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In search of allelopathy: an eco-historical view of the investigation of chemical inhibition in California coastal sage scrub and chamise chaparral

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RICHARD W. HALSEY (Southern California Chaparral Field Institute, P.O. Box 545, Escondido, CA 92033). In search of allelopathy: an eco-historical view of the investigation of chemical inhibition in California coastal sage scrub and chamise chaparral. J. Torrey Bot. Soc. 131. 343–367. 2004.—Allelopathy between plants, whereby one species influences another by chemical means, has been speculated upon since the Greeks. During the second half of the twentieth century, southern California was the focal point of allelopathic research by several influential investigators. Frits Went suggested *Encelia farinosa*, a common desert shrub, inhibited annuals from growing under its canopy by chemical inhibition. Reed Gray and James Bonner conducted further investigations. Cornelius H. Muller questioned the allelopathic explanation for *Encelia*, but later felt chemical inhibition was the cause for vegetation patterns found in both southern Californian coastal sage scrub, primarily around *Salvia leucophylla* and *Artemisia californica*, and *Adenostoma fasciculatum* (chamise) chaparral. Various investigators challenged Muller's conclusions, but Muller remained convinced allelopathy was an important ecological variable in southern California's shrublands. Muller's passionate belief in his scientific models led him to ignore contrary evidence, yet his dedication to science and the education of his students inspired many. Allelopathy remains a controversial topic today despite hundreds of investigations because of the difficulty in isolating all the possible variables affecting plant growth.

Key words: allelopathy, seed dormancy, coastal sage scrub, chamise chaparral, bare zone, chamise-fire cycle, multiple working hypotheses, bioassay.

Plants and microorganisms produce a variety of chemicals, as byproducts of their metabolic processes, capable of either inhibiting or encouraging the biological actions of other organisms, including their own species. Understanding allelopathy is an attractive research goal, especially when considering its potential application to the commercial production of natural herbicides.

The notion of plants influencing their neighbors has been around since the ancient Greeks. By the mid 1800's, the hypothesis that plants influenced each other by chemical means became widely accepted, especially after the work of French botanist, A.P. DeCandolle in 1832. Hans Molisch, an Austrian plant physiologist, introduced the term ''allelopathy'' to identify the process in 1937. The word is based on the Greek *allelo* meaning ''one another'', and *path* for ''suffering'' or ''disease.'' Molisch (1937) applied a broader definition by including both negative as well as positive impacts of chemical interactions occurring between plants, as well as microorganisms. However, by the time Molisch coined the word, the idea had lost considerable scientific support in favor of a different hypothesis explaining the causes of vegetation patterns; the depletion of soil nutrients by competition. Allelopathy became a troublesome variable for the soil depletion model because it created an intolerable degree of uncertainty. It is difficult enough to develop conclusions about plant competition based on soil nutrients without worrying about some unknown chemical interaction influencing experimental results. Consequently, the notion of chemical influence was generally ignored. Yet the subject continued to be of interest to many and was given a new life in the deserts of southern California.

Desert Symbiosis. During field trips into southern California's deserts, Caltech botanist Frits Went noticed there was a strong tendency for annual plants to locate themselves under or near larger, woody species. For desert wildflowers, he felt physical factors, such as shading or soil conditions, did not adequately account for the germination and vegetation patterns he observed. Went decided to quantify his ideas in

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1942 with a study of two small shrubs. One, the dusty-gray *Ambrosia dumosa* (burro-weed) with low growing, brushy stems, harbored an abundant array of annuals under its shady canopy. The other, *Encelia farinosa* (brittlebush), was an erect, sparsely stemmed shrub with little more than bare ground below. If *Encelia* shrubs were dead, however, the frequency of annual growth beneath its skeletal frame increased dramatically. In discussing his observations, Went (1942) wrote,

> . . . there is a specific effect of shrubs, which must be ascribed to specific materials given off by them. These materials seem to be produced especially by the living shrub and they determine the specific occurrence of definite annuals. No guess as to the nature of these materials will be given; this can safely be postponed until experimental evidence is available.

The Substance. In 1948 Went's investigation attracted the interest of plant physiologist James Bonner, a Caltech colleague of Went. Bonner pursued his interest by accepting a student's research proposal to investigate the chemical cause of *Encelia's* inhibiting qualities. Working in Bonner's lab, Reed Gray analyzed the plant's roots, leaves and chemical extracts in an effort to identify the toxic principle's source.

Gray and Bonner (1948a) first tested the roots by growing barley, tomatoes and *Parthenium argentatum* (guayule) in sand next to *Encelia*. No significant effects were observed. The next test involved placing various quantities of chopped *Encelia* leaves on the surface of sand in pots containing young tomato plants. This time, after watering through the leaves for eleven days, inhibition was observed. The greater the concentration of *Encelia* leaves, the less the tomato plants grew. Interestingly, when the same experiment was tried with garden soil instead of sand, the level of inhibition was reduced. In a final test, 12-day-old tomato seedlings were exposed to an aqueous extract made from whole *Encelia* leaves. All the plants died within three days. When chopped leaf extract was used, three-fourths of the plants died within 24 hours. A comparable tomato leaf extract proved to have little affect on seedlings.

Gray and Bonner wrote, ''The results presented above show conclusively that there is a powerful inhibitor of growth of tomato seedlings contained in *Encelia* leaves.'' Adding later, ''The presence of the growth inhibitor in the leaves of *Encelia*, may have ecological importance in relation to the fact that only a few specimens of desert annuals are to be found growing in close relationship with the *Encelia* shrub on the desert.''

After further work, Gray and Bonner (1948b) isolated and synthesized the shrub's toxic principle, 3-acetyl-6-methoxybenzaldehyde. The synthesized material demonstrated the same inhibitory effects as the natural product. However, despite experimental results indicating a toxic affect, the scientists maintained a healthy skepticism. They made clear that actual ecological applications in the field remained untested.

A Paradox. With the soil nutrient depletion model dominating plant ecology, the notion of allelopathy being responsible for desert vegetation patterns attracted very little attention except from a young botanist named Cornelius H. Muller from the University of California, Santa Barbara. Based on his own experiences, Muller regarded Gray and Bonner's conclusions as ridiculous and decided to conduct a detailed study of his own with the intent of demonstrating that their laboratory results were artificial and did not apply to the field (Bruce Mahall, pers. com. June 03). After extensive work, Muller published his experimental results and conclusions in 1953. Ironically, the young man's decision to challenge Gray and Bonner would mark the beginning of a renaissance for allelopathy and permanently attach his name to the field.

C.H. Muller received his B.A. and M.A. in botany at the University of Texas, Austin in 1932 and 1933 and his Ph.D. in 1938, from the University of Illinois. He established his early reputation by focusing on the genus *Quercus* (oaks), doing most of his work on species found within Texas and northern Mexico. He was one of the first investigators to recognize the propensity for the genus to hybridize. Muller thoroughly enjoyed collecting specimens and studying plants where they grew and placed a high value on detailed field observations. For him, understanding the individualistic environmental tolerances and characteristics of species in nature was a fundamental part of any botanical inquiry. Consequently, he saw Gray and Bonner's reliance on sophisticated chemical and analytical laboratory methods as overly narrow and too removed from the real world of plants to provide much insight (Mooney 1999).

To produce evidence for his interpretation, Muller (1953) expanded Gray and Bonner's laboratory studies. In addition to watering tomato seeds with *Encelia* extract, he included a companion experiment with an extract from the other plant Went studied, *Ambrosia dumosa* (burroweed). His results confirmed the toxicity of *Encelia*, but revealed an interesting paradox. The extracted chemicals from *Ambrosia*, the plant harboring large numbers of desert annuals, were more injurious to seedlings than the compounds from *Encelia*. How could one species producing extremely toxic substances support ''a miniature flower garden'' beneath its canopy whereas another, less harmful plant successfully inhibit all undergrowth?

Muller proposed a simple explanation for the inconsistency between lab observations and what was actually occurring in the field. Annuals failed to grow under *Encelia* because of poor soil conditions, not due to chemical toxins. On the other hand, *Ambrosia* encouraged annuals because of humus-rich soil that was produced from the accumulation of leaves dropping from the plant's low hanging branches. Muller also suggested that toxic chemicals leaching into the ground were irrelevant since soil microorganisms likely destroyed them before having an impact on germination. Gray and Bonner mentioned the denaturing role of microbes in rich soils as well, but considered it unimportant since *Encelia* only grows in sandy, well-drained locations. ''Since shrub-dependent herbs will not grow in the open except upon decaying remains of former shrubs,'' Muller wrote, ''there is no reason to expect them to grow upon soil covered by, but little changed by, *Encelia*.''

In concluding his discussion of results, Muller wrote an eloquent statement reflecting the difficulties in studying plant ecology.

> The natural habitat, even in a relatively simple community of the desert, is far too intricate a system of influences and factors, physical and biological, to hope that there may be found a single factor controlling the complicated life of a perennial species. An explanation, when it is arrived at, will be at least as intricate as the situation it seeks to describe.

Muller's paper was dramatically different from Gray and Bonner's in both objective and tone. While Gray and Bonner were following up Went's investigations and narrowly focusing on one species, Muller widened the inquiry in order to disprove a hypothesis. In doing so, he contributed an important component of the scientific process: clarifying the reasons for an observed phenomenon by pointing out other variables effecting experimental results. With the systematic precision of a well-prepared district attorney, Muller presented his case and supported his hypothesis; soil conditions rather than plant toxins determined the distribution of annuals. However, his prosecutorial style was not helpful in convincing others of his viewpoint. By implying Gray and Bonner were overly simplistic and failed to understand the true complexities of the natural world, Muller diverted attention away from the scientific merits of his paper and toward personalities. It revealed an approach he would use many times in the future when responding to those with whom he disagreed, subtly characterizing their viewpoints as less than enlightened.

''Oh yeah, I remember him,'' Reed Gray said when reflecting upon his career in 2003. After a brief pause, he let out a soft laugh. ''Yes, he was the guy who said we were all wet.''

Unfortunately neither Gray nor Bonner published a response to Muller, but both men vigorously disagreed with his conclusions (Reed Gray, pers. com. July 03). Bonner's opinion is especially significant because of his reputation for being open minded and willing to change if presented with convincing evidence. Frank Salisbury (1998), who went on to become a successful plant physiologist himself wrote, ''Some scientists develop a hypothesis and defend it to their deaths without flinching and in spite of any contrary evidence that might appear. James was not cast in that mold. For him, only the truth mattered.''

C. H. Muller published a follow up manuscript on desert allelopathy with a close, but unrelated colleague, Walter Muller (Muller and Muller 1956). Their paper described further field research and experimental results confirming the presence of toxins in desert plants but also their ineffectiveness as growth inhibitors in the field. Refining the statements Muller made in 1953 about the importance of understanding the complexity of nature they wrote,

> It should be emphasized that the natural habitat is a complex of physical and biological factors that influence growth. Even though distributions may give the impression of an antibiotic effect by some of the individuals, careful investigation may indicate that the situation cannot be explained

> in such a fashion. Environmental influences and the metabolic activities of organisms are complex factors which are variously intermingled, and in most cases it is doubtful whether any one factor would be distinguishable as the primary causative influence.

