YEAR	+	r
PPT-JUNE	t-1	+	0.57
TEMP-APRIL	t	+	0.68
TEMP-AUGUST	t-1	+	0.72
FRUIT CROPS	t	-	0.73

F = 89.7 (4,130)   P<0.001

MID ELEVATION

PARAMETER	YEAR	+	r
PPT-JUNE	t-1	+	0.56
TEMP-APRIL	t	+	0.78
PPT-DECEMBER	t-1	+	0.83
TEMP-AUGUST	t-1	+	0.86
PPT-SEPTEMBER	t-1	-	0.87

F = 77.7 (5,129)   P<0.001

ARCTOSTAPHYLOS GLANDULOSA (COAST) INFLORESCENCE PRODUCTION

MID ELEVATION

PARAMETER	YEAR	+	r
TEMP-DECEMBER	t-1	-	0.52
PPT-OCTOBER	t-1	-	0.65
TEMP-WINTER	t-1/t	+	0.78
TEMP-MARCH	t	-	0.82
PPT-JANUARY	t	+	0.84

F = 61.6 (5,129)   P<0.001

HIGH ELEVATION

PARAMETER	YEAR	+	r
TEMP-FALL	t-1	-	0.41
FRUIT CROPS	t	-	0.59
TEMP-MARCH	t	+	0.70
PPT-SUMMER	t-1	-	0.71

F = 33.6 (4,130)   P<0.001

ARCTOSTAPHYLOS GLAUCA (DESERT) INFLORESCENCE PRODUCTION

LOW ELEVATION

PARAMETER	YEAR	+	r
PPT-JUNE	t-1	+	0.67
TEMP-APRIL	t	+	0.80
TEMP-AUGUST	t-1	+	0.85
PPT-DECEMBER	t-1	+	0.86

F = 91.1 (3,130)   P<0.001

MID ELEVATION

PARAMETER	YEAR	+	r
PPT-JUNE	t-1	+	0.68
TEMP-APRIL	t	+	0.81
PPT-SPRING	t	+	0.84
TEMP-SEPTEMBER	t-1	+	0.85
FRUIT CROPS	t	-	0.86

F = 75.0 (5,129)   P<0.001

ARCTOSTAPHYLOS GLANDULOSA (DESERT) INFLORESCENCE PRODUCTION

MID ELEVATION

PARAMETER	YEAR	+	r
PPT-JUNE	t-1	+	0.81
TEMP-APRIL	t	+	0.93
PPT-SPRING	t	+	0.94
FRUIT CROPS	t	-	0.94
PPT-FEBRUARY	t	-	0.94

F = 213.2 (5,129)   P<0.001

HIGH ELEVATION

PARAMETER	YEAR	+	r
PPT-JANUARY	t	-	0.46
TEMP-JUNE	t-1	-	0.62
PPT-SUMMER	t-1	+	0.69

F = 39.6 (3,131)   P<0.001

CONCLUSIONS

A simple model that attempts to integrate these factors is shown in Fig. 3. We suggest that the size of the fruit crop is a function of the level of available carbohydrates at the time of fruit maturation in late spring and early summer. Photosynthate production in chaparral shrubs is strongly influenced by soil moisture levels during the growing season (Miller 1981), and there is evidence that soil moisture levels in arid lands are linearly correlated with precipitation (Nobel 1987). Additionally, temperature and precipitation could affect flowering directly, or indirectly via pollinators. Low flowering success would exert a strong control on fruiting. Likewise, flowering would potentially be limited by the number of nascent inflorescences produced in the previous year and which survive until flowering.

Spring of Year (t-1)   Spring of Year (t)

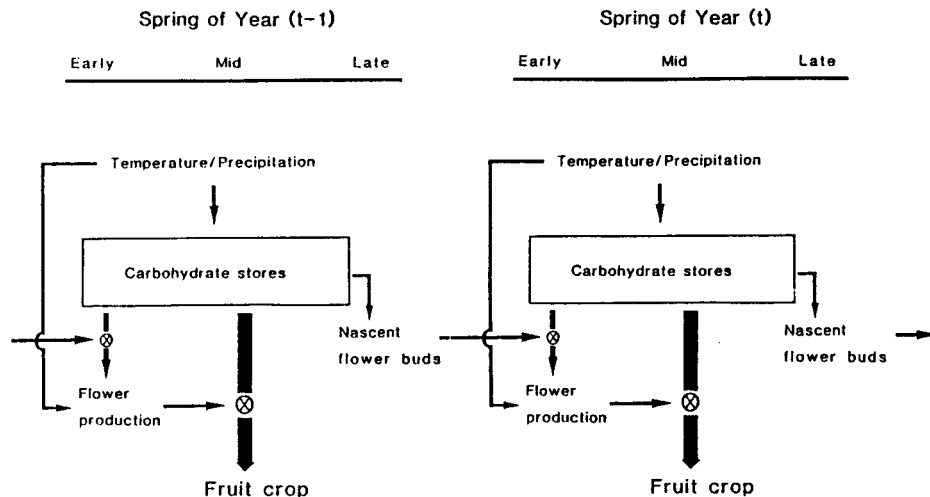Early   Mid   Late   Early   Mid   Late

Fig. 3. Model of factors controlling fruit and inflorescence production

In this model, inflorescence production is dependent upon carbohydrate pools in the plant in late spring and early summer. Since fruit crops can deplete carbohydrate pools at this time, there may be an internal competition between fruits and nascent inflorescences for carbohydrate and mineral resources, and this could lead to the negative relationship between fruits and inflorescences seen in Table 2. This model suggests that nascent inflorescence production is purely a function of sufficient carbohydrate stores in late spring. However, there may be indirect effects; e.g., low carbohydrate pools may limit branchlet growth, which in turn would limit nascent inflorescence production because inflorescences are differentiated from aprical meristems on such shoots.

Clearly more work is needed in the form of a longer period of observation and detailed physiological studies, both of which are planned for these sites.

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