Vegetation: Identification of Typal Communities

Stratification of samples and attention to population
structure reveal the existence of discontinuities.

R. Daubenmire

Throughout the brief history of scientific interest in vegetation, which becomes highly tenuous as one proceeds backward for more than a century, botanists have recognized *types* of vegetation. The recurrence of closely similar plant assemblages wherever the net influence of climate, soil, animal, and time factors have provided closely equivalent environments was early recognized, and these concrete units were combined to form abstract classes or types, each of which had consistent distinguishing characters. This perspective has prevailed to the present date, but in its century of development neither the methods of analysis of vegetation nor of organizing the subsequent data have shown much trend toward standardization. There has accumulated instead a spectrum of concepts, terms, and methods so broad as to discourage the novice and confuse even the specialist at times. The entire area of endeavor is rendered difficult by the facts that vegetation is a continuous variable and that under man's disturbing influences the distinctiveness of types is greatly weakened. But if there is to be such a thing as vegetation science, there must be a framework for organizing, storing, and retrieving the information, and one might expect the eventual triumph of that system which is most meaningful—one in which the mere indication of a position in the system automatically makes possible the maximum predictions about the unit.

In the last decade there has arisen a new perspective in the organization of vegetation data, the "continuum viewpoint," the supporters of which stress the continuity of vegetation and hold that classification of vegetation into

The author is professor of botany at Washington State University, Pullman.

types is arbitrary and unwarranted. In North America, at least, H. A. Gleason was first to challenge the validity of the type concept. In a paper published in 1926 (*1*) he held that species distributions are not correlated and that therefore any classification of vegetation is purely arbitrary. (There is an implicit assumption here that one species can never rise to such a dominant position over a portion of the landscape as to warrant recognition of a discontinuity on the basis of it alone.) Gleason offered no data. In 1939 he reworded his argument and republished it (*2*), again with no data.

In North American literature the idea lay dormant until 1951, when it was taken up by J. T. Curtis and his students. These workers developed special methods for collecting data and special methods of processing them arithmetically. For data collection they emphasized plotless techniques, which had been developed originally for timber inventory in the forests of Europe and which were seized upon by many North American ecologists because they were said to require less field labor than sample plots. Likewise, the methods for mathematical manipulation of data which these workers advocated have had an obvious appeal in an era when ecology is becoming more quantitative. Curtis's methods (*3*) yield one abstract number representing all the trees in each stand (15 acres or larger) studied in the field, and since this number—a "continuum number" or "index" with values ranging from 300 to 3000—is an adjusted sum of values, that is, it is influenced jointly by the kinds, densities, sizes, shade tolerance, and patterns of distribution of individual trees, no two stands are likely to yield the same sum. Curtis's continuum was

interpreted as representing vegetation gradation from wet to dry extremes of environment. Bray and Curtis (*4*) and others have experimented with methods involving more than one axis of variation, but the complexity of these techniques as they attempt to cope with the vast array of environmental gradients operating concurrently makes the results more satisfying to a mathematician than to a botanist.

An arrangement of stands according to one or more axes of variability, for example, the continuum index, is called an "ordination," and since the continuum indices for one region form a series lacking nodes, such a series appears to prove the absence of discontinua among stands such as would permit their grouping into *types* (or *associations*), each characterized by constantly reappearing features that distinguish it from other types.

Since continuum data have been produced wherever a continuum champion has chosen to work—and Curtis's group by no means furnishes the sole contributors to the continuum hypothesis as may be seen from the bibliography in a recent summary, by McIntosh (*5*), of continuum studies—whereas community-types have been defined and mapped in practically all parts of the world, we have a paradox demanding resolution. In my own work I have found significant discontinua, comparable to those documented by hundreds of workers following continental European methods. It appears to me that if one selects any of several appropriate methods, one can demonstrate a continuum anywhere. The crux of the problem, as I see it, lies in the validity of methods of gathering data, or in their subsequent manipulation, if not in both. I should like to demonstrate some continua that I consider significant bases for vegetation classification, and then comment on how the same mosaics of vegetation might have been sampled, or how my data might be manipulated, to provide an apparent verification of the continuum hypothesis. But before turning to this, let us examine briefly some concepts of the continuum champions.

Gleason (*2*, p. 106) expressed an opinion that "the forests of the foothills of the Rocky Mountains of Colorado, composed there largely of *Pinus ponderosa,* might be traced northward with . . . gradual variation, thence eastward along the northern boundary of the grassland in Canada, and again southward to the forests of Illinois, and lead

us to the extraordinary conclusion that the *Pinus ponderosa* forests of Colorado represent the same association as the *Quercus velutina* forests of Illinois and the aspen groves of Manitoba."