So it appeared allelopathy was once again relegated to its status as a rejected hypothesis. It would be a very short period of exile.

A New Set of Circumstances. Between 1957–58 inquisitive students from the University of California, Santa Barbara kept asking their botany professor about unusual bare zones they saw around stands of *Salvia leucophylla* (purple sage) during field trips to a coastal sage scrub plant community in the Santa Ynez Valley, northwest of campus. The ''halos'' of naked ground were so striking it was as if they had been created by herbicide. Bare areas were observed around *Artemisia californica* (California sagebrush) as well. What was preventing plants from growing in these zones? Could *Salvia* or *Artemisia* themselves be responsible?

The students' professor was in a unique position to evaluate the possibility because he was already familiar with allelopathy. He had just completed a major paper on the subject concluding it was not responsible for vegetation patterns elsewhere. But this was different. It was a new setting, a different group of plants. So demonstrating a remarkable level of intellectual flexibility, he decided to re-examine the possibility and let the data speak for itself. The professor's name was C. H. Muller.

As he had done with *Encelia*, Muller began collecting large amounts of data from the field with special attention to surrounding environmental conditions. But demands of the new endeavor and his responsibilities at the university were consuming an inordinate amount of time, keeping him away from his family on weekends. So with the gentle urging of his wife Katherine, and recently available grant money, he hired an assistant, Bruce Haines, a friend of the family who had just transferred to the University of California at Santa Barbara as an undergraduate. Haines' primary task was to travel out to the bare zone sites each weekend and collect data. Every Monday morning, Haines appeared in Muller's office and was quizzed in detail about his observations.

''The game became one of me trying to anticipate all of his questions and come up with answers before we met,'' Haines (pers. com. May 03) recalled. ''I would think it all through while driving back from fieldwork on Saturday or Sunday. It was pretty stressful at times, but he really coached me well on how to become a successful observer and thinker. He taught me how to do science, something I will always be grateful for.''

Along with demanding accurate record keeping and directing his students to solve their own problems, Muller stressed Chamberlin's model of *multiple working hypotheses,* a process designed to help prevent personal attachment to a favored theory. ''After awhile, I realized Muller wasn't interested in telling me what to do. He wanted me to figure everything out for myself,'' Haines added. ''He was constantly drilling into my head Chamberlin's model, reminding me that I needed to keep emotions out of my work.''

In a paper read before the Society of Western Naturalist in 1889, Thomas C. Chamberlin (1890) described the critical role played by formulating multiple working hypotheses in discovering ''new truths.'' Chamberlin's basic point was that if an investigator focuses on a single, original hypothesis, which seems to be satisfactory for a particular phenomenon, he has a tendency to view the explanation paternalistically. It becomes his ''intellectual child.'' Affections for such a favored hypothesis become a blinding influence.

''Love was long since represented as blind,'' Chamberlin wrote, ''and what is true in the personal realm is measurably true in the intellectual realm. Important as the intellectual affections are as stimuli and as rewards, they are nevertheless dangerous factors, which menace the integrity of the intellectual process.'' With experimental data in mind, he added, ''There is an unconscious selection and magnifying of the phenomena that fall into harmony with the theory and support it, and an unconscious neglect of those that fail of coincidence. There springs up, also, an unconscious pressing of the theory to make it fit the facts, and a pressing of the facts to make them fit the theory.''

Muller's rejection and then decision to re-examine allelopathy as a cause for vegetation patterns demonstrated an important application of Chamberlin's advice. He had not permanently discarded the allelopathic model, but rather retained it within his own quiver of multiple working hypotheses.

The Results. With Haines collecting in the field, Muller finalized laboratory tests in the greenhouses at UCSB. The experimental design was not the same as his effort in 1953 with desert plants because he was hypothesizing a different delivery system for toxic agents; evaporates into the air rather than rain-drip off leaves.

To set up appropriate germination tests or bioassays to measure possible toxic effects, leaves of both *Salvia* and *Artemisia* were crushed and placed in separate dishes. Moist filter paper resting on a wire mesh an inch and a half above the leaves was sprinkled with cucumber seeds. The entire arrangement was then covered and sealed. Two days later Muller et al. (1964) observed, ''In every instance volatile materials emanating from the crushed leaves radically inhibited seedling root growth.'' Bioassays using sliced instead of whole leaves on *Cucumis sativus* (cucumber) and *Avena fatua* (wild oat) seeds showed similar results.

Muller recognized sealed containers in a lab could not replicate natural conditions in the field, so he attempted to design a delivery pathway more closely resembling the natural distribution of volatile materials into the soil. He suggested dew formation.

By using cooling coils, dew was condensed from an atmosphere in which *Salvia* was growing. The dew was then collected and used to soak cucumber seeds. After several unsuccessful trials, Muller was able to show reduced root growth. He concluded, ''Although field experimentation is still to be performed, it appears that whole plants of *Salvia leucophylla* release a volatile substance that condenses in dew and that significantly inhibits the growth of cucumber roots.''

The effect Muller was classifying as an allelopathic response in the field was dramatic. He suggested that the volatile substances from these aromatic species appeared to be responsible for inhibiting growth of plants as far as 27 feet away. If true, allelopathy in coastal sage scrub would be considered one of the most remarkable ecological interactions on earth.

The coastal sage scrub ''bare zone'' model was presented in Science under the title, ''Volatile Growth Inhibitors Produced by Aromatic Shrubs.'' The paper was considered important enough to be the subject of the magazine's cover photo (Fig. 1). The picture is an aerial shot of coastal sage scrub stands of *Salvia leucophylla* and *Artemisia californica* bordering grassland. Surrounding the clumps of sage were the characteristic ''halos'' of bare ground. The photo's title read, ''Chemical Plant Competition.''

Along with Walter Muller, Bruce Haines was listed as a coauthor to the 1964 paper, a significant accomplishment for a young undergraduate.

Cowpaths. It was not long before others began examining the data and making their own conclusions, as Muller had done with Gray and Bonner's work several years before. In May, four months after publication, Philip Wells (1964) from the University of Kansas wrote a critique listing several alternative explanations for the bare zones, using details of the Science cover photo as a focal point. ''The interconnecting and in part rectilinear character of the network of white lines does not suggest origin by chemical inhibition,'' Wells suggested. ''An equally good explanation is that most of them are cattle trails.''

In referring to Muller's suggestion that the shrubs were invading the grassland by way of inhibiting grass plants, Wells pointed out the top center of the photo where there were over 100 smaller shrubs scattered in the open grassland without grassless ''halos.'' Why would isolated bushes be without bare zones? Wells wondered. This suggested the halos actually appeared long after *Salvia* had expanded into the grassland not as a preparatory step to their initial invasion.

Wells also noted what he saw as failures in Muller's experimental design such as use of cucumber seeds instead of natives, testing procedures remote from field conditions, and ignoring the impact of herbivores in bare zone creation. Ironically, the same criticisms Muller had leveled at Gray and Bonner. Wells concluded by saying the idea of chemical inhibition emanating from the sages was an interesting idea, ''but it seems premature to imply that antibiosis ranks high in the complex of ecological factors determining the vegetation patterns depicted in the cover photograph.''

As is often the case with criticisms of published papers, Muller and Muller (1964) were given the opportunity to write a response and have it printed immediately below Well's letter. The two men dismissed several of Wells' criticisms as not pertinent and repeatedly made the point that their paper was only an initial report providing ''scant space for monographic completeness.'' They also discounted concerns over the lack of data relating to the role of cattle and herbivores because to include such information

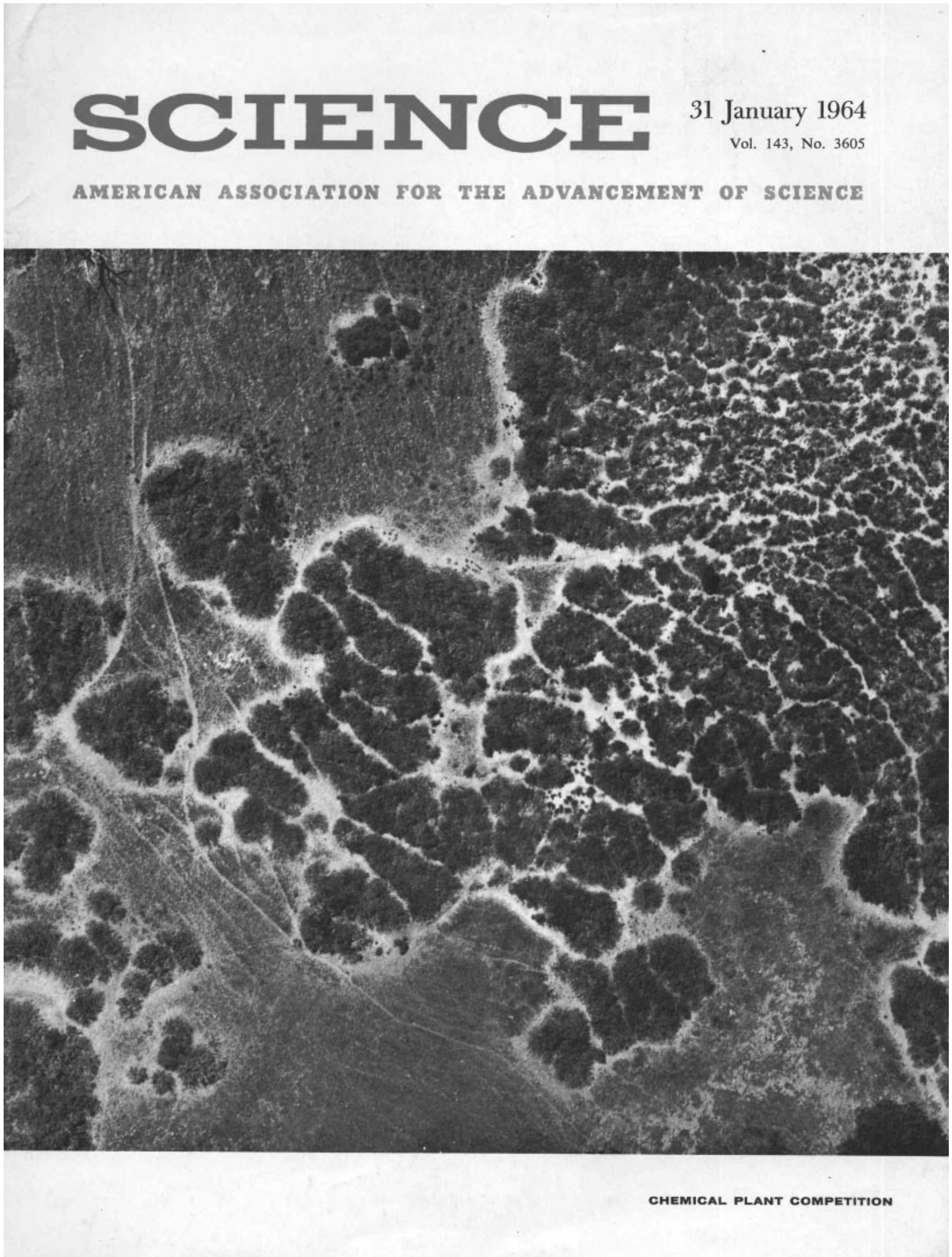

FIG. 1. Cover Photo of Science, January 31, 1964. Mosaic pattern created by bare zones around *Salvia leucophylla*, *S. apiana*, and *Artemisia californica*. Reprinted with full permission from 1964 Science 143, cover. Copyright AAAS.

adequately would ''require several pages and is being saved for the summary treatment, which will not be submitted until all possible factors have, so far as is practical, been investigated, evaluated, and fitted into the complex.''

