If my statements had no other effect than to bring out the valuable information presented by Dingle, it would have been a worthwhile effort. Perhaps my remarks on the possible influence of ice cloud streaks produced by airplanes on rainfall from lower natural clouds could have been more judiciously worded. While freely admitting that such cases indeed exist and perhaps, as Dingle implies, are not uncommon, I believe that their restriction in time and space on a global scale makes it likely that their effect on climate is minimal and disappears in the "noise" discussed in my article.

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## Role of Animals in Suppression of Herbs by Shrubs

Bartholomew (*1*) has challenged the idea that phytotoxins are causative in the production and maintenance of bare zones associated with shrub borders impinging upon annual grassland in California. However, we feel he has oversimplified the problem. In our descriptions (*2*) of the interactions of phytotoxins, animal grazing and seed predation, and variable physical and competitive factors in the production of "bare" zones and inhibition zones separating *Salvia leucophylla* from annual grassland, we have tried to dissuade readers from accepting any simplistic, "single-factor" explanation of the phenomenon, and have admitted repeatedly that even phytotoxins fail to control in some situations.

We hold that Bartholomew's and our experiments combined permit no definitive characterization of animal roles. More instructive have been our negative results, that is, the frequent failure of animal pressure to reduce herb growth within its sphere and also the failure of phytotoxins to have effect under certain circumstances. More pertinent still are the instances in which bare zones develop in the absence of animal pressure. The following observations required few counts or measurements because they exhibited "all-or-none" attributes. Each manipulation and observation of natural variables was fully controlled by corresponding checks; most results with statistical qualities were recorded in the form of data for which there is no space here.

1) Some herb species (for example, *Bromus rigidus*) were absent from the inhibition zone which extended several meters past the range of rodents as revealed in our baiting experiments (Fig. 1), although only rodents feed on the seeds of *B. rigidus*.

2) Seeds of *Bromus rubens* and *B. mollis* were not taken by birds and were taken only sparingly by rodents in baiting experiments. Seeds of *Festuca megalura* were taken only by harvester ants which were absent over most of the area examined.

3) Natural shade and the resulting conservation of moisture permitted dense growth of these species which eliminated the bare zone, thus proving that the seed supply was undiminished, that *Salvia* toxic effectiveness required normal drought stress, and that animal pressures failed to support a bare zone.

4) Repeated observation of young seedling mortality without evidence of animal grazing in typical bare zones negated the requirement of grazing.

5) Exclosure cages (with or without sides) in bare zones contained seedlings from 10 to 50 percent the height of the same species at the same time in adjacent unprotected grassland early in the growing season.

6) Fog drip and conservation of moisture beneath all cages resulted in lush growth later in the season so that harvesting and weighing at the season's end missed the period of toxic stunting and were therefore meaningless.

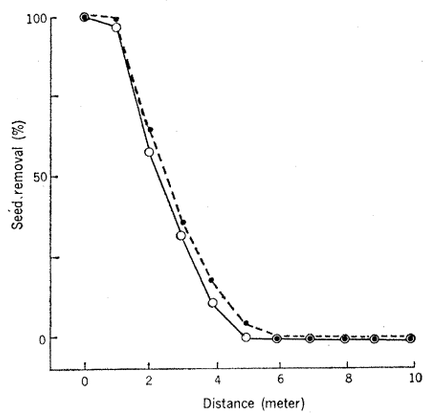


Fig. 1. Nocturnal (mammalian) removal of the most palatable seeds during March 1966 (a period of low availability of seed and high density of animals). *Salvia* zone (0 m), bare zone (0 to 2 m), and inhibition zone (2 to 10 m); solid line, *Bromus rigidus*; dashed line, *Avena fatua*.

7) Lush growth in the protection of sideless cages strongly contrasted with death of stunted (ungrazed) seedlings due to drought in adjacent open bare zones.

8) Total removal of isolated *Salvia* thickets left a bare zone with no grass the first year and only stunted, sparse growth the second; this fact indicated some persistence of toxic effect where there was no cover for animals.

9) Gross differences in grassland inhibition characterized shrub thickets of different species, *Salvia leucophylla* being distinctly more effective than *Ceanothus cuneatus, Adenostoma fasciculatum*, or *Artemisia californica*.

10) The areas beneath the cover of artificial shrubs of nontoxic *Ceanothus* branches within grassland, heavily inhabited by *Peromyscus* and *Sylvilagus bachmani*, were barren of herbs after 2 years, but after 7 years there was no diminution in the size or density of herbs beyond their limits.

From these facts we conclude that (i) early stunting of grass seedlings by toxins and their eventual failure in the bare zone require the moderate stresses of periodic drought characteristic of normal conditions of rainfall in southern California (without protection such as cage roofs); (ii) grazing by small animals in exposed grassland without the support of phytotoxins does not result in bare zones; (iii) very favorable conditions of soil moisture can counteract phytotoxic and animal effects combined; (iv) the pattern of bare zones is neither initiated nor maintained by animals acting alone; (v) the pattern is maintained by phytotoxins even where animal pressure is lacking and may be initiated largely by inhibition of germination.

Bartholomew has criticized our failure to demonstrate sufficient concentrations of *Salvia* terpenes in soil to give positive inhibitory results in vitro. These toxins must act in our bioassays within 48 to 72 hours under optimum growing conditions, but their activity in the field extends over several weeks of slow growth under normal periodic drought stress. Stunting of herbs in the first few weeks of growth in the absence of grazing cannot be otherwise explained. We have recently obtained good positive results (*3*) from in vitro bioassays of soil from *Artemisia cali-*

*fornica* and *Arctostaphylos glandulosa* stands which also produce bare zones. Bartholomew, in not addressing himself to the stunting and differential exclusion of species from the inhibition zone, where both his and our data show minimum animal activity, completely overlooks the strong cumulative effects of even low concentrations of toxin. In failing to identify the grass species in his exclosures and using commercial grain rather than seeds of the pertinent grasses in his baiting experiments, he obscured important facts of differential impact by both animals and phytotoxins.