Curtis and McIntosh (*6*, p. 491) concluded that "the entire physiognomic upland hardwood forests [of southern Wisconsin are] to be interpreted as an entity (or portion of an entity) without discrete subdivisions."

According to McIntosh (*5*, p. 264), "the patterns of overlapping curves of species populations on environmental and compositional gradients defy attempts objectively to bound and enumerate unit communities."

Maycock and Curtis (*7*, p. 8) state that "if all species involved [in one association] are characterized by similar tolerances and no overlapping or integration of tolerance amplitudes occurs with species considered components of other vegetation types, then a separation of distinct associational units would appear to be justified." More briefly, these authors would consider units as distinct only if they had wholly different floristic lists.

Whittaker (*8*, p. 32) wrote, "When population curves of species are drawn together along 'an environmental' gradient . . . the resulting picture is not one of associations marked off from one another, but of a pattern of curves flowing into one another, a continuum of populations."

Cain (*9*, p. 198) commented that plant aggregations exhibit "unlimited variables, combinations and permutations," thus suggesting even less order in the landscape than is claimed by continuum advocates.

Stable Vegetation along a
Climatic Gradient across Steppe

I have located and analyzed nearly 200 well-preserved remnants of virgin-steppe vegetation in Washington, obtaining both vegetational and environmental data for small sites of maximum homogeneity. The various kinds of vegetation that may be found in this steppe region differ from each other as a result of (i) macroclimate, (ii) microclimate (this chiefly a consequence of slopes that face steeply to the north or to the south), (iii) soil (loam to sand, shallow to deep, saline or nonsaline), and (iv) disturbance (fire and grazing). Each of these environmental variables tends to have a distinctive influ-

ence on vegetation structure and composition. If a scientist wishes to make a clear test of the character of species distribution in relation to a gradient in one of these variables, he can hold all the other three constant. Let us consider responses of the steppe species in stable communities to a gradient of macroclimate. According to the continuum hypothesis, the gradual change in climate across our gently sloping plateau should result in imperceptible change in vegetation, with each species having a clearly defined optimal region and declining in abundance in both directions from this point, and with no two species showing coordinate patterns of distribution. To make our test critical we will reject all disturbed sites, and likewise reject rock outcroppings with average soil depth less than 25 cm, saline-alkali soils with pH 8.4 and above, dunes, marshes, and other special types of substrate, accepting only stabilized vegetation occurring on deep, well-drained silt-loam. Even loamy sites will be excluded if the slope exceeds 15 percent and thus produces significantly specialized microclimates.

I have drawn on a map (Fig. 1) a rectangle defining a broad transect that extends from the center of the rain-shadow of the Cascade mountains, where annual precipitation is very low and temperature relatively high, eastward up the gentle slope of the Columbia Plateau to the foothills of the Bitterroot mountains of Idaho, where precipitation is over 300 percent greater and temperatures are relatively low. Twenty-one of my study sites within this rectangle fit the requirements I have listed for a valid test of macroclimatic influence. Two stands of forest located just beyond the steppe boundary have also been included (on the extreme right in Fig. 1) in order to indicate the extent of penetration of steppe plants into forest. It is pertinent to note that every stand was located and analyzed prior to my decision to use the data for the present discussion.

In Table 1 the actual (not relative) coverage of plant canopies is given for all species that have as much as 5-percent coverage in at least one of the steppe stands. The horizontal arrangement of the 23 stands reflects their relative east-west position along the transect. The vertical arrangement of the species reflects shifting positions of the species distributions, from predominantly western to predominantly eastern.

In the western end of the transect the conspicuous shrub *Artemisia tridentata* and the large grass *Agropyron spicatum* provide about 90 percent of the total biomass of the communities, and these stands have been grouped into an *"Artemisia tridentata–Agropyron spicatum* association."