Muller and Muller were not, however, willing to ignore the comment about cowpaths. They described observations comparing the presence of cow droppings between grassland and bare zones revealing more per square meter in ''remote uninhibited grassland'' than any other locale. ''It is clear from these figures,'' they wrote, ''that cows go where grass is and that they do not linger about shrub patches trampling down depauperate herbs over wide areas. . . The great broad white zones of bare ground both inside and outside the shrubs are curved (not ''rectilinear'') and *can scarcely be explained* except as inhibition.'' The roles of smaller herbivores such as sparrows were dismissed as well because ''*never do they* produce a bare area unaided by initial biochemical inhibition'' (italics added).

In their response, Muller and Muller were treating biochemical inhibition as a forgone conclusion. According to their interpretation, inhibition was the only reasonable explanation for bare zone formation, a pattern that ''never'' occurs without it. In defending their hypothesis with such determination, they were demonstrating a confidence unjustified by available data. ''The criticism,'' they continued, ''that cowpaths are visible within the shrub zone and may therefore be responsible for the patterning involves the most surprising failure to observe. Steps are being taken to preserve an area of the more instructive patterning. We are desirous of showing this to anyone who will look.''

Wells had looked and came away with a different viewpoint. What was not revealed was the intimate awareness Wells had with not only the site but also Muller's investigation. Wells (pers. com. May 03) had been Muller's sabbatical replacement in 1958. He spent time in the summer of 1959 with Muller in Happy Canyon, the Santa Ynez Valley study site, debating the cause of the bare zones and the role of herbivores.

''He playfully asked me why the bare areas surrounded the soft chaparral,'' Wells remembered. ''From the start I said it was due to animal activity, and he just smiled in his fatherly way. He had a good four years to think about the role of animals, but chose to ignore it.''

Although the ''cowpath'' explanation would ultimately prove to be wrong, the possibility of other animal activity was important enough to warrant more consideration than Muller accepted. Muller also neglected factors he suggested in 1956 as capable of eliminating the effectiveness of inhibiting chemicals such as ''microbial activity, adsorption to soil colloids, or inactivation under xeric (dry) conditions.'' The omissions are especially curious in light of his criticism of Gray and Bonner's work, suggesting, as he said, a ''single factor'' capable of controlling vegetation patterns under *Encelia*. By discussing only chemical variables in his paper, Muller's scientific methodology and conclusions were vulnerable to the same weaknesses he criticized eleven years before.

Further Clarification. Muller (1965) continued his research by isolating the volatile terpene compounds in *Salvia* and identifying them as cineole and camphor. He realized the artificial dew technique was not the best model for the natural deposition of these compounds so he searched for another. Since both cineole and camphor have a high affinity for oils, Muller hypothesized the compounds could *adsorb* or collect on the surface of the fatty cuticles of nearby seedlings directly from the atmosphere, inhibiting or terminating their growth. This contrasts with *ab*sorption, where a substance is pulled into some region rather than remaining on the surface. He experimented by exposing paraffin wax to crushed *Salvia* leaves and found the solid wax readily adsorbed the volatile terpenes from the air. The direct adsorption model appeared more realistic because volatile compounds would be much more concentrated during warm temperatures in the summer than during cooler, dew-producing periods.

However, with additional research, Muller rejected this hypothesis as well. In a paper coauthored with Roger del Moral in 1966, it was suggested the volatile compounds were adsorbed by colloidal particles in the soil first. The toxins were then dissolved by the first winter rains and adsorbed by the seedlings. Their supporting experiments were straightforward and clearly demonstrated soil adsorption of terpenes released from *Salvia leucophylla*. Muller and del Moral (1966) hypothesized that during late spring and summer months, when the aroma of sage is most obvious, toxic terpenes collect on the surfaces of soil particles and remain unchanged until moisture dissolves them. As seedlings germinate, the toxins are transported through cell membranes and into the plant body, inhibiting or terminating growth, possibly through the suppression of mitosis.

In contrast to the response to Wells and more in keeping with the multiple working hypothesis model, Muller and del Moral included a clear statement regarding the impact of variables other than allelopathy.

> It must be emphasized, however, that inhibition by 'last year's' terpenes may be only one of a series of factors subtly interplaying to produce the observed patterning of herbs about *Salvia* shrubs. Perhaps a combination of several factors is necessary to produce the phenomenon. We have a high degree of confidence that *Salvia* terpenes are a mandatory condition, but we would not be surprised if small animal activity, soil type, semi-arid climate, and the like proved at least significant contributors to the phenomenon.

Muller published his full description of sage scrub allelopathy in the fall of 1966, providing an excellent summary of his work thus far. He presented detailed descriptions of both laboratory and field work and speculated upon the origin of allelopathic compounds. As a testament to his resourcefulness, Muller was able to obtain the first gas chromatograph on campus, normally the domain of the chemistry department. This allowed chemical analysis of the vapors produced by *Salvia*. Factors concerning bare zone patterns were also delineated. The width of each zone on the uphill side of a *Salvia* thicket was about equal to those on the downhill side. This was considered evidence supporting vapor transport of allelochemicals rather than moisture because water would wash toxins off the plant and send them down slope.

Unfortunately, the precise techniques used to measure the effects of animals continued to remain vague despite reassurances they remained an ongoing research focus. After describing a simple transect observation showing minimal effects from grazing, Muller (1966) briefly concluded, ''although grazing by small animals may augment the effect of differential inhibition, it is not capable of initiating or maintaining unaided the observed phenomenon. Our study of animal influences continues with increased emphasis.''

In speculating upon the evolutionary history of inhibitory mechanisms, Muller suggested ''that all, or at least most'' of plant-produced inhibitors, ''originated as metabolic by-products of the plants in which they are found, regardless of what functional role they may now play.'' In order to rid themselves of such by-products, plants such as *Eucalyptus* and *Salvia* produce highly volatile compounds that are released into the atmosphere in large quantities. The possibility of inhibiting a competitor, resisting a pathogen, or repelling a browsing animal with such excretions is an ''added advantage.''

Volatile substances released by *Salvia* and other aromatic shrubs in coastal sage scrub are complex compounds. In terms of energy required for a plant to produce them, they are quite expensive. This suggests there may be reasons other than simple excretion of wastes to account for their presence (Bruce Mahall, pers. com. June 03). Proving original causation for any plant or animal trait, however, is extremely difficult if not impossible. Such thoughts would seem to be relatively unimportant when considering the entire allelopathic model, but Muller was willing to mount a passionate defense when questioned. Dennis Breedlove and Paul Ehrlich (1969) experienced Muller's intensity when they briefly referenced his view discounting ''the primary role of plant biochemicals as herbivore poisons'' in a short article discussing predation on lupine flowers by butterfly larvae.

After calling Breedlove and Ehrlich's notation of his idea ''irrelevant'' to their article, Muller (1969a) added, ''I appreciate their publicizing my viewpoint on this basic evolutionary question, but I feel that the isolation of this reference in a report on a subject so slightly related must necessarily have left most readers wondering why it was included at all.''

After discussing evidence supporting his viewpoint, Muller concluded, ''. . . the toxicity to animals of these metabolic wastes, no matter how important eventually, is subsequent and secondary to their elimination from protoplasm. No useful purpose is served by simplifying this explanation beyond the limits of reality.''

Finding Allelopathy in the Chaparral. Convinced allelopathy accounted for vegetation patterns in coastal sage scrub, Muller and two of his students, Ronald Hunawalt and James McPherson (1968) turned their attention to another familiar phenomenon, the lack of herbs under mature stands of chaparral and the sudden surge in seed germination after fire. ''It is quite clear,'' they wrote, ''that, except for the bulb-forming perennials, the explosive herb growth with which we are concerned has its basis in temporary relief from some control of seed germination.''

For Muller's team, the ''control'' was most likely chemical because the bare zone phenomenon found in coastal sage scrub also appears under and adjacent to chaparral shrubs. In referencing an unpublished study from his lab of two common manzanita species, Muller et al. wrote, ''Among the non-aromatic chaparral shrubs, *Arctostaphylos glauca* and *A. glandulosa* have recently been studied in detail and shown to inhibit herbs for a distance of 1 to 2 m from the edge of the drip lines of their canopies.''

However, instead of merely *inhibiting growth* of herb and shrub seedlings as hypothesized for bare zone allelopathy in sage scrub, Muller et al. proposed a distinctly different model for chaparral, the *suppression of seed germination* by allelopathic compounds. Since chaparral shrubs do not release volatile chemicals into the air, as is the case for coastal sage scrub species like *Salvia*, another mechanism was needed to account for the transport of toxins. Muller and his students found it in water-soluble compounds on the foliage of dominant chaparral shrubs like *Adenostoma fasciculatum* (chamise) and *Arctostaphylos glauca* (Eastwood manzanita). They proposed the same delivery system Gray and Bonner suggested for *Encelia*, water falling off leaves and stems during rainstorms. They suggested that toxic compounds washed off plants and accumulated in the soil, thereby chemically inhibiting seeds from germinating. When fire swept through chaparral, toxin-producing shrubbery was removed, toxic leaf litter burned away, and accumulated soil toxins were denatured by heat. No longer chemically restrained, seeds were free to germinate as soon as water was delivered during the next rainstorm, causing the post burn environment to explode with wildflowers and shrub seedlings.

In reviewing their preliminary findings, Muller et al. wrote, ''The chaparral fire cycle thus emerges as a sequence of events consequent to the destruction of toxins and their shrub sources by fire. This is followed by the germination of seeds no longer inhibited by shrub toxins.'' After reviewing additional details, they concluded confidently ''allelopathy is the primary basis of the herb fire cycle in California chaparral.'' McPherson and Muller (1969) published a complete report on what later became known as the ''chamise-fire cycle'' model the following spring.

