Antibiosis as a Factor in Vegetation Patterns

The report by Muller, Muller, and Haines (31 Jan., p. 471) is admirable in its experimental approach to the subject of antibiosis in higher plants, but I fail to see that this has genetic significance for the striking mosaic patterns involving subligneous shrubland and grassland shown in their interesting photograph on the cover. One notices in this photograph a number of linear cattle trails running through the grassland area (lighter tone) and connecting with a complex network of anastomosing lines within the shrubland area (darker tone). No mention is made in the paper of the possible influence of disturbance by cattle and native herbivores in the origin of some of these details of the vegetation pattern, which are apparently attributed to "chemical plant competition." The area in the photograph is said to be "representative of vast areas where similar patterning has occurred after biochemical inhibition of herbs. White borders surrounding shrub zones are areas of maximum inhibition; the soil is almost devoid of herbs." There are not only linear white borders surrounding the shrub zones, but also intricate patterns of white lines *within* the main body of shrubland, producing the mosaic effect in the center of the photograph. The interconnecting and in part rectilinear character of the network of white lines does not suggest origin by chemical inhibition. An equally good explanation is that most of them are cattle trails. No mention is made of the fact that the dominant annual grasses (*Avena fatua, Bromus mollis*) are not indigenous but were introduced from Europe, and that annual grasslands of this type in California are a product of a long history of severe overgrazing and burning, beginning with the Spanish colonial period.

The shrubs (*Salvia leucophylla* and *Artemisia californica*) are said to be invading the grassland. One of the areas of invasion apparently lies in the top center of the photograph, where over 100 shrubs are scattered in the grassland with no white borders in evidence among them. This would appear to be a pattern developing *before* and not "after biochemical inhibition of herbs."

No mention is made in the paper of the possibility that shrubland and grassland may be underlain by soils differing in characteristics other than those involved in the putative biochemical inhibition. For example, are there any differences in texture or depth of soil under the different types of vegetation?

The experimental procedure which assayed the effect of volatile growth inhibitors on seedlings enclosed in containers sealed with petrolatum is rather remote from field conditions, where high temperatures at the soil-air interface may cause a rapid dissipation of volatile substances hypothetically deposited with dew. Chemical inhibition of seedling growth of herbs by unidentified volatile substances emanating from aromatic shrubs rich in terpenes is 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.

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A report provides scant space for monographic completeness; admittedly, we did not mention that *Avena fatua* and *Bromus mollis,* as well as *B. rigidus, B. rubens,* and *Erodium cicutarium,* were introduced from Europe, where Deleuil [*Compt. Rend.* **230**, 1362 (1950)] reports herbs inhibited by shrubs. We did not ascribe the origin of this grassland to "a long history of severe overgrazing and burning," because this is not true. The original bunch grasses, *Stipa pulchra, S. lepida,* and *Poa scabrella* are eliminated by even very light grazing. In this type of grassland dense stands of bunch grasses regenerate when an area is protected from grazing even though subjected to annual burning. Under any circumstance, the introduced European species persist among the annual indigenes which they closely resemble in habit and ecological relations. We also did not mention "the possibility that shrubland and grassland may be underlain by soils differing in characteristics other than those involved in the putative biochemical inhibition" because (i) we have implied no soil characteristics involved in biochemical inhibition, and (ii) in five trenchings across three shrub-grass boundaries soil differences were not detectable. We recognize that some shrub zones are centered upon areas of shallow soil, but whether this is cause or effect remains to be shown. We made no mention of our identification, assay, and tracing *in the field* of the chemical inhibitions by means of gas chromatography, because these are separate studies about to be submitted as additional reports.

The points of criticism mentioned above are thus not pertinent to the subject. The critique may be judged in the light of the principles treated by Green and Henson [(*Can. Entomologist* **85**, 227 (1953)]. Our report did not treat the degree to which "cattle and native herbivores" are involved in the intricate system of influences that have produced the patterning. To do so adequately will 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 practicable, been investigated, evaluated, and fitted into the complex. There follows, however, a brief set of data that will illustrate our consideration of herbivore influence. A lobe of *Salvia leucophylla* covering an area of 192 m^2 extended out into a level and edaphically uniform grassland which was divided into the following zones: (i) a bare zone of 52.8 m^2 surrounding the shrub area, (ii) an area of visibly inhibited grassland totaling 145.4 m^2, (iii) an arbitrary zone next adjacent apparently not inhibited and totaling 162.5 m^2, and (iv) a more remote uninhibited area on the same flat totaling 734.1 m^2. In each of these zones an accurate count of fresh cow droppings was made at a time when cattle had recently been returned to the pasture after an absence of several months. From the counts and areal measurements, we computed areas per dropping which were distributed as follows: (i) bare zone, 52.8 m^2 per dropping, (ii) heavily inhibited grassland, 20.7 m^2 per dropping, (iii) apparently uninhibited grassland, 11.6 m^2 per dropping, and (iv) remote uninhibited grassland, 3.65 m^2 per dropping. It is clear from these figures that cows go where grass is and that they do not linger about shrub patches trampling down depauperate herbs over wide areas (20 times wider than cowpaths).

The criticism that cowpaths are visible within the shrub zone and may therefore be responsible for the patterning involves a most surprising failure to observe. Cowpaths within a shrub zone cut off at both ends by grassland and not going anywhere are no longer cowpaths. The photograph shows the currently used paths in the grassland bowed toward the lower left by encroaching shrubs while faint scars above reveal where the paths once passed. In the grassland these old paths are obliterated by grass; in the shrub zone they remain bare and become broader. 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. Since severe inhibition 6 to 9 m distant from the shrubs is commonplace, with or without transverse cowpaths, it is impossible to ascribe the phenomenon to characteristically narrow cowpaths.