Complexes such as those described here do not yield to measurement of single factors and correlated plant responses. The studies here briefly summarized comprise a selection from many undertaken in an attempt to evaluate the relative influences of factors such as animal behavior, herb and seed palatability, susceptibility of herbs to toxins, variation in microsites, shrub structure, and chemistry of shrub toxins as they may participate in the development of bare zones adjacent to thickets of *Salvia leucophylla*. There is no universal solution to a problem with so many variables, and certainly there is no acceptable simplistic one.

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### References and Notes

1. B. Bartholomew, *Science* **170**, 1210 (1970).
2. C. H. Muller, *Bull. Torrey Bot. Club* **93**, 332 (1966); *Rec. Adv. Phytochem.* **3**, 105 (1970); in *Biochemical Coevolution*, K. L. Chambers, Ed. (Oregon State Univ. Press, Corvallis, 1970), p. 13; ——— and R. del Moral, *Bull. Torrey Bot. Club* **93**, 130 (1966).
3. J. P. Halligan and C. H. Muller, in preparation; C.-H. Chou and C. H. Muller, in preparation.
4. The several studies here drawn upon were supported by NSF contracts GB-149, GB-4058, GB-6814, and GB-14891 and by the Faculty Research Committee, University of California, Santa Barbara. We gratefully acknowledge the work of B. L. Haines, D. T. Bell, and I. Gardner as field assistants.

22 April 1971

All of the points presented by Muller and del Moral as evidence for chemical inhibition could be subjected to experimentation. However, as presented the points are not conclusive evidence for chemical inhibition. My specific criticisms of their points are as follows.

1 and 2) In addition to chemical inhibition the differences in species composition away from shrubs may involve an interaction of selective foraging and grazing with interspecific competition of grass species (*1*).

3) The dense growth of annuals in natural shade conditions illustrates the obvious point that drought is involved in any temporal and spatial patterning of annual plants and says nothing about either animal or chemical inhibition.

4 and 5) The fact that there is seedling mortality in the bare zone and that, even if seedlings are protected, there is an initial lag in the growth rate over that in the grassland should not be surprising. The physical and biotic environments under which the germination takes place are very different. One is a hard, bare mineral soil which has a reduced soil microflora (*2*), whereas the other is a soil with a much higher organic content, which is covered with a layer of organic litter from previous years. These differences will influence both the availability of water to the seedling roots and the microclimate of the blades.

6 and 7) I have previously shown (*3*) that with both *Salvia leucophylla* and *Baccharis pilularis* annuals will grow in the bare zone in wire mesh exclosures that are closed on all six sides, but these annuals are essentially eliminated from exclosures that have a top and bottom but are open on all four sides. These results do not agree with the statements of Muller and del Moral.

8) The removal of shrubs shows that there is a residual effect after both the toxin source and the animal domicile are removed. The initial lack of grass and subsequent stunting would be the same as in points 4 and 5 above. The fact that there was a gradual change says nothing about the factors that caused the phenomenon but merely that these factors have been removed.

9) In addition to differences in toxicity some of these plants contain volatile toxins and others contain water-soluble toxins that would not be effective beyond the crown of the shrubs (at least on the uphill side of the shrubs). Also, there may be differences in the suitability of these shrubs as domiciles for animals and differences in the climatic and soil conditions under which each shrub grows. These and other factors would interact to make a spectrum of grassland inhibition between different species of shrubs and adjacent grassland.

10) Artificial shrubs (an isolated pile of *Ceanothus* branches a few meters in diameter) are hardly comparable to a shrub community in its suitability as an animal domicile and could hardly be "heavily inhabited" by the rabbit *Sylvilagus bachmani*.

In regard to my comment on differences in concentration of volatile toxins in bioassays and the concentrations found under field conditions, a difference in time of action cannot be equated to differences in concentration without quantitatively showing that this is the case. I look forward to the forthcoming results of "in vitro bioassays of soil from *Artemisia californica* and *Arctostaphylos glandulosa*." The first of these plants produces volatile toxins and the second produces water-soluble toxins. Muller and co-workers should also show a gradient of soil toxicity between the edge of the shrubs and the grassland.

In conclusion, Muller and del Moral appear to agree with the position I expressed in my report (*3*): "The extent of the relative contribution of chemical and animal inhibition to the formation and maintenance of the bare zone needs further investigation." It is likely that this overall question has no universal answer even for a single kind of shrub at a given locality, much less for different shrubs in different localities. Thus to insist on, for example, chemical inhibition as the universal answer for such a phenomenon would undoubtedly be unwarranted. Although volatile plant toxins might be the main factor in the production and maintenance of the bare zone and inhibition zone adjacent to some species of shrubs, an interaction of other factors will produce the same results in cases such as that of *Baccharis pilularis* which lacks volatile plant toxins. In order to dissect a complex ecological phenomenon of this nature, it is necessary to hold constant as many factors as possible and to measure the effect of single variables upon the system. Counts and measurements are as necessary in this as in other fields of scientific investigation because not all workers may agree on what is obvious about a given situation.

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### References

1. J. L. Harper, *Brookhaven Symp. Biol.* **22**, 48 (1969).
2. W. H. Muller, *Bot. Gaz.* **126**, 195 (1965).
3. B. Bartholomew, *Science* **170**, 1210 (1970).

24 May 1971