McPherson and Muller's first task was to eliminate variables other than chemical. After conducting experiments and concluding nutrient depletion, shading, moisture and oxygen levels in the soil were not significant factors in preventing germination, they turned their attention toward fire. Soil under chamise shrubs was collected (with leaf litter removed) and heated at various temperatures then watered. As temperature levels were raised, more seedlings emerged, with the greatest increase in germination appearing between 80–90° C (175–195° F). ''Since heating of the soil and litter mass which contains the seeds brings about increased germination,'' McPherson and Muller concluded, ''it is strongly suggested that the heat degrades some substance in the soil which otherwise suppresses germination.''

To eliminate soil as a variable and test the effect of heat alone, seeds of nine native species were heated in ovens and allowed to germinate on wet sponges covered with filter paper. After running experiments at three different temperatures (70°, 80°, 90°C, plus a control), McPherson and Muller wrote, ''No species found to be stimulated to germinate in the soil heating experiment could be so stimulated by direct heating of its seeds.''

The largest portion of their study focused on establishing the level of toxicity of suspected chamise allelochemicals. Bioassays were conducted in a manner similar to those used in previous experiments. All parts of the plant were tested, but leachate of intact aerial portions (leaves on branches) provided the most positive results. The solutions were prepared by sprinkling water over chamise foliage and concentrated to various strengths. Although seeds treated with normal leachate and then concentrated 1.3 times did show slightly depressed growth patterns, the results failed to demonstrate statistically significant differences when compared to seeds moistened with plain water. However, when concentrated 4 to 10 times, leachate collected during natural rainfall reduced growth of *Bromus diandrus* (rip-gut grass) seedlings 34% to 75% respectively. Since *B. diandrus* (species names reflect current taxonomy after Jepson 1993) is non-native and typically not found within undisturbed sites, additional bioassays were attempted with native herbs but the tests were rendered meaningless by mold growth.

The important question of whether or not leachate actually inhibited germination, as Muller's hypothesis suggested, was not resolved.

To measure the effect of shrub cover removal

Table 1. Seedling data collected under shrub cover from exclosure experiments to examine animal effects. Adapted from McPherson and Muller (1969).

Site	Inside fenced control plots under shrubs	Outside fenced area under shrubs
Large exclosure Site III	71 seedlings/m^2	11 seedlings/m^2
Small exclosures Site III	70 seedlings/m^2	11 seedlings/m^2
Large exclosure Site IV	20 seedlings/m^2	4 seedlings/m^2

without fire, a clearing test was conducted. Four 6 × 6 meter quadrants of chamise were carefully pruned all the way to the ground. The clearings were fenced to prevent small animals from entering. Adjacent to each clearing was another fenced plot with undisturbed brush to act as a control. After the first rains Muller and McPherson said they observed an ''explosive growth of native herbs'' in the clearings, averaging 1000/m^2, ''presenting an aspect strikingly similar to that of first-season herb growth following a burn.'' In the control plots under the shrubbery, few seedlings were found, averaging 40/m^2. McPherson and Muller concluded the results fit in well with their chamise-fire cycle model; due to the removal of the chamise, toxins were no longer added to the soil and their effectiveness was drastically reduced by ''mild heating or by passage of time and simple exposure to rain and sun.''

Unfortunately the clearing data was only presented as a list of species rather than a quantitative measure of abundance. Disturbed areas along roadsides can have similar densities of annual species with occasional post fire endemics, but their composition has no relationship to fire. It is impossible to tell if the ''explosive growth'' was dominated by only a few weedy species like *Filago californica* and *Conyza canadensis* (horseweed) or some other combination (Jon E. Keeley, pers. com. July 03). Without quantitative data, the actual impact of artificial shrub clearing remained ambiguous.

The test did provide, however, some insight concerning another variable, animal activity. ''A surprising feature of the clearing experiment,'' they wrote, ''was the relatively large number of herbs in the fenced control areas where the shrubs were intact.'' The description ''relatively large'' was used in reference to their expectation that ''none would be present.''

To examine the effects of animals, samples of herb populations were taken both inside and outside the fenced control areas. The data showed a significant difference between the two areas. At one site in an eleven year old stand an average of seventy seedlings were found per square meter within the fenced plots as opposed to eleven seedlings per square meter in unprotected areas. Investigating further, they set up an additional experiment with five small exclosures (16″ × 16″ × 8″) between chamise shrubs. Unlike the larger exclosures, these were completely enclosed with mesh hardware cloth on top as well as along the sides. After an unspecified period of time, seedlings were counted, showing remarkably similar results to the first data set (Table 1).

It was clear, McPherson and Muller wrote, ''that small animals have an impact upon seedling populations.'' However, the data were dismissed as relatively unimportant with a brief sentence. ''The same results show that some effect of the shrubs themselves is by far the predominant influence.''

Their opinion was based on analysis of data from their large exclosure experiments; areas cleared of shrubbery and ''poorly protected'' against little animals produced over 1000 herbs per square meter, whereas ''well protected'' plots under the cover of shrubbery only produced about 70 herbs per square meter ''which were stunted, depauperate, and failed to mature.'' The chaparral shrubbery, they concluded, was responsible for the depressed herb numbers.

While something different was obviously going on to allow so many seedlings to germinate in the clearings, were the exclosure experiments properly evaluated? Was fencing effective in eliminating animal activity as a significant variable? Were animals spending as much time in the clearings as they were under the shrub cover? Was the composition of plant species in the clearings reflective of actual post-fire flora found in the local area? Would another investigator, a plant physiologist or mammalogist for example, have interpreted the data in the same way?

It wasn't long before someone else decided to find the answers.

The Question of Herbivores. In 1970, Bruce Bartholomew, a graduate student at Stanford

University, published a short paper in Science re-examining the cause of bare zones around *Salvia* in coastal sage scrub. Although Muller acknowledged animals played some role in the maintenance of these areas, he insisted they were not involved in their origin; allelopathy was the primary causative agent of the ''halos'' around certain coastal sage scrub species.

Bartholomew (1970) offered an alternative view. ''In California, the chaparral and coastal sage shrubs form excellent cover for rodents, rabbits, and birds. The adjacent grassland provides poor cover for most of these animals yet furnishes an excellent food supply for grazers and seedeaters. One would expect then that feeding activity of these small animals would be concentrated in grassland areas immediately adjacent to stands of shrubs.''

To little rodents like *Peromyscus californicus* (California mouse) and *Dipodomys agilis* (pacific kangaroo rat) the world is a dangerous place. Cover is critical to their survival since they are on the dietary preference list of local carnivores like coyotes and hawks. Consequently, they have a tendency to remain under shrubbery with only occasional, quick forays into the grassland to nibble on available seeds and new growth. They will stray only as far as they can quickly leap back to safety. Bare zones, therefore, can be viewed as ''calculated-risk terrain'' where rodents have a fair chance of grabbing food without getting caught. And since boundaries between two different habitats are often the richest in terms of food resources, mammal activity is highest where shrubbery abuts grassland (Christensen and Muller 1975b).

To test his theory, Bartholomew set up feeding stations and traps to determine where animals spent their time within the shrub/grassland interface zones of southern California's Los Angeles County and the more northern county of San Mateo. After collecting his data, he found significantly more seed was eaten and animals captured in bare zones than in the adjacent open grassland. To test whether or not there was enough animal activity to produce or maintain the ''halos'', Bartholomew set up various types of one-foot square exclosures in both grassland and bare zone areas. Some exclosures were total, excluding herbivores completely, while others were open on the sides as controls for the effects of shading and dew formation caused by exclosure materials. After a two-year study, areas protected from herbivore entry showed significant plant growth when compared to unprotected areas (Fig. 2). ''The extent of the relative contribution of chemical and animal inhibition of the formation and maintenance of the bare zone,'' Bartholomew wrote, ''needs further investigation. However, annuals will grow in the bare zone with either the presence or absence of volatile toxins if animal activity is excluded.''

Noteworthy, in terms of speculation, is how Bartholomew phrased his conclusions. He avoided saying allelopathy did not exist and that bare zones were primarily the work of herbivores. Rather, he reported his data and left the more general question of causation open to further debate.

Muller was not impressed. He wrote a letter to Bartholomew's department at Stanford questioning the appropriateness of permitting a graduate student to publish a paper questioning such a well-known and well-documented case for allelopathy. The following summer Muller submitted a formal response in Science with his former student Roger del Moral, who was then working at the University of Washington. They listed ten additional observations not mentioned in previous papers as supporting a minimal role for herbivores, and characterized Bartholomew's perspective as short sighted. Muller and del Moral (1971) wrote, ''. . . 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.''

Again, reminiscent of Muller's earlier criticism of Gray and Bonner they concluded, ''There is no universal solution to a problem with so many variables, and certainly there is no acceptable simplistic one.''

Bartholomew had not suggested animals were the ''universal solution'' for bare zones. He had only presented data showing annuals will grow in areas protected from their activity. This was in contrast with some of the definitive statements Muller was making, implying the primacy of allelopathy above all other variables. Although he clearly did not believe ecological phenomena could be explained by a single factor, Muller's spirited defense of his work and zeal to promote chemical inhibition as an important process gave the impression allelopathy was all that really mattered in determining chaparral and coastal sage scrub vegetation patterns. The contradiction

