



**Energy Allocation Patterns of a Sprouting and a Nonsprouting Species of
Arctostaphylos in the California Chaparral**

Jon E. Keeley, Sterling C. Keeley

American Midland Naturalist, Volume 98, Issue 1 (Jul., 1977), 1-10.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Midland Naturalist is published by University of Notre Dame. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

American Midland Naturalist
©1977 University of Notre Dame

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 98

JULY, 1977

No. 1

Energy Allocation Patterns of a Sprouting and a Nonsprouting Species of *Arctostaphylos* in the California Chaparral

JON E. KEELEY and STERLING C. KEELEY

*Department of Botany and Institute of Ecology,
University of Georgia, Athens 30602*

ABSTRACT: The r- and K-selection theory was used to generate testable hypotheses about patterns of energy allocation in two chaparral shrubs of different reproductive strategies. Terminal-branchlet vegetative and reproductive biomass of the nonsprouting *Arctostaphylos glauca* and the sprouting *A. glandulosa* were sampled in a 23-year-old and a 90-year-old stand of chaparral to test the predictions that: (1) the terminal vegetative growth (g dry weight/m² of areal coverage) would be equal in the two species, in both stands; (2) oven dry weight (g) of reproductive parts/m² of areal coverage would be greater in *A. glauca* than in *A. glandulosa* in both aged populations; (3) allocation to reproductive parts by the shrubs in the 23-year-old stand would be greater than (or equal to) that of the 90-year-old shrubs. The amount of terminal vegetative growth was equal for both species in the 23-year-old and the 90-year-old stands. There was no statistically significant difference in the weight of fruits produced by the two species in the 23-year-old stand. However, fruit production by *A. glauca* was significantly greater than by *A. glandulosa* in the 90-year-old stand. Fruit production was also significantly greater for the older *A. glauca* shrubs than for those in the 23-year-old stand. The relationships of rainfall pattern and age of shrubs to fruit production are discussed.

INTRODUCTION

The southern California chaparral is a vegetation of predominantly evergreen sclerophyllous-leaved shrubs adapted to the mild, wet-winter, summer-drought climate of that region. During the long, hot summers these shrubs become extremely dry and flammable, and, once ignited, the dense nature of the vegetation makes it susceptible to widespread conflagrations. After fire, these shrubs regenerate rapidly by sprouts from underground burls or from large numbers of seedlings. Some species regenerate by both sprouts and seedlings, but many are restricted to one mode. The restriction to sprouting or nonsprouting reproduction is most pronounced in the two largest genera of chaparral shrubs, *Arctostaphylos* (Ericaceae) and *Ceanothus* (Rhamnaceae).

Nonsprouting shrubs were regarded by Jepson (1939) as "fire-type" species, better adapted and "biologically specialized" to the fire cycle of the California chaparral. Sprouting from belowground vegetative

parts was considered by Wells (1969) to be an ancestral trait which has been lost by these obligate seeding shrubs, and he hypothesized that this loss is responsible for the high degree of speciation in these genera.

This shift from the sprouting to the seeding mode of reproduction has several consequences for the life history of these shrubs. In the immediate postfire years sprouting species rapidly regain their original prefire size. However, few seedlings of these sprouting shrubs become established (Jepson, 1916; Plumb, 1961; Vogl and Schorr, 1972), and the distribution and population size of these species remain relatively constant through time. The nonsprouting species, on the other hand, are replaced following fire with an abundance of seedlings which require 10-20 years to regain their original prefire size. Evolutionarily, these two reproductive modes represent opposite extremes. Sprouting shrubs depend on well-adapted genotypes with an immediate competitive edge, whereas nonsprouting shrubs face each fire cycle with a new variety of phenotypes which are then acted upon by the selective forces present at that time and during the years up to the next fire. However, both of these alternatives are obviously successful, so what are the forces which have acted to select for one type of strategy or the other?

Cody (1966) argues that natural selection determines how an organism will allocate its energy, by choosing the optimal "performance" for given environmental conditions. The result of this selection is to maximize the contribution of a particular suitable genotype to following generations as well as to meet the contemporary environmental requirements. Reproduction is requisite for the continuance of any species, but the amount of energy allocated to the purpose must be balanced against the amount of energy necessary to allow the organism to survive until the point when it can reproduce.