Wells overlooked the fact that we did not credit White-crowned Sparrows (*Zonotrichia leucophrys*) and Golden-crowned Sparrows (*Z. atricapilla*) with contributing to the vegetational patterning. This they do in perceptible degree, but never do they produce a bare area unaided by initial biochemical inhibition. Their contribution consists of grazing more heavily near shrubs for a brief period after initial germination and results in a slight intensification of the patterning.

Steps are being taken to preserve an area of the more instructive patterning. We are desirous of showing this to anyone who will look.

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Radiocarbon Dating of Mollusk Shells: A Reply

W. Broecker's criticism (*1*) of our hypothesis (*2*) that humus contributions affect the radiocarbon age of fresh-water mollusk shells is based partly upon the misconception that our hypothesis requires oxidation of humus "within the water body *rather than* in the soils of the drainage basin" (italics added). His phrase "rather than" should read "as well as" in order to be in accord with our evidence and stated conclusions. Humus oxidation begins in soils and ground water, of course, but a second-stage oxidation of humus takes place in suspension in river waters and to a lesser extent in lakes; they are not sterile environments. A third-stage humus effect depends upon the nature of the food web and upon the food selectivity of mollusks. We have shown in a separate study of $C^{13}:C^{12}$ ratios (*3*) that river mollusks adapt themselves to digest humus or humus-derived material, which is relatively deficient in both C^{13} and C^{14} (as compared with atmospheric carbon dioxide). Our conclusion that humus is an important source of shell carbon was based largely upon that study, and the radiocarbon data are regarded as supplementary evidence. This was perhaps not sufficiently emphasized.

Because of C^{13} enrichment (about 15 per mil) and C^{14} enrichment (about 30 per mil) in mollusk shell relative to the food web (the major source of metabolic carbon), projections made in order to estimate the probable age of contributing humus should be drawn through points representing the food web (Fig. 1) rather than through those representing shell isotopic composition. Failure to do that, and to allow for carbon fractionation by mollusks, probably explains Broecker's conclusion that "humus of about 4000 years in age is needed in order to yield the observed compositions of river mollusk shells. . . ." Our projection gives a maximum necessary humus age of less than 3000 years (Fig. 1).

We do not dismiss the contribution of inactive carbon from limestones, which Broecker emphasizes so strongly; it should be pointed out, however, that the limestone-dissolution effect is a local one, not generally significant in limestone-free areas. Relative contributions of the several carbon reservoirs probably can be more exactly defined by a detailed study of the C^{13} and C^{14} content of bicarbonate, food web, and mollusk flesh and shell in biologic communities of rivers. We have proposed an investigation to be made in collaboration with Broecker.

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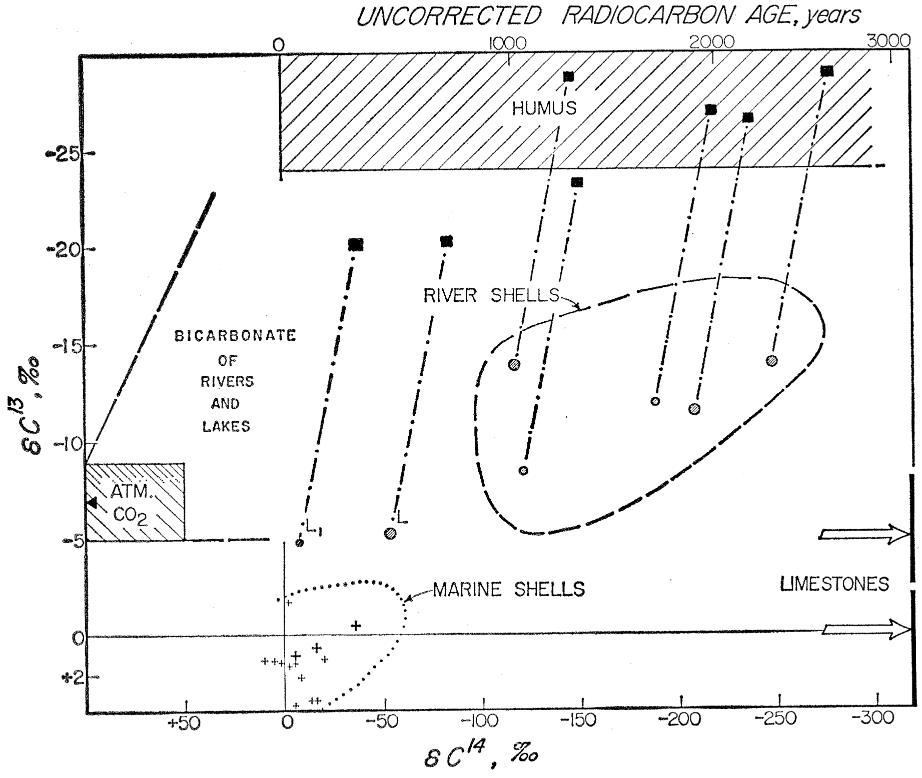

Fig. 1. Carbon isotopic composition and radiocarbon age of mollusk shells. This figure is identical with Fig. 1 in the earlier report by Keith and Anderson (*2*), except for showing fractionation tie-lines and the approximate isotopic compositions of food web (filled squares) to be expected in relation to the analyzed fresh-water shells (circles). Specimens L and L_1 are from lake-water environments.

References

1. W. Broecker, *Science* **143**, 596 (1964).
2. M. L. Keith and G. M. Anderson, *ibid.* **141**, 634 (1963).
3. ———, *Geol. Soc. Am., Spec. Paper* **73**, 185 (1963); *Geochim. Cosmochim. Acta*, in press.

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