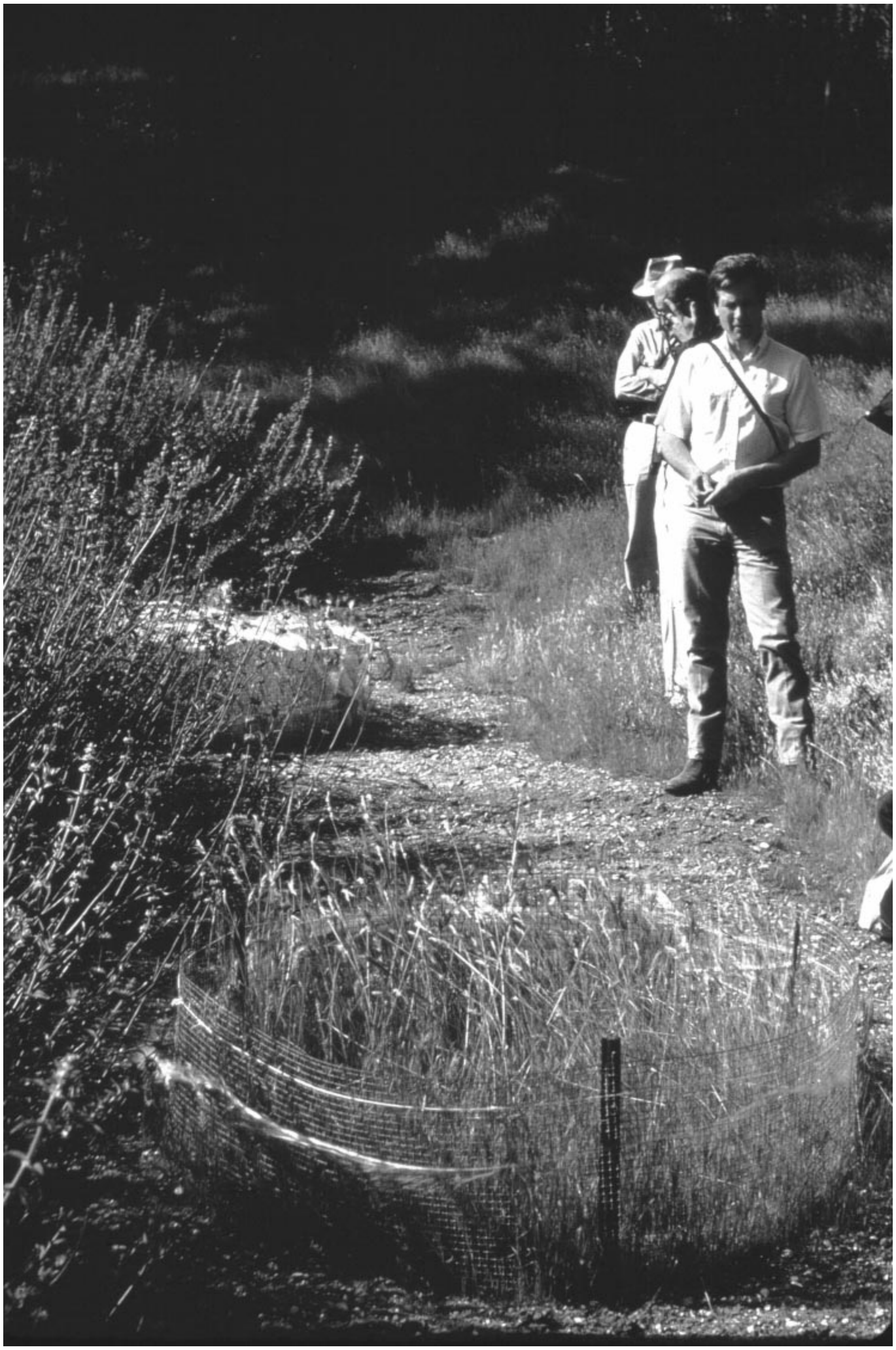

Fig. 2. How Fencing Affects Bare Zone Formation. Exclosures preventing entry by herbivores resulted in a significant increase in herbaceous growth within protected areas. Photo taken in the Santa Ynez Valley, Santa Barbara County, California in 1968. Photo provided by J.E. Keeley.

between these two positions was an issue Bartholomew (1971) alluded to in his rebuttal.

> Muller and del Moral appear to agree with the position I expressed in my report: '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 a 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* (chaparral broom) which lacks volatile plant toxins.

Bartholomew stressed the importance of holding ''constant as many factors as possible and to measure the effect of single variables.'' Because his own data provided evidence this was not properly done in earlier work he concluded, ''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.''

At the invitation of Muller's students, Bartholomew came to UC Santa Barbara to discuss his data and view the study sites on his way to Baja California. Arriving with his major professor Hal Mooney and several other graduate students in the department's field van, Bartholomew participated in lively conversations comparing data and perspectives. Muller himself was not present during the discussions and took a dim view of the entire affair, becoming angry with his students for arranging it. He viewed it as Stanford University questioning the quality of his work as a scientist, rather than a theory's validity. To the students, the visit marked a turning point in their analysis. After examining the available information, consensus was reached. Bare zone formation and maintenance was primarily the work of animals, not chemicals.

''I was in Washington when Bartholomew came down, so I wasn't part of the discussions,'' del Moral (pers. com. June 03) said later. ''But looking back, we didn't fully appreciate the synergistic actions of all the variables.''

The Turning Point. By the time of Bartholomew's research in 1970, Muller and his students had applied the concept of allelopathy to explain a wide range of vegetation patterns in California including:

—The succession of grasslands by aromatic shrub species such as *Salvia leucophylla* and *Artemisia californica* through the release of volatile inhibitors, known as the coastal sage scrub ''bare zone'' model. Other common species identified as toxic and capable of inhibiting growth around them included *Salvia apiana* (white sage), *Salvia mellifera* (black sage), *Heteromeles arbutifolia* (toyon), *Prunus ilicifolia* (holly-leafed cherry), and *Artemisia tridentata* (Great Basin sagebrush) (Muller 1966).

—The ''deteriorated interiors of older stands'' of *Salvia leucophylla* and *Artemisia californica* caused by the concentrated release of volatile toxins (auto-toxicity) (Muller 1966).

—The suppression of germination under the canopy of *Adenostoma fasciculatum* (chamise) chaparral (McPherson and Muller 1969). The dramatic post-fire bloom of herbaceous species is the result of heat denaturing allelopathic chemicals in the soil and the elimination of toxin-producing shrubbery (Muller et al. 1968). This explanation has been identified as the ''chamise-fire cycle'' model.

—The exclusion of certain herb species from grasslands by chemical inhibitors released as decomposition products of grasses like *Avena fatua* (wild oats) (Muller 1966).

—The invasive nature of *Brassica nigra* (black mustard) (Muller 1969). With David Bell, he suggested rainwater leachate from dead black mustard stalks and leaf material containing toxic chemicals could account for the plant's pure stands and the bare zones around them. Their experimental data was based on concentrated rainwash solutions and bioassays as used in previous investigations (Bell and Muller 1973).

After 1970, the swirling controversy over the significance of herbivore activity and the questionable strength of some earlier experimental data forced a more critical examination of allelopathy by Muller's students. Pat Halligan revisited the ''bare zone'' model and Norman Christensen investigated the question of herb suppression within chamise chaparral.

Examining the toxicity of *Artemisia californica* between 1970 and 1972, Halligan (1976) investigated two coastal sage scrub sites near Santa Barbara; one off the mountainous road through San Marcos Pass and the other at La Purisima Mission near Lompoc. Studying the ''halo'' areas made famous by Muller's original paper, Halligan focused on four herb species for evidence of chemical inhibition: native *Madia sativa* (coast tarweed), and non-natives *Hypochoeris glabra* (smooth cat's-ear), *Bromus diandrus* (rip-gut grass), and *Vulpia myuros* (fescue grass).

The important difference between Halligan's work and previous efforts was his experimental methodology. Six different materials were tested as seedbeds for germination studies as opposed to just one, revealing an important variable previously unexamined, the effect of the growth medium on seedling health. Halligan discovered that the cellulose sponge underlying the filter paper used in Muller's lab was actually *toxic* to seeds. By replacing the sponge with cheesecloth and rinsing the filter paper before use, Halligan was able to find a more neutral media. ''All other seedbeds,'' he reported, ''presented problems of toxicity or excessive variability with one or more of the bioassay species.''

Using animal exclosures similar to Bartholomew's, Halligan (1973) also examined the effects of small herbivores. ''By the end of the growing season, the grasses had grown to normal size in the closed exclosures, but had been truncated at ground level in the open exclosures.'' In an additional test, a 48 × 60 ft. protected zone was set up ''extending from within the shrub zone to well within the grassland'' and was ''trapped extensively for small mammals.'' After one year, grassland invaded nearly 1½ feet into the bare zone. Outside the fence, grasses actually regressed from the shrubs, increasing the bare zone by more than 2 feet. Rabbits left their tell-tale feces in abundance where the bare zone widened. ''These experiments and observations,'' Halligan concluded, ''strongly suggest a central role for small mammals in causing the bare aspect around stands of *A. californica*.'' In commenting on the Muller/Bartholomew controversy Halligan suggested both men were correct in their studies regarding the influence of allelopathy and herbivores respectively, but both oversimplified herb distribution patterns and overrated their individual theories.

Regarding the allelopathic potential of *Artemisia*, Halligan's 1976 data suggested the plant produced terpene toxins capable of inhibiting herb growth when applied at natural concentrations. The hypothesized mechanism of transport of volatile compounds was the same as Muller's, from leaves to air to soil to seed. His tests also supported Muller's contention that toxic effects were strongest during the first rain. The toxins disappeared entirely by early spring.

''Some plants were difficult to grow in the soils I collected before the rains,'' Halligan (pers. com. July 03) recalled, ''but by early spring I could grow almost anything.''

From Halligan's bioassays, *Hypochoeris glabra* and *Madia sativa* were much more inhibited by toxins of *Artemisia californica* than *Bromus diandrus* and *Vulpia myuros*. In exclosure experiments, designed to minimize herbivore activity, *H. glabra* and *M. sativa* also appeared to be inhibited in the shrub zone. *B. diandrus*, on the other hand, grew freely in the shrub zone, especially when protected from grazing (this contradicted earlier data from Muller and his previous students showing toxins inhibited *B. diandrus*). From his experimental results, Halligan concluded his original hypothesis was correct; some plant species are allelopathically excluded from thickets of *A. californica* while others are not.

In narrowing the scope and application of his paper, Halligan wrote in 1976, ''I have found greatly varying responses of bioassay species to almost every material bioassayed.'' After listing several examples, he continued, ''Knowing that each species reacts to toxins in its own unique way, it would seem to be of paramount importance to use those species which are directly involved with the vegetation pattern under study. However, in the literature I find many examples of the use of irrelevant species being used for bioassays, such as 'oak leaf' lettuce, radishes and *Cucumis sativus*. These species are of relevance mainly to farmers, not naturalists. The notion that one species' response can be extrapolated to other species is untenable, as indicated by the great disparity of response between species in this article.''

In closing, Halligan acknowledged that although his ideas contradicted Muller's conclusions ''regarding the relative importance of grazing and allelopathy'' some of Muller's ''recent views are no longer completely opposite those in this article.'' The ''recent views'' referred to were from a paper written by Norman Christensen and Muller in 1975.

The Chamise-fire Cycle. Christensen was one of Neil Muller's last graduate students. In re-examining some of the data published by McPherson and Muller (1969) on chamise chaparral, Christensen designed several innovative experiments to test variables controlling germination and seedling growth. He also did something missing from the previous investigation, a direct comparison between a burned and unburned stand of chamise in the Santa Ynez Mountains, northwest of Santa Barbara.

In one series of experiments, eight test plots were established under the chamise canopy to examine the effect of four factors: animal activity, soil heating, additional nutrients, and heating plus nutrients. As had been the case before, the herbivore component presented particular challenges.

''When trying to isolate areas to eliminate animal interference,'' Christensen (pers. com. May 03) recalled, ''we kept catching rodents over and over in traps within exclosures designed to keep them out. Their ability to get over fencing had been completely underestimated.''

The resulting paper was different from any other in which Muller participated; animals were acknowledged as playing a central role. ''There can be little doubt from these data,'' Christensen and Muller (1975a) wrote, ''that animal grazing plays a very significant role in seedling survival in chaparral. It appears virtually certain that any unprotected seedling, not succumbing to some other malady, will eventually be eaten.''

Although allelopathy was still the primary focus, it was no longer being treated in such an exclusive manner, but rather as one of several variables.

> It may be concluded that numerous ecological factors associated with the chaparral understory result in an extremely low probability of seedling survival. Among these are animal grazing, low soil fertility, plant toxins, and, perhaps, low light levels. Following fire, the negative effect of each of these factors is removed or reduced.