Progressing eastward, we reach a point where a second large grass, *Festuca idahoensis*, joins *Agropyron*, with *Artemisia* continuing as an overstory. On both a local and a geographic scale it is easily demonstrated that the *Festuca* has higher moisture requirements than *Agropyron*, so that its appearance on the uplands may be interpreted as approximating the point along a climatic continuum where increasing precipitation and decreasing temperature make it possible for *Festuca idahoensis* to maintain populations in the face of intense competition from *Agropyron*. If this botanical boundary is worth recognizing, and all botanists who have published papers on steppes of the Columbia River drainage have recognized the distinction, those *Artemisia* stands that contain the *Festuca* seem appropriately distinguished as an *"Artemisia tridentata–Festuca idahoensis* association." Although from a taxonomic standpoint this node is marked by the presence or absence of only a single dominant, from an ecosystemic standpoint two features are involved: the grass and a biologically meaningful point on the moisture-balance gradient. Not all species deserve as much recognition as this—for example, *Poa cusickii* and *Stipa thurberiana*, whose distributions in Washington bear no evident relation to climate, soil, animal influences, fire, or time, and which present no patterns over the landscape. *Agropyron spicatum* extends across all the steppe associations involved in this discussion, and so is of no more value in distinguishing the types than is day length of value in distinguishing environmental conditions along this east-west transect. Thus one must recognize the principle that, while all species limits must have some explanation (even if only on the basis of chance dissemination), not all species are of equal value in community characterization.

Very few ecotones in the region outlined are marked by a large change in the species lists. In species taxonomy it is a commonplace that two taxa may share so many characters that they are distinguished by only a fraction of their structural complexity. This principle
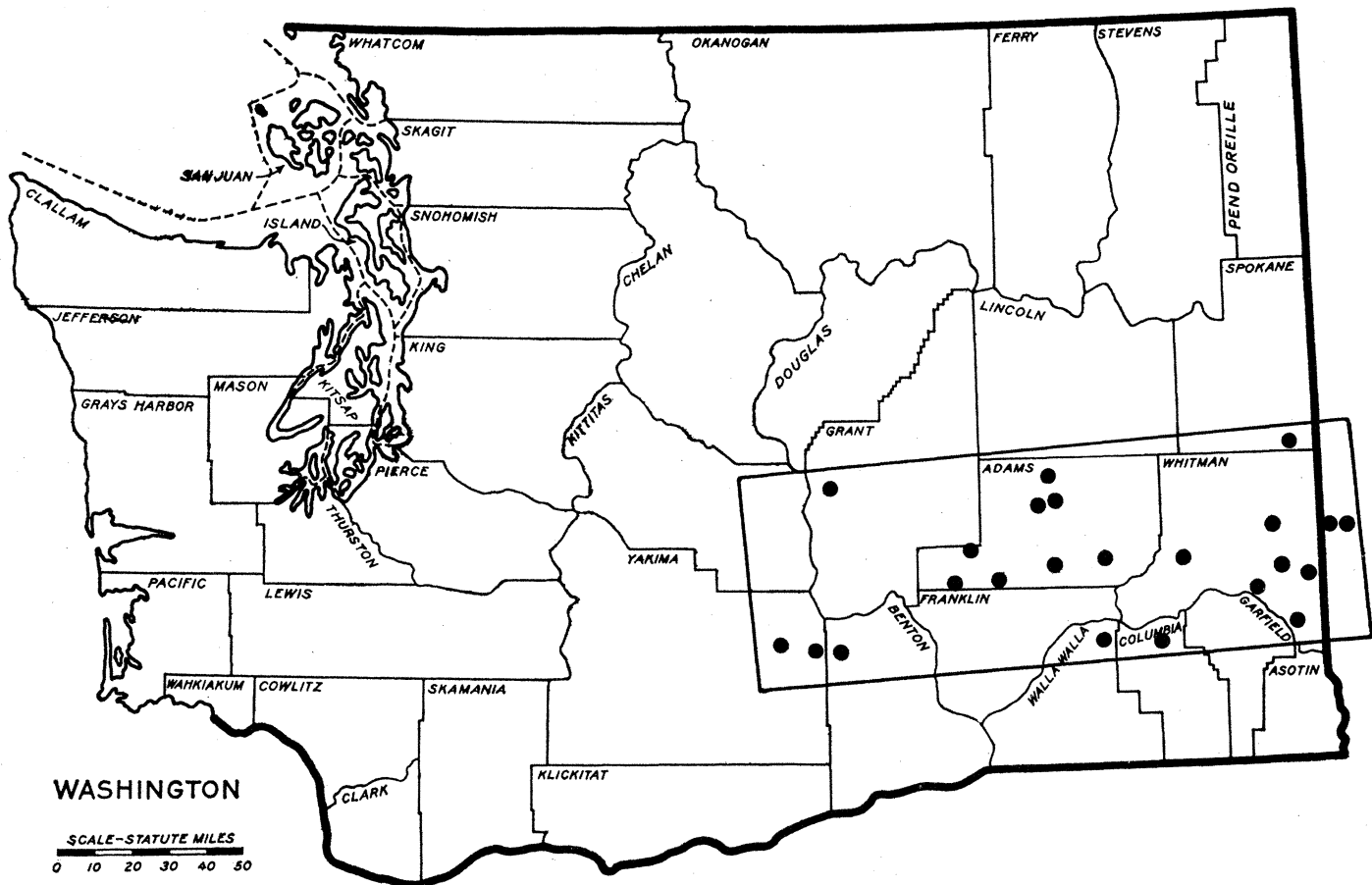
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Fig. 1. Locations of stands for which data are presented in Table 1. The geographic discontinuity that segregates the four western-most stands does not correlate with any of the vegetational discontinuities apparent in Table 1.