In recent years an effort has been made to put this allocation of energy theory into a framework from which the relative apportionment of energies in an organism can be predicted in terms of its environment (MacArthur and Wilson, 1967; Gadgil and Bossert, 1970; Hairston *et al.*, 1970; Gadgil and Solbrig, 1972). The central idea of r- and K-selection is that organisms living in environments imposing high density-independent mortality will be selected to allocate a greater proportion of resources to reproductive activities at the cost of their capabilities to propagate under crowded conditions. This has been called r-selection; thus, colonizing species are considered to be r-selected. Conversely, populations under high density-dependent regulation allocate a greater proportion of resources to nonreproductive activities at the cost of their capabilities to propagate under conditions of high density-independent mortality. This has been called K-selection; thus climax species are considered to be K-selected. The more predictable that a given unfavorable environmental phenomenon is, the more likely an organism will be able to increase its "fitness" by diverting some of its resources to ameliorating its effect. Under

density-dependent regulation, organisms can enhance their future reproductive success by diverting some of their resources to nonreproductive activities. Diversion is of less value for organisms subjected to less predictable density-independent mortality.

There are certain aspects of the life history of chaparral shrubs which suggests that these species cannot be viewed strictly within the framework of r- and K-selection. For example, reproduction by all shrub species is confined almost entirely to the immediate postfire year. Thus the initial colonizers are also the climax species. However, perhaps r- and K-selection theory can be useful in generating testable hypotheses about patterns of energy allocation. For example, in the mature chaparral density-dependent factors exert strong selective pressure on all species. This would be expected in view of the intense limitations on the community imposed by low levels of available light and moisture (Bauer, 1936; McPherson and Muller, 1967; Mooney and Dunn, 1970; Mooney and Chu, 1974). However, unpredictable density-independent disturbance, *i.e.*, fire, is also an integral part of this system and must be dealt with by all species. We would predict that a nonsprouting species, such as *Arctostaphylos glauca* Lindl., would react to density-dependent and density-independent forces in a different way than would a sprouting species such as *A. glandulosa* Eastw. A pictorial model of how these two types of shrub species might have reacted evolutionarily to these different selective regimes in their allocation of energy is illustrated in Figure 1.

Since *Arctostaphylos glauca* is entirely dependent upon seedling establishment following fire, we would expect a large proportion of its energy to be allocated to (sexual) reproductive effort (*sensu*, Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Ogden, 1974). In *A. glandulosa*, resprouting following fire is very successful, thus we would not predict a large allocation of energy to sexual reproductive effort. Presumably much of the energy would go to belowground parts such as the burl. The aboveground portions of both shrubs are under similar conditions of density-dependent and density-independent mortality factors; we would, therefore, expect similar proportions of energy allocated to terminal vegetative growth in both species. However, the degree to which density-independent selection will operate will depend in some way upon the frequency of fire. If these shrubs have evolved under and are "attuned" to a frequent fire cycle of every 20-25 years (Vogl, 1967; Muller *et al.*, 1968; McPherson and Muller, 1969), we would expect allocation for combatting density-independent mortality to be maximized very early in the life cycle of the nonsprouting *Arctostaphylos glauca*.

In light of these ideas we propose the following three hypotheses: (1) that annual allocation of energy to terminal branchlet vegetative growth will be equal in both the nonsprouting *Arctostaphylos glauca* and the sprouting *A. glandulosa*; (2) that the nonsprouting *A. glauca* will allocate a greater proportion of its annual fixed carbon to sexual reproductive effort than will the sprouting *A. glandulosa*, and (3)

that the nonsprouting *A. glauca* will maximize reproductive effort very early in its life cycle.

METHODS

To test these hypotheses, only terminal vegetative and reproductive growth was sampled due to the problems involved in obtaining adequate samples of entire shrubs (*viz.*, burls, roots, stems, etc.). We assumed that the annual gross production, when expressed on a per m² of areal coverage basis, would be the same in both *Arctostaphylos* species. This assumption is supported by the findings of Cole (1967) which showed that chaparral species of *Eriogonum* (Polygonaceae) from the same habitat were physiologically very similar, particularly with regard to their carbon balance (rates of photosynthesis/respiration). The similarity in leaf density (Kittredge, 1945), size and shape, as well as branching pattern in *A. glauca* and *A. glandulosa*, suggests that the proportion of grams of leaf material/m² areal coverage would also be similar. Thus, the amount of terminal vegetative and reproductive biomass per m² of areal coverage reflects the relative percentages of biomass allocated to these two functions.