In further studies to evaluate the effects of fire on animal grazing, Christensen and Muller (1975b) placed trays of *Bromus diandrus* seedlings approximately two inches high in burned and unburned chamise stands. After 24 hours, seedlings under the chaparral canopy were completely eliminated, grazed to the ground. Those in the burn area were untouched. A likely explanation for the difference is the same as that which Bartholomew suggested for grass growth outside the bare zones around *Salvia*: small animals avoid open spaces to limit exposure to predators.

When examining the effects of fire, Christensen's data initially confirmed McPherson's results by demonstrating, ''heat treatment of soil significantly affected overall germination.'' However, in a later set of experiments, where heat was examined separately from soil, the test results diverged from McPherson's. Employing a much wider range of temperatures and heating times, Christensen found two of the nine species listed as unresponsive to heat by McPherson actually showed dramatic increases in their germination rates when subjected to both 100° and 120° C (210 and 250° F): *Lotus scoparius* (deerweed) and chamise.

Christensen's results indicated heat alone was more significant than previously thought. Further, he revealed an important measurement that seriously questioned one of the primary assumptions of the ''chamise-fire cycle'' model, namely that heat from fire denatures inhibiting chemicals. By using chromatographic analysis, Christensen discovered the concentration of suspected allelopathic toxins was actually *greater* in burned soils rather than less.

When preparing leachate from chamise foliage to test the effect of suspected allelochemicals on seeds, Christensen used the same method employed by McPherson and Muller (1969), but only utilized the natural, non-concentrated form rather than 4x–10x concentrated forms. After employing three different bioassay techniques, Christensen found four of eleven plant species tested showed depressed or zero germination rates when exposed to natural leachate. Two of these were non-natives. To verify that leachate was actually suppressing germination rather than killing the seeds, the un-germinated seeds were later planted on seedbeds with plain water. They germinated as well as untreated seeds.

Interestingly, of the six native fire-followers exposed to chamise leachate, none showed significant differences in germination rates from the control. More revealing, however, was how the seeds were prompted to germinate in the first place. Each had to be carefully pre-treated with scarification, the seed coats being ruptured by laborious scratching with a sharp scalpel (Table 2).

The requirement of pre-treatment demonstrated the presence of *innate* dormancy in the seeds,

Table 2. Seed Response to Chamise Leachate. The effect of natural chamise leachate on the germination of seeds of eleven selected species present after a burn. *Bromus diandrus* was included in experiment to compare with previous work. Adapted from Christensen and Muller (1975b).

Response to leachate	Affected species
Germination inhibited	*Lactuca serriola* (prickly lettuce): non-native *Centaurea melitensis* (tocalote star thistle): non-native *Cyrptantha intermedia* *Erigeron divergens* (fleabane daisy)
No significant affect on germination (not found after burn)	*Bromus diandrus* (rip-gut grass): non-native
No significant affect on germination and requiring *minor* scarification	*Lotus scoparius* (deerweed) *Calystegia macrostegia* spp. *cyclostegia** (morning glory)
No significant affect on germination and requiring *major* scarification	*Allopyllum glutinosum* (phlox) *Emmenanthe penduliflora* (whispering bells) *Eurcypta chrysanthemifolia* *Phacelia grandiflora*

dormancy present *before* coming in contact with any suspected allelopathic inhibitors in the soil. This revealed another critical flaw in the entire ''chamise-fire cycle'' model. If seeds of chaparral species were already deeply dormant at the time of dispersal, there was no reason to hypothesize the presence of other inhibitors in the environment capable of *inducing* seed dormancy. Although Christensen showed shrub-derived toxins depressed germination and growth in some plant species, he was careful to describe the results in such a way as not to imply allelopathy was the most significant factor in determining natural vegetation patterns.

''It's one thing to show inhibiting chemicals are there in the plant,'' Christensen said later, ''it's quite another to show they have an impact in the field (pers. com May 03).''

Innate Dormancy Confirmed. By 1976 Muller retired and became Emeritus Professor at UCSB. Although he was no longer engaged in active research, he continued to maintain a presence in the field of plant ecology. Despite the ongoing controversy concerning the validity of the ''bare zone'' and ''chamise-fire cycle'' models, Muller had successfully presented both so that they were becoming common topics in ecology textbooks and college biology courses.

''Allelopathy was a concept I felt needed to be covered in the classes I taught,'' Jon E. Keeley remembered (pers. com. Dec 03). ''The models developed for coastal sage scrub and chaparral plant communities were excellent ones to use because I wanted to show my students as many local examples as I could.''

Keeley, a professor at the time at Occidental College in Los Angeles, encouraged his students to analyze experimental design and actively challenge assumptions. In doing so, however, they often expressed confusion over some of Muller's methodology. ''My student's kept asking questions like, 'why did they keep using non-native weeds in their tests?' or 'why did they flash evaporate and concentrate suspected allelochemicals before testing them?' I couldn't answer their questions. It was clear that if we wanted answers, we needed to carry out some germination studies ourselves and examine the seed dormancy issue under more natural conditions.''

The first results of their investigations were published in the Journal of Ecology in 1985. They wrote, ''Part of the confusion surrounding chaparral herb germination behavior is the assumption that one mechanism works for all species as suggested by certain investigators working on single non-native species'' (Keeley et al. 1985). Instead, Keeley and his students felt chaparral plant species with ''a diversity of life histories and of seed germination behaviors'' were best examined on a separate basis.

For their study, thirty different native species' seeds were collected in late spring. These included a wide range of typical fire-followers including 22 annuals, 6 herbaceous perennials, and 2 subshrubs (woody species that die back to near ground level every year). The seeds were heated dry at various temperatures (80, 120, and 150° C) and planted in potting soil. Each species was then subjected to three different treatments: aqueous leachate from chamise foliage, powdered charred chamise wood, and leachate and charred wood. Natural level and 4x concentrated leachates were used, both being collected in the same manner Muller employed, from living chamise foliage during middle to late summer. In contrast to previous studies, each species was

Table 3. Comparative Results. Species concluded as not being stimulated by heat to germinate (0) by McPherson and Muller (1969) and compared to later experimental results by others. Cue responsible for stimulating germination listed. (—) indicates not tested.

Species tested	McPherson and Muller (1969)	Christensen (1975b)	Others
Lotus scoparius (deerweed)	0	heat	heat (5)
Helianthemum scoparium	0	—	heat (2)
*Vulpia octoflora** (vulpia grass)	0	—	—
Calandrinia ciliata (red maids)	0	—	—
Phacelia grandiflora	0	scarification	smoke (1)
Lotus strigosus	0	—	heat (3)
Silene multinervia (catch-fly)	0	—	smoke (1)
Oenothera micrantha (camissonia)	0	—	—
Adenostoma fasciculatum (chamise)	0	heat	charred wood (5)
Calystegia macrostegia ssp. *cyclostegia** (morning glory)	—	heat	heat (4)
Emmenanthe penduliflora (whispering bells)	—	scarification	smoke (1)

* Species name has been changed to reflect recent taxonomy in Jepson (1993). Source of information: (1) Keeley and Fotheringham, 1998; (2) Keeley et al., 1985; (3) Westermeier, 1978; (4) Parker, 1987; (5) Keeley, 1991.

subjected to multiple tests. ''All treatments were carried out in combination for a total, including controls, of sixteen treatments per species. Each was replicated eight times.''

In experiments on twenty-two native annuals, only two, *Apiastrum angustifolium* (wild celery) and *Cryptantha muricata* (popcorn flower) were inhibited by chamise leachate. And these results could only be obtained by using a concentrated 4x solution.

''Even more difficult to reconcile with the theory of allelopathy,'' Keeley wrote, ''is the observation that nine species in this study showed an enhanced germination rate in response to *Adenostoma* leachate.''

In comparing the species tested by Keeley with McPherson and Muller (1969) and Christensen and Muller (1975b), it becomes clear that the importance of fire cues in germination was underestimated in the earlier work. Further investigations have now documented that most fire-following species produce innately dormant seeds and that some aspect of fire, not allelopathy, provides the primary cue for their germination (Table 3).

''The best way to do these experiments,'' Jon Keeley explained (pers. com. July 03), ''is to include a response curve that covers a wide range of temperatures and durations. For example, if you hit the right combination with *Lotus strigosus* and *Helianthemum scoparium*, you can get extremely high germination rates, even 100%. Also, heat and chemicals can have both stimulatory and lethal effects dependent on their levels. Consequently, failure to find a positive response can not be interpreted as conclusive because the treatment levels could have been either lethal or insufficient to stimulate.''

After the publication of his 1985 paper, Keeley went to UCSB and talked with Muller. ''He suggested I may not have examined the right things, but that was about it,'' Keeley remembered. ''We really didn't have any substantive discussions on the matter.''

Is it Still a Possibility? For chaparral, it is clear innate dormancy in seeds can account for the lack of herbs under the community's canopy. The remarkable post-fire germination cycle can be explained without invoking environmentally induced chemical inhibition. Poor growing conditions under mature shrubs selected for traits postponing germination until those conditions improved, such as after a fire, including higher available nutrients levels, more space and light, and lower herbivory.

The possibility of environmentally induced dormancy still remains, however. Two fire following herbs, *Papaver californicum* (fire poppy) and *Nicotiana attenuata* (coyote tobacco), are absent under the chaparral canopy, yet germinate freely under lab conditions (Jon E. Keeley pers. com. Dec. 03). ''Rather than these two species being suppressed by shrubs to reduce competition as described in the 'chamise-fire cycle' model, I think it may be the other way around,'' Keeley suggested. ''Sensitivity to shrub chemicals by some annuals may have been selected for by the evolutionary process as a way to time germination during more desirable post fire conditions. So perhaps in these two cases, allelochemicals may be causing an induced dormancy. But without further investigation, we just don't know.''

While factors other than chemical inhibition can account for bare zones around *Salvia leucophylla* and *Artemisia californica*, the possibility of some allelopathic influence remains open. Do volatile compounds in coastal sage scrub ever play a significant enough role to make a difference in naturally occurring vegetation patterns? ''As far as I know, the question of why grasses grow within bare zones during wet years, despite animal activity, has never been adequately addressed,'' Bob Muller said when reflecting upon his father's work (pers. com. July 03). ''Why don't animals *always* eliminate seedlings, regardless of the level of moisture?''

The hypothesis favored by Muller to explain this observation and supported by Halligan's data on *Artemesia* suggests that heavy rains leach toxins from the soil, removing inhibitory chemicals and thus permitting seedling success. Muller also felt this accounted for the lack of bare zones on the Santa Barbara Channel Islands. The islands' sandy soils were more susceptible to leaching than the clay soils in the Santa Ynez Valley where bare zones were plentiful (V. Thomas Parker pers. com. April 03). Before the hypothesis can be accepted with a convincing level of confidence, however, replication of Halligan's data over longer time frames and measurements collected under a wider variety of conditions are needed. Unfortunately, there is little interest in pursuing the matter much further. Plant ecologists generally view the entire concept of allelopathy with understandable skepticism because hundreds of investigations have produced little more than ambiguity. As demonstrated in Muller's work, ecological variables are notoriously difficult to isolate. In commenting on the need for researchers to recognize this difficulty, John Harper (1975), the prominent plant population biologist from England, wrote, ''It would be surprising if, among the variety of plant interactions in nature, there were not cases in which toxins played an important ecological role, but it does not help the discovery of such cases to preach their existence as though it were gospel.''

