

moved by the ice interface. This movement will of course be impeded by mechanical constraints on the small particles, which reduce the relative motions of the various particles. There are thus two distinct sorting processes at work during freezing of a soil: (i) the motion of stones and large objects as described above; and (ii) the direct sorting action of the ice-water interface on small particles. Both these processes tend to sort the largest particles to the surface and the finest particles deeper into the soil.

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Vegetational Continuum

Daubenmire's criticism of the "continuum viewpoint" ["Vegetation: Identification of typical communities," *Science* **151**, 291 (1966)] is a result of misunderstanding the late J. T. Curtis's concept of the vegetational continuum. In *The Vegetation of Wisconsin* (Univ. of Wisconsin Press, Madison, 1959) Curtis says, "The entire series of communities whose floristic composition gradually changes along an environmental gradient has been termed a 'vegetational continuum', to emphasize the fact that no discrete divisions, entities, or other natural discontinuities are present." He goes on to say, "It must not be assumed that this gradual blending of one community into another or one vegetation type into another is always expressed in the field. On the contrary, there are many examples of abrupt shifts from one assemblage to another, sometimes along a line so sharp that it may be crossed at a single step." These statements clearly dismiss the paradox that Daubenmire thinks exists.

As a student of Curtis, I interpret these statements to mean that plants or groups of plants vary continuously in time and in space, but *not necessarily in space at a given time*. Time is defined as actual time or theoretical successional time; the concept is thus a corollary to the theory of succession and has implications in taxonomy and evolution. The continuum viewpoint is founded in the principles of biological variability and the amplitude of tolerance. These principles are that no two species, and no two individuals of the same species (unless genetically identical), have the same amplitudes of tolerance.

The continuum and its relation to succession can be illustrated by hydrarch succession, where the vegetation varies gradually and continuously as a site progresses from hydric to mesic. One plant assemblage blends into another, and it is difficult and often arbitrary to decide the precise moment in time when a sedge-shrub association becomes a forest community. The continuum concept eliminates the need for this decision.

But not all communities are seral; many have reached a climax, a terminus of stability, or a state of quasi-equilibrium. Other communities are retrogressive as a result of catastrophe. But even in these communities, individual plants vary continuously in time, as one individual replaces another. Only abrupt, catastrophic breaks in succession result in breaks in the time continuum.

The discontinuities cited in Daubenmire's article do not refute the continuum concept. Curtis acknowledged discontinuities in space or on the land, and he and his students have used the community approach in vegetation classification. Part of the confusion and irritation concerning the continuum has resulted from publications by "continuum champions" that glorify the special methods of processing data arithmetically (indices, ordinations, 3-D diagrams), making them the focal point of their work, rather than using them in proper perspective as tools (as Curtis intended) in community classification. Daubenmire's specific complaints (concerning shortcomings in sampling methods, in the treatment of data, and so on) should be lodged not against the continuum concept but against individual investigators. These faults are by no means restricted to "continuum champions." It would be

more profitable if adversaries of the continuum concept directed their attack to the theory of succession itself, to reconcile inconsistencies existing between that theory and what actually takes place in many plant communities.

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. . . If "closely similar plant assemblages" which can be combined to form types with "consistent distinguishing characters" exist, as Daubenmire asserts, why then the "spectrum of concepts, terms and methods so broad as to discourage the novice and confuse even the specialist"? The facts are that the consistent, distinguishing characters needed to recognize an association type vanish upon close examination. As Daubenmire says, a "century of development" of the type concept of vegetation has produced little trend toward standardization of "methods of analysis nor of organizing the subsequent data." The consequent state of confusion, to which Daubenmire alludes, casts doubt upon the typological approach and is a primary reason that a different viewpoint on vegetation was called for.

A major methodological difference between Daubenmire's "continuum champions" and his "hundreds of workers" who support the typological view of vegetation is the emphasis by the former upon methods of quantitative analysis; Daubenmire's comment that the results are "more satisfying to a mathematician than to a botanist" is simply rhetoric. The simple arithmetic methods of the original continuum [Curtis and McIntosh, *Ecology* **32**, 476 (1951)] and the more involved techniques of Bray and Curtis [*Ecol. Monographs* **27**, 325 (1957)] will probably prove inadequate and be replaced by more refined mathematical methods. But it is most unlikely that the "vast array of environmental gradients operating concurrently, in Daubenmire's apt phrase, will be amenable to the subjective methods which have characterized the traditional approach to vegetation studies exemplified in Daubenmire's article. His own reduction of the "vast array" to a single factor, operating independently, is a simplification unsupported even in his geographical area by the limited data he presents.