Two sites were chosen for the study, one a 90-year-old stand of chaparral and the other a 23-year-old stand (ages were determined by

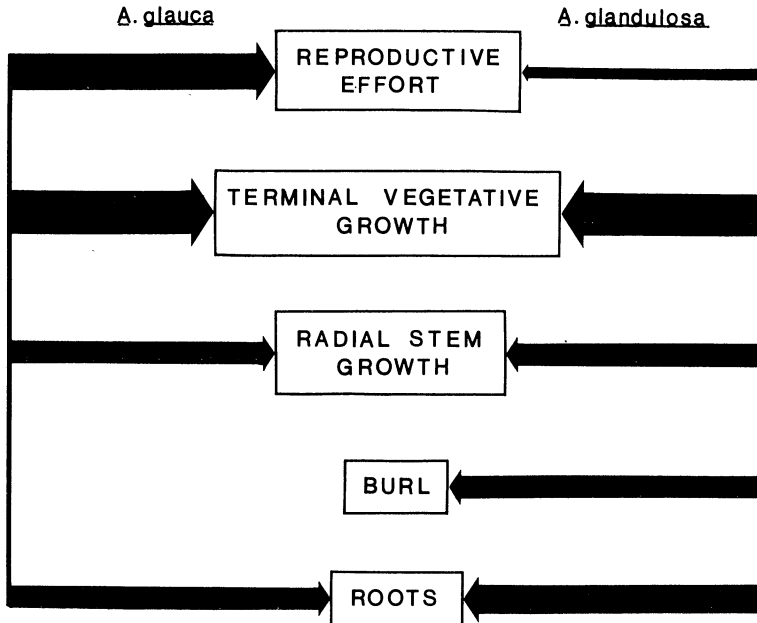


Fig. 1.—A pictorial model of the predicted relative apportionment of net annual fixed carbon by the two species of *Arctostaphylos* (arrow width indicates relative proportion)

ring-counts of several species). Both stands were located on E-facing slopes at an elevation of 700 m on the E ridge of Lawson Peak, San Diego Co., Calif. Sampling was undertaken at the end of the growing seasons in August 1973 and in June 1974. By the end of summer each year all vegetative growth is completed, as also is the production of flower buds and inflorescences for the following year. Flowering and fruiting from the previous year's inflorescences are completed by early summer. Since flower and fruit production was almost nil at this site in 1973 (Keeley, 1973), the dormant flower buds and inflorescences were taken as the total reproductive effort for that year. Fruits produced by the buds initiated in 1973 were collected in June 1974. The total reproductive effort for the reproductive cycle 1973-74 was obtained by adding the biomass of flower buds and inflorescences produced in 1973 with the biomass of fruits produced in 1974, plus an estimate of the biomass of pedicels and flowers produced in 1974. These estimates were obtained by multiplying the average weight of pedicels and flowers ($n = 50$) for each species by the total number of fruits produced by that species.

The shrubs sampled during the study were located along a randomly placed line in each site. The first 15 shrubs encountered of each species were sampled; height and areal coverage were recorded. The shrubs were divided into quarters, and all the terminal branchlets from one of these quarters were removed and returned to the laboratory. The sample was then separated into current year's vegetative growth and reproductive parts. These samples were oven-dried to constant weight and weighed. The results were expressed as grams of oven dry weight/m² of areal coverage (g ODW/m² AC). Calorific studies were not undertaken; rather biomass was used as an "estimate" of the amount of energy involved (*sensu* Harper and Ogden, 1970). In 1974 the same sampling procedure was used but only fruits were collected. The following predictions were tested: (1) g of current year's terminal vegetative ODW/m² AC would be equal in *Arctostaphylos glauca* and *A. glandulosa* in both aged populations; (2) g ODW of reproductive parts/m² AC would be greater in *A. glauca* than in *A. glandulosa* in both aged populations; (3) g ODW of reproductive parts/m² AC in the 23-year-old population would be greater than (or equal to) the 90-year-old population. These predictions were tested statistically with the Student's t-test and accepted at the 95% confidence limit. Where the variances were nonhomogeneous (by the F-test), the alternative method of Snedecor and Cochran (1967) was used.