Consequently, due to past errors, a climate of apprehension has formed a dark cloud over the field, requiring more stringent levels of proof than demanded within other areas of ecology (Williamson 1990). ''To my knowledge,'' wrote J. H. Connell (1990), ''no published field study has demonstrated direct interference by allelopathy in soil. . . while excluding the possibility of other indirect interactions with resources, natural enemies, or other competitors.''

''The critical issue,'' Harper (1975) identified, ''is to determine whether such toxicity plays a role in the interactions between plants in the field. Demonstrating this has proved extraordinarily difficult—it is logically impossible to prove that it doesn't happen and perhaps nearly impossible to prove absolutely that it does.''

When concentrated, as was done in many of the sage scrub and chaparral studies, many biological compounds can inflict damage to living systems, including the inhibition of seed germination or growth. Reflecting on this question while studying allelopathy in Illinois, Lawrence Stowe (1979) suggested, ''that virtually any species can be shown to have allelopathic properties by testing it in bioassays, and that positive results in bioassays may have nothing to do with the interactions among plants in the field.'' Stowe also found an unfortunate tendency for some investigators to ignore the lack of correlation between their laboratory bioassay results and what they found in nature. Interestingly, Muller pointed out the correlation issue in his 1953 study of the two desert shrubs, *Encelia farinosa* and *Ambrosia dumosa*, demonstrating that inhibition found in the lab did not always translate into inhibition in the field.

''Literally hundreds of plant extracts have been tested for bioactivity and shown to be active,'' Romeo and Weidenhamer (1998) wrote. Because of failure to properly test under natural conditions, they noted, ''there is both garbage and confusion in the literature. Many reported effects are not real, and probably many real ones have been overlooked simply because the bioassay used was faulty.''

The primary cause for faulty conclusions from experimental data rests with poor design of controls allowing more than one variable to affect results. This was one of the issues clouding Muller, Hunawalt, and McPherson's (1968) conclusion that seeds were released from inhibition when fire detoxified allelopathic chemicals in the soil rather than heat itself being the direct causative agent. Investigating resource competition, a hypothesis uncritically accepted by many ecologists, suffers similar problems.

The question of what happens to suspected allelochemicals once they enter the soil also remains an incredibly complex matter. Soil particles, moisture content and the multitude of microorganisms soil harbors have dramatic effects on organic chemicals, the details of which are also extremely difficult to quantify and accurately measure over time. Ray Kaminsky (1981), working in the same UCSB facilities Muller used, concluded ''the allelopathic potential of *Adenostoma fasciculatum* may, to a large degree, be attributable not to the substances from the shrub itself, but to its association to phytotoxin-producing soil microorganisms.'' However, as a testament to the complexity of such studies, Phil Pack, a student at Occidental College in Los Angeles working on a Master's thesis could not replicate Kaminsky's data when testing native species by using longer time frames for germination (J.E. Keeley, pers. com. July 03).

Some interesting work has been done recently on the allelopathic potential of *Centaurea maculosa* (knapweed), an extremely invasive weed in the western United States. Harsh P. Bais and colleagues (2003) discovered the plant exudes (-)-catechin, a phytotoxic chemical, from its roots. By adding the compound in natural concentrations to field soil in pots they found ''the germination and, to a lesser extent, the growth of *Festuca idahoensis* and *Koeleria micrantha*, two native North American grasses, were sharply reduced.'' Strengthening their argument was the observation that the inhibitory effect was much less on Eurasian grasses, suggesting an evolutionary response within knapweed's original community. Although these results clearly show *C. maculosa* produces toxins capable of inhibiting growth in other species, the same two questions remain as they have with all previous allelopathic investigations: 1) do the plant's chemical products actually have an inhibiting effect in the field, and 2) if they do, is the effect significant enough to play an important role in the plant's success over other species?

Ironically, one of the most prescient reflections concerning the problems facing the investigation of allelopathy came from C.H. Muller himself when he rejected Gray and Bonner's analysis in 1953. It is worth repeating.

> The natural habitat even in a relatively simple community of the desert, is far too intricate a system of influences and factors, physical and biological, to hope that there may be found a single factor controlling the complicated life of a perennial species. An explanation, when it is arrived at, will be at least as intricate as the situation it seeks to describe.

Perspective. Muller was a talented botanist as well as an independent thinker who clearly understood how science worked. He was well versed in Chamberlin's method of multiple working hypotheses and keenly aware of the pitfalls of becoming overly attached to a theory. Throughout his career, he constantly impressed upon his students the value of designing appropriate controls and maintaining objectivity.

''The question of the day in Muller's lab was always, 'Give me ten other reasons for getting the data you're collecting''', former graduate student Nancy Vivrette said (pers. com. July 03). ''Just obtaining a positive result wasn't enough.''

''Muller was as fair a scientist and human being as I've ever met,'' Roger del Moral remembered (pers. com. June 03). ''Every Tuesday night while I was at Santa Barbara, he would run a lively ecology discussion group. People from every biological discipline you can imagine would come and present their papers. Muller really enjoyed arguing. He would take one position and argue for that, then take the exact opposite perspective later on. The amazing thing was, he'd win both sides!''

Muller's ''bull sessions'' were legendary. He viewed science as a sort of intellectual coliseum where ideas could be attacked and defended with ferocious intensity. Once he decided a particular position was wrongheaded, Muller would charge into the fray with self-righteous determination and slay its supporters with debating skills few could match. He was equally forceful in defense of his own positions. For him, there were very few shades of gray.

''He got so mad at me for suggesting moisture was an important variable in bare zone formation,'' Haines remembered. ''He thought I had been brainwashed by the drought specialists at Duke University. I didn't understand it, because he always stressed the value of maintaining multiple working hypotheses. I'd only done what he'd taught me to do.''

Pat Halligan (pers. com. July 03) experienced a similar reaction when re-examining Haines' work in the early 1970's. ''C.H. became really irritated because he felt I kept getting the wrong results, so I started all over again from the bottom with a year of fieldwork behind me. The atmosphere was almost unbearable. It was easier to use Dale Smith's lab on campus during the day, and Muller's lab at night when no one else was around.''

Muller's last graduate student, V. Thomas Parker (pers. com. Apr. 04), remembered, ''Although Muller rejected my results the first few times I presented them, it wasn't because he was mad, he just wanted my controls to be uniform and extensive. He always said 'they had to be beautiful.'''

Parker was tasked with investigating possible allelopathic inhibition by *Quercus agrifolia* (coast live oak) upon *Avena fatua* (wild oat), a common grass in surrounding grasslands but rare under the canopy of isolated oaks. While he found *Quercus* had no effect on *Avena*, his data did suggest the grass was being inhibited by a different source, the dominant understory herb *Pholistoma auritum* (fiesta flower) (Parker and Muller 1979, 1982).

The contradiction between Muller's scientific philosophy emphasizing open-mindedness and his frequent dismissal of evidence contrary to the allelopathic model seems inexplicable until one appreciates the determination required to champion an unpopular idea. Muller saw some of his detractors as the usual crowd of doubters who were overly attached to outdated theories, unable to properly evaluate new ideas. In part, his reaction to them was shaped by the desire to counter the remaining followers of Frederic Clements (1905) who was a major influence in plant ecology for over fifty years and who dismissed allelopathy as a viable theory (Robert Muller pers. com. July 03).

In private moments, Muller would readily agree allelopathy was just one of many variables affecting the ecology of plants. But in an effort to promote the idea in papers and during scientific conferences he gave the impression the process was a dominating ''single factor.'' In striving to disprove every challenge, Muller did not treat competing hypotheses with equal intensity. The observation confirmed by Christensen's research that post-fire species are deeply dormant without chemical inhibition playing a role was never fully acknowledged. Despite evidence to the contrary, Muller continued to support his ''secondarily induced dormancy'' hypothesis in chaparral whereby seeds remain dormant due to external, environmental inhibitors.

Muller was, however, very successful in developing an elegant series of experiments to test his coastal sage scrub ''bare zone'' model by focusing on the inhibition of seedling *growth.* He uncovered and was able to describe a potentially important variable in the community structure of coastal sage scrub vegetation. His error was utilizing the same techniques in chaparral as he did in bare zone studies, namely exposing seedlings to vegetation leachate. Demonstrating chamise or manzanita leachate was inhibitory or lethal to seedlings was not relevant to the ''chamise-fire cycle'' model. Chaparral allelopathy calls for inhibition of seed *germination*, not seedling *growth* after germination. If chemicals were indeed toxic to seeds and seedlings, the chaparral seed bank would eventually become decimated, as seeds germinated each spring only to be killed by inhibiting chemicals. Few seeds, if any, would remain to account for the explosive post-fire germination response.

Judging Muller by his mistakes, however, or as an investigator blinded by passion to prove a favored theory belies the man's intentions and his success as a scientist. Emotional attachment to a particular position is not necessarily contrary to objectivity. The desire to discover something new and the competitive drive it engenders, are critical components to the scientific process. Little advancement in knowledge would be gained without them. Propelled by the emotional energy that moves knowledge forward, the scientist strives to maintain a delicate balance between desire and truth, knowing full well one is capable of influencing the other in unconscious, yet dramatic ways. It is a balance we struggle with in every aspect of our lives.

The Gnarly. As Muller's days of active research came to a close and he assessed nearly twenty years of data, he modified his perspective on allelopathy to account for the new data his students collected. Although he continued to maintain chemical inhibition was an important ecological process in southern California's shrublands, he accepted some changes to his original hypotheses that he felt were warranted. His co-authorship with Norm Christensen in 1975 reflects his willingness to accept conclusions contrary to his own. Muller was meticulous about where he allowed his name to appear.

''My work did not take me where he had hoped it would go,'' Christensen said later (pers. com. Aug 03), ''but in the end he was pleased that we had a pretty coherent story to tell. I think he felt that allelopathy was still a factor, but could see that the patterns we observed were more complex and that animals were very important.''

Bruce Haines visited his old mentor in the mid-1970‘s and was surprised to hear Muller describe the impact of two wet years on the bare zones they first studied together in the early 1960‘s. ‘‘He told me they were completely filled in with grass,’’ Haines recalled. ‘‘I was surprised by his comment because it was the same issue I raised in my thesis that caused me so much trouble. He said that he now saw drought as playing an important role in how effective plant toxins could be. We talked a bit more and then he looked me right in the eyes and said, ‘You were right!’ I’ll never forget it.’’