Proponents of the typological point of view believe that they can recognize

homogeneous vegetation types intuitively. The more advanced of these ecologists then sample representative areas of the recognized types, and the resultant data support their choices, as one would expect. The "consistent distinguishing characters" are of course justified, since areas that do not have them are excluded; the "closely similar" quality is always reasonable but rarely stated precisely; and the abstract classes always conform to the botanist's initial intuitions. This is precisely what is questioned by many ecologists, who suggest that if vegetation is comprised of discrete classes of types these should be apparent in objectively sampled areas.

Daubenmire's "critical test" of the continuum hypothesis in steppe vegetation rests upon 21 samples of unstated size, in an area about 160 by 60 miles (256×96 km). These sites are of "maximum homogeneity" and in a "pristine and stable condition"; all "disturbed sites" are rejected. At no point does he state the criteria by which these elusive qualities are determined in an area poorly represented in the ecological literature (no references are cited). Anyone who has considered vegetational homogeneity recognizes the difficulty of assessing it. Daubenmire's footnote definition of homogeneity calls for a degree of omniscience that no ecologist will ever attain.

On the basis of these carefully selected examples, he recognizes four associations. The two westernmost are distinguished by the presence or absence of a single species, *Festuca idahoensis*. Somehow this one distinction is parlayed into two by the assertion that the entrance of the species marks "a biologically meaningful point on the moisture-balance gradient." No data on moisture balance are offered or cited. A third association is distinguished by the disappearance of one species—*Artemisia tridentata*—again at a "botanically significant" moisture level, identified only by the absence of *Artemisia*. It is interesting to note that *Artemisia* is described as disappearing "abruptly." But in the table offered in evidence the three stands of the *Artemisia-Festuca* association from west to east show frequencies of 25, 13, and 4, respectively—more a gradual decline

than an abrupt disappearance. In fact, the four most common species in this association show east-west gradients, and there is a greater difference in over-all composition between the easternmost and westernmost examples of the *Artemisia-Festuca* association than there is between these and the closest geographical example of the *Artemisia-Agropyron* association to the west or the *Agropyron-Festuca* association to the east.

It is of course crucial to Daubenmire's argument that the significant difference is the presence, in the *Artemisia-Festuca* association, of any amount of *Festuca idahoensis*, since this is the single criterion by which he has distinguished the associations. It is difficult to dispute effectively a one-species difference. The species is either there or it is not. Few ecologists, however, would accept a single-species difference as an adequate criterion for delimiting associations. It would not be acceptable to proponents of certain European schools of plant ecology. It is not acceptable to the many plant ecologists who prefer to use all species, weighting them by objectively determined values for quantity or importance. . . .

Daubenmire asserts in his forest example that population structure and dynamics are important in synecological research and that these are ignored by continuum studies. Early studies of forest continua in Wisconsin were in fact based on a premise of dynamic relations between the component species and interpreted as a successional series. It should not be simply his "impression" that they included seral stands; this was one of the major points which was emphatically made in these studies. Only later studies suggested that a continuum did not necessarily imply dynamic relations between stands.

It would be unfortunate if Daubenmire's parody of a continuum ordination were accepted as representative of the methodology used in continuum studies. No continuum study incorporates samples including as few as six mature trees. No such study is based on as few as eight samples. Only the earliest and most primitive of continuum studies simply lined up the samples in a linear sequence, and then only in the initial stages. Forest continua have not been

based solely on trees but have been demonstrated with herbaceous vegetation, either by itself or in addition to the tree species.

It is difficult to accept, as Daubenmire does, the concept of a floristic continuum and then assert that the product of the flora and the environment—the vegetation—is discontinuous. The argument assumes that the boundaries of dominance of a species are abrupt, while the total range of the species shows considerable overlap with species of other associations. To buttress his views of abrupt and coincident species boundaries Daubenmire cites the work of E. Dahl on Rondane Mountain. The portion of this work he refers to describes a transect across an area illustrated in a photograph as sharply defined vegetational zones. Dahl specifically laid his transects across these apparent zones. However, even here, close examination of the diagrams in which Dahl represents the species distributions in the transects does not support the claim of simultaneous species change with homogeneous areas between. The presumed coincident boundaries overlap for substantial fractions of their total distance on the transect, and composition changes within the area of dominance of one species so that the presumably uniform sections are not internally homogeneous.

An alternative interpretation of Daubenmire's data, based on his own criteria of stand selection and type delimitation, would be that from a search of a large area (about 9000 square miles) one may select a minute portion of the area that is susceptible, on superficial examination, to being grouped into discrete associations. If vegetation study is to be meaningful, however, it must apply to the vegetation as it exists over most of the landscape. This is the vegetation that covers the watersheds, provides food for the animals, and determines the aesthetic and economic qualities of the area.

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