RESULTS

In 1973 *Arctostaphylos glauca* and *A. glandulosa* produced similar amounts of terminal vegetative growth in both the 23-year-old and 90-year-old stands of chaparral (Table 1). The only statistically significant difference in the four populations was a decrease in terminal vegetative growth in the older *A. glauca* shrubs. Allocation of biomass to reproductive parts in 1973 (*i.e.*, buds) was not statistically different

among the four populations. There was no statistically significant difference between the two species in the amount of biomass allocated to fruits in the 23-year-old stand; however, in the 90-year-old stand, *A. glauca* fruit production was statistically greater than that of *A. glandulosa*. (Table 1). Also, there was a greater production of fruits by the older *A. glauca* shrubs. The total amount of biomass (g ODW/m² AC) allocated to reproduction for the full reproductive cycle, 1973-74, was twice as great in the 90-year-old *A. glauca* shrubs than in the 23-year-old ones. *Arctostaphylos glandulosa* reproductive effort appears to remain constant.

DISCUSSION

Annual allocation to terminal vegetative growth was equivalent in the two species in both stands. This finding supports our first hypothesis and probably reflects the intense competition for light in the mature canopy. However, the prediction that the nonsprouting *Arctostaphylos glauca* would allocate a greater proportion of its total annual fixed carbon to reproductive effort than the sprouting *A. glandulosa* seems to have exceptions. At least in some years, 23-year-old *A. glandulosa* are capable of producing similar amounts of fruit biomass as *A. glauca*. The third hypothesis which was proposed was also not supported by the data from this study. Where we predicted that the nonsprouting *A. glauca* would maximize its reproductive effort early in its life cycle, we found instead that the older shrubs produced a much greater biomass of fruits.

We need to ask whether or not the amount and pattern of biomass partitioning found is "typical" for these species. Possibly the quantity of both vegetative and reproductive growth is not typical; the amount of rainfall during the 1972-73 season was above average (Keeley, 1973), and annual biomass production by chaparral shrubs is quite sensitive to moisture availability (Harvey and Mooney, 1964; Mooney

TABLE 1.—Terminal vegetative and reproductive growth (g ODW/m² AC) by the two *Arctostaphylos* species in the 23-year-old and the 90-year-old stands of chaparral (n=15)

	Age	<i>A. glauca</i>		<i>A. glandulosa</i>	
		\bar{X}	SE	\bar{X}	SE
Vegetative biomass—1973	23	563.0 ± 42.1 ¹		493.8 ± 32.8	
	90	434.5 ± 28.8 ¹		498.2 ± 52.2	
Reproductive biomass—1973	23	20.8 ± 7.6		18.9 ± 3.6	
	90	24.0 ± 6.2		26.1 ± 3.7	
Fruit production—1974	23	49.4 ± 19.6 ¹		62.6 ± 15.4	
	90	124.8 ± 33.1 ^{1, 2}		55.8 ± 13.2 ²	
Total biomass for the reproductive cycle—1973-74 ³	23	71.2		87.0	
	90	151.3		86.8	

¹ Difference between age classes is significant at $P < .05$

² Difference between species is significant at $P < .05$

³ Includes inflorescences and buds produced in 1973 and flowers, pedicels and fruits produced in 1974 (flower and pedicel biomass was estimated by multiplying the average weight of a flower and pedicel, n=50, by the number of fruits produced in 1974)

et al., 1973). While annual production varies, the pattern of reproductive effort between species may change from year to year.

In a 3-year study of fruit production from the 90-year-old stand of chaparral at the Lawson site (Keeley, 1973), the number of fruits produced/m² AC by *Arctostaphylos glauca* for 1972, 1973 and 1974 was 3.8, 1.6 and 349.5, respectively, and by *A. glandulosa* 10.0, 0 and 916.8 for those same 3 years. Thus, in the 1st and 3rd years of this study, *A. glandulosa* produced greater numbers of fruits than *A. glauca* and in the 2nd year it produced fewer fruits than *A. glauca*.