A little later, Muller wrote a letter to Pat Halligan (pers. com. July 03). It was Halligan’s research in 1976 that documented the effect of excessive moisture on the inhibitory effectiveness of volatile compounds. ‘‘My project was to prove the allelopathic mechanisms of *Artemisia* because C.H. didn’t like the results Haines came up with,’’ Halligan said. ‘‘But he didn’t agree with mine either, so I had a difficult time there. But several years after I left Santa Barbara, C.H. wrote me a note saying he felt I had done a lot of good work and agreed with my conclusions. He acknowledged to me that allelopathy was just part of the mix and not the dominating factor.’’

According to those who knew him best, C.H. Muller was an ‘‘old-school’’ Texan willing to fight an honorable battle for what he believed. His passion led his science and sometimes influenced his conclusions, but his love for botany and the natural world led many to follow his vision and become outstanding scientists themselves.

‘‘He was certainly an inspiration for young students because he made them feel part of the ‘grand battles’ in which he always seemed to be engaged,’’ Harold Mooney (1999) one of Muller’s earliest students, wrote.

As a sophomore, Mooney listened to Muller reject allelopathy as he discussed Gray and Bonner’s work on *Encelia*. Then, after a two-year stint in the US Army, Mooney returned to find his teacher ‘‘engaged in research that purported to demonstrate that allelopathy did indeed exist’’ in the foothills of Santa Barbara. ‘‘This was pretty exciting for a budding young ecologist, to see the stuff of science so close up: the proposal and counterproposal in trying to work out the complexities of the operation of natural systems.’’

‘‘It was such an interesting time,’’ Norm Christensen said when reflecting upon his work with Muller. ‘‘I look back on it all now and it was by far the best research I’ve ever done. It was so much fun. Behind his back, we affectionately knew C.H. as ‘the gnarly’. We all loved his crustiness and knew well that he would march into the jaws of hell on our behalf. I am grateful to have had the opportunity to work with him. He is an exemplar of the fact that scientists are also very human. That’s not a bad thing.’’

By the mid-1970’s, Muller’s deteriorating vision and brush with a near fatal illness made fieldwork impossible, but he continued writing research papers into the 1990’s. In 1975, he was selected as the Ecological Society of America’s Eminent Ecologist. The photo accompanying an article about the award shows the famous oak taxonomist with a wry smile holding a sprig of *Toxicodendron diversilobum* (poison oak) (Fig. 3). V. Thomas Parker remembered, ‘‘He wanted to see if anyone would notice.’’ In 1982, Current Contents, a source for bibliographic research, declared Muller’s 1966 paper, ‘‘The Role of Chemical Inhibition in Vegetational Composition’’, a Citation Classic having been referenced more than 125 times.

As for others involved in the story, their paths diverged in a multitude of ways. Reed Gray, who co-authored the desert allelopathy paper with James Bonner in 1948, entered the private sector as a chemist after he was awarded a Ph.D. in biochemistry for his research on *Encelia*.

‘‘That paper helped me all through my life in getting jobs and recognition,’’ Gray said in 2003. ‘‘I remember the local Pasadena newspaper even did an article on it. It was titled something like ‘the biochemical warfare among plants’.’’

The potential of using plant allelochemicals as herbicides prompted Gray to isolate and synthesize a toxic compound from the genus *Leptospermum*, commonly known as tea trees. He recorded two patents for the compound while working for the Stauffer Chemical Company in 1980. He is retired now, living with his family in Northern California.

Phil Wells went on to do pioneering work on the dramatic vegetation displacements of Great Basin forests since the last glacial period by using a unique source of information, fossilized remains of plants preserved in *Neotoma* (wood rat) nests occupied over the past 12,000 years (Wells 1983). ‘‘The idea first came to me when I spotted one of their nests at Indian Springs, near Las Vegas in the early 1960’s. The material wood rats accumulate can be preserved for tens

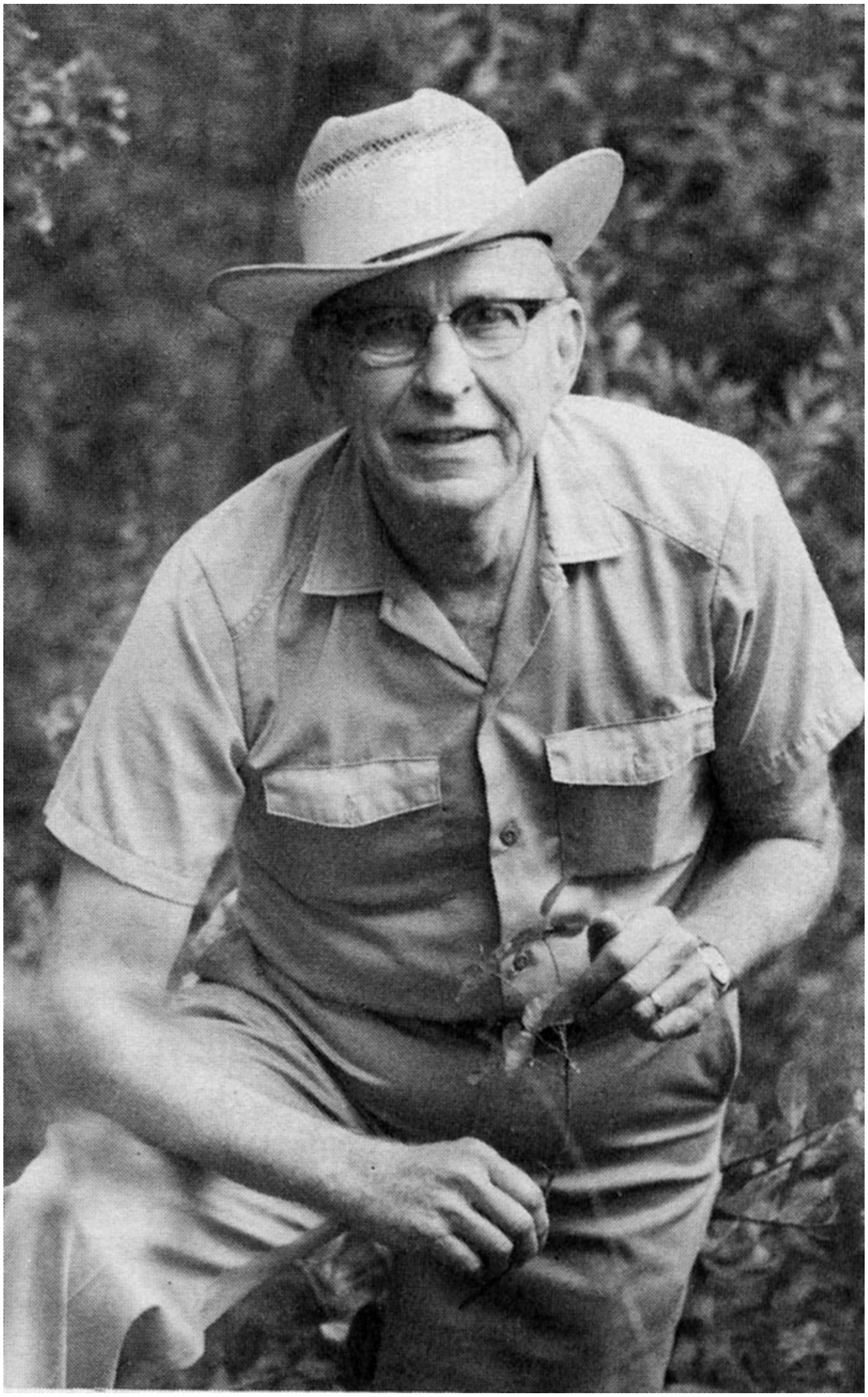

FIG. 3. C.H. Muller, in the field, demonstrating his well-know sense of humor. Being a recognized expert on the genus *Quercus*, Muller is holding a sprig of poison oak. Photo accompanied the announcement of his award as Eminent Ecologist in 1975 in the Bulletin of the Ecological Society 56 (4): 23, 1975.

of thousands of years and contain samplings of all the plant communities existing around them,'' (Wells pers. com. June 03). Well's techniques are now the standard for studying Holocene and late Pleistocene paleoecology in arid parts of the world.

Wells became Professor Emeritus at University of Kansas. He died October 29, 2004.

Helped by Muller's training, Bruce Haines designed a successful dissertation research project at Duke University involving work at the Smithsonian Tropical Research Institute in Panama. It was there he developed a life-long interest in the biological and biophysical processes controlling the abundance of leaf-cutting ants. He remains a professor of botany at the University of Georgia.

Hal Mooney became a professor of biological sciences at Stanford University and has built a significant portfolio of excellent scientific work in plant ecology, chaparral plant physiology, convergent evolution and global climate change. He was also Bruce Bartholomew's doctorate advisor. Mooney continues to teach and research at Stanford and is a member of the National Academy of Science.

James McPherson became professor of botany at Oklahoma State University and distinguished himself as an outstanding teacher. He worked tirelessly as a conservationist, managing the Nature Conservancy's Springer Prairie Preserve, contributing his expertise to the development of the Tallgrass Prairie Preserve, and actively participated in the Sierra Club. He died unexpectedly of a heart attack in 1994.

Bruce Bartholomew remained in northern California and was hired to care for the botanical collection at the University of California in Berkeley. He eventually left to become curator of the herbarium at the California Academy in San Francisco and has become a renowned ethnobotanist.

Pat Halligan taught at the University of Nebraska for a short time, but ultimately went back to school to become a dentist and opened a practice in the state of Washington. ''I was an abysmally poor teacher,'' Halligan remembered with a smile in his voice, ''so it became clear to me that I needed to find another profession.'' Despite leaving academia, he has continued his interest in botany by becoming a respected expert on rhododendrons.

Norm Christensen was hired by Duke University and began working on the effects of fire in southeastern coastal plain ecosystems and responses of southeastern forests to human disturbance. His career has evolved considerably over the past thirty years; first focusing on the basic science of ecology then shifting towards applications to ecosystem management, especially in regards to fire. He was selected to chair two congressional committees to study fire, one in 1986 after public complaints about how prescription burning charred giant sequoias in California and in 1988 after the great Yellowstone blaze.

V. Thomas Parker completed his work at UCSB and is now professor of biology at San Francisco State University. He has done extensive work involving changes in plant populations, dispersal, seed bank dynamics, seedling establishment, and mycorrhizal ecology. One of his specialties include the genus *Arctostaphylos* (manzanita), leading to his selection as one of the authors to the group's new treatment in the upcoming second edition of California's Jepson Manual.

Jon Keeley left Occidental College and is currently a research scientist with the U.S. Geological Survey, Western Ecological Research Center in Sequoia National Park as well as an adjunct biology professor at the University of California, Los Angeles. His work in botany and fire management has earned him the reputation as being both a rigorous scientist and one of the foremost fire ecologists in the world.

Neil Muller inspired 12 Ph.D and two master's students from 1966 to 1977 and published over 100 research papers from the 1930's into the 1990's. He died January 26, 1997. His ashes were scattered over a field of bull thistles in Texas.

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