Although *Arctostaphylos glandulosa* produced a greater number of fruits in two of the years, the amount of biomass was not greater since the fruits of *A. glauca* are larger than those of *A. glandulosa*. Even so, it is difficult to explain why in *A. glandulosa*, a very successful sprouting shrub which seldom establishes new seedlings, natural selection would select for allocation of almost as much energy to sexual reproduction as in *A. glauca*. This is particularly interesting in light of the axiom that organisms will optimize their fitness for any given environment (Levins, 1968) or, more specifically, reproduction will seldom be attempted when on the average it fails (Willson, 1971). The answer may lie in the distinction between the best possible phenotype and the best available phenotype (Cody, 1974). For example, as Cody points out, the best plant phenotype for survival in the driest deserts will exist only if the mutations that control water economy have actually occurred. Surely the very conservative form of reproduction in *A. glandulosa*, *i.e.*, repeated sprouting, possibly for many hundreds of years, would not be conducive to the production of novel genotypes (Wells, 1969; Raven, 1973). Consequently, in a rapidly changing region such as California there may not have been a very close evolutionary tracking of the environment by *A. glandulosa*.

Thus, there is much to suggest that the relative amounts of reproductive effort in these two species will vary from year to year and it is likely that it will vary from site to site. However, we have little reason to suspect the pattern of biomass partitioning to reproductive effort to vary between age groups within a species. That is, the results of this study agree well with our personal observations from other areas, that older *Arctostaphylos glauca* shrubs have a much greater reproductive potential than younger shrubs.

While making comparisons on a proportionate basis is essential in determining the "strategy" of energy partitioning (Gadgil and Solbrig, 1972), we feel that comparisons at the population level would be instructive in this instance. To obtain a picture of the changes in cover and reproductive potential, we reconstructed the 90-year-old stand as it would have appeared at 23 years of age (Table 2). We assumed that the density of shrubs, live and dead, in the 90-year-old stand was the density of shrubs which were alive at 23 years of age. This is reasonable since in the 90-year-old stand there were very few dead *Arctostaphylos glandulosa*, and the basal diameter of the smallest dead *A. glauca* was larger than any of the *A. glauca* shrubs in the 23-

year-old stand (Keeley, 1973). Using the average AC/shrub, the average terminal branchlet vegetative production/m² AC for 1973, and the average fruit production/m² AC for 1974 from the 23-year-old stand, we were able to calculate the total AC, the annual vegetative production and the annual fruit production for that point in time (given the same meteorological conditions as 1973-74).

One of the striking aspects of this comparison is the very large increase in areal cover from 23 years to 90 years in *Arctostaphylos glauca*. This is a reflection of the low mortality in this species coupled with the large difference in size between the two age classes; 90-year-old *A. glauca* shrubs have over eight times more AC/shrub and are nearly twice as tall as the 23-year-old *A. glauca* shrubs. Concomitant with this large difference in areal cover is a large increase in annual vegetative biomass production. The *Arctostaphylos glandulosa* population also shows this pattern of an increase in vegetative biomass production from 23 to 90 years.

Fruit production is also increased between 23 years and 90 years of age by both species. Other things being equal, *Arctostaphylos glauca* shrubs are capable of producing over 15 times more fruits at 90 years of age than at 23 years of age. This tremendous increase in reproductive potential does not suggest a species which evolved under a frequent fire cycle of every 20-25 years as suggested by some authors. Perhaps it would be more appropriate to regard chaparral as having evolved under a fire cycle of an unpredictable time span. Thus, the chaparral is adapted to both short and long fire-free periods.

In conclusion, we should emphasize that the results from this study illustrate the pattern of biomass allocation in one locality in one year. Further studies will be needed to show how representative these data are for these two species and these particular life history strategies.

TABLE 2.—A comparison of the areal coverage and fruit production for the two *Arctostaphylos* species¹ populations in the 90-year-old stand with that predicted at 23 years of age in the same stand

	Density (Shrubs/ha)		Total areal cover (m ² AC/ha)		Terminal vegetative production (kg/ha/year)	
	23 ¹	90	23	90	23	90
	<i>A. glauca</i>	1133	859	793	5197	417
<i>A. glandulosa</i>	1719	1562	3060	4733	1511	2357

TABLE 2.—(continued)

	Fruit production (kg/ha/year)		Fruit production (#/ha/year)	
	23	90	23	90
	<i>A. glauca</i>	56.5	786.3	62,200
<i>A. glandulosa</i>	266.2	410.8	1.7 x 10 ⁶	2.4 x 10 ⁶

¹ Estimate based on total number alive and dead in the 90-year-old stand of chaparral

LITERATURE CITED

- ABRAHAMSON, W. G. AND M. GADGIL. 1973. Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). *Am. Nat.*, **107**:651-661.
- BAUER, H. L. 1936. Moisture relations in the chaparral in the Santa Monica Mountains, California. *Ecol. Monogr.*, **6**:409-454.
- CODY, M. L. 1966. A general theory of clutch size. *Evolution*, **20**:174-184.
- . 1974. Optimization in ecology. *Science*, **183**:1156-1164.
- COLE, N. H. A. 1967. Comparative physiological ecology of the genus *Eriogonum* in the Santa Monica Mountains of Southern California. *Ecol. Monogr.*, **37**:1-24.
- GADGIL, M. AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. *Am. Nat.*, **104**:1-24.
- AND O. T. SOLBRIG. 1972. The concept of r- and K-selection: Evidence from wild flowers and some theoretical considerations. *Ibid.*, **106**:14-31.
- HAIRSTON, N. G., D. W. TINKLE AND H. M. WILBUR. 1970. Natural selection and the parameters of population growth. *J. Wildl. Manage.*, **34**:681-690.
- HARPER, J. L. AND J. OGDEN. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol.*, **58**:681-698.
- HARVEY, R. A. AND H. A. MOONEY. 1964. Extended dormancy of chaparral shrubs during severe drought. *Madroño*, **17**:161-163.
- JEPSON, W. L. 1916. Regeneration in manzanita. *Ibid.*, **1**:3-11.
- . 1939. A flora of California, Vol. 3. Associated Students Store, University of California.
- KEELEY, J. E. 1973. The adaptive significance of obligate-seeding shrubs in the chaparral. M.S. Thesis, San Diego State University. San Diego, Calif. 82 p.
- KITTRIDGE, J. 1945. Some quantitative relations of foliage in the chaparral. *Ecology*, **26**:70-73.
- LEVINS, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J. 120 p.
- MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J. 203 p.
- MCPHERSON, J. K. AND C. H. MULLER. 1967. Light competition between *Ceanothus* and *Salvia* shrubs. *Bull. Torrey Bot. Club*, **94**:41-55.
- AND ———. 1969. Allelopathic effects of *Adenostoma fasciculatum* "chamise," in the California chaparral. *Ecol. Monogr.*, **39**:177-198.
- MOONEY, H. A. AND C. CHU. 1974. Seasonal carbon allocation in *Heteromeles arbutifolia*, a California evergreen shrub. *Oecologia*, **14**:295-306.
- AND E. L. DUNN. 1970. Convergent evolution of mediterranean-climate evergreen sclerophyll shrubs. *Evolution*, **24**:292-303.
- , D. J. PARSONS AND J. KUMMEROW. 1973. Plant development in mediterranean climates. Technical Report 73-6. Origin and structure of ecosystems. San Diego State University, San Diego, Calif. 14 p.
- MULLER, C. H., R. B. HANAWALT AND J. K. MCPHERSON. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. *Bull. Torrey Bot. Club*, **95**:225-231.
- OGDEN, J. 1974. The reproductive strategy of higher plants II. The reproductive strategy of *Tussilago farfara* L. *J. Ecol.*, **62**:291-324.

- PLUMB, T. R. 1961. Sprouting of chaparral by December after a wildfire in July. *U.S. For. Serv. PSW Tech. Pap.* 57. 12 p.
- RAVEN, P. H. 1973. The evolution of Mediterranean floras, p. 213-224. *In*: F. di Castri and H. A. Mooney (eds.). *Mediterranean type ecosystems — origin and structure*. Springer-Verlag, New York.
- SNEDECOR, G. W. AND W. G. COCHRAN. 1967. *Statistical methods*. 6th ed. Iowa State University, Press, Ames. 593 p.
- VOGL, R. J. 1967. Fire adaptations of some Southern California plants. *Proc. Tall Timbers Fire Ecol. Conf.*, 7:79-109.
- AND P. K. SCHORR. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. *Ecology*, 53:1179-1188.
- WELLS, P. V. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. *Evolution*, 23: 264-267.
- WILLSON, M. F. 1971. Life history consequences of death rates. *Biologist (Phi Sigma Soc.)*, 53:49-56.

SUBMITTED 24 NOVEMBER 1975

ACCEPTED 12 JANUARY 1976