Table 1. Percent canopy-coverage of species in stands located in Fig. 1. Stands are arranged according to longitude, progressing from west to east in a belt 96 × 31 kilometers (153 × 63 miles) which crosses vegetation zones nearly at right angles. Species with coverages never rising to 5 percent are omitted. Plus (+) sign indicates less than 1 percent.

Median annual precipitation 167 mm ←——————————————————————————→ 526 mm
Mean annual temperature 11.2° C ←——————————————————————————→ 7.9° C

Species	Artemisia–Agropyron							Artemisia–Festuca			Agropyron–Festuca					Festuca–Symphoricarpos						*	†
Stipa thurberiana	5		3																				
Poa cusickii	2	9	+																				
Stipa comata	2	+	13	2	9	14		1		13	6												
Artemisia tridentata	18	18	9	9	16	19	11	25	13	4													
Chrysothamnus viscidiflorus			+			2	9	+	+	8	1		+										
Plantago patagonica			14	8		11			3	6	3	7	2	2	+								
Phlox longifolia	+	12		+	7	8	12	2	+	1		1	3	1	5	1							
Erigeron filifolia				3		5		+	+					+									
Astragalus spaldingii								2	1	2	+	+	6	2	13								
Poa secunda	40	50	29	61	55	73	36	44	38	5	19	39	16	23	45	2	+	2	+	+	+		
Achillea millefolium			+		+	+			+	2	1	2	3	1	+	22	10	6	9	25	25	1	
Agropyron spicatum	41	63	46	35	41	55	36	40	39	26	42	77	33	34	71	79	57		77	78	78	13	
Festuca idahoensis								9	23	39	29	7	71	75	8	81	30	41	35	40	40		
Senecio integerrimus																+	2	8	3	2			
Myosotis stricta																2				5	5		
Haplopappus liatriformis																10	8			+	+		
Koeleria cristata																5	3		+	4	4		
Hieraceum albertinum																5	+	4	11	1	1		
Lupinus sericeus																6	1	2		3	3		
Festuca scabrella																		51					
Sidalcea oregana																	8						
Castilleja lutescens																	+	2	9	5	5		
Arnica sororia																5			+				
Solidago missouriensis																29						1	
Balsamorhiza sagittata																		41	14	51	51		
Helianthella uniflora																				31	31		
Astragalus arrectus																				18	18		
Poa ampla																57	53					9	
Rosa nutkana + R. woodsii																1	2		+	1	1	1	
Iris missouriensis																+	29		2	1	1	+	
Potentilla gracilis																6	21	+	45	5	5	2	
Geranium viscosissimum																	21	+	4			1	
Galium boreale																+	11			1	1	1	+
Symphoricarpos albus																4	15	2	11	17	17	42	30

* Pinus ponderosa–Symphoricarpos albus association. Only those species which occurred in the steppe stands are shown. † Pseudotsuga menziesii–Physocarpus malvaceus association. Only those species which occurred in the steppe stands are shown here.

should not be debarred from ecosystem taxonomy, as it is by the argument that vegetation types must be distinguished by a complete difference in floras.

As we continue eastward, *Artemisia* disappears abruptly from upland silt-loams (Table 1), leaving only a monotonous herbaceous cover in which the same two grasses (*Agropyron* and *Festuca*) are overwhelmingly dominant. Here again, a botanically significant higher level on the moisture-balance scale is indicated by the dropping out of one species, *Artemisia* (along with shrub-dependent birds, epiphytic lichens, and all their parasites and epiparasites); the name "*Agropyron spicatum-Festuca idahoensis* association" will be used for stands of this character. This phytogeographic line winds across the steppe region in Washington and continues southward into Oregon. Like the other vegetational discontinuities revealed by this type of study, this one is capable of precise climatic definition, with all climatic stations on the *Artemisia-Festuca* side having drier climate than all those on the *Agropyron-Festuca* side. Again the limits of one dominant species constitute the chief biologic phenomenon, marking an ecologically important node along the climatic gradient.

Eastward, one more discontinuity is strikingly shown by a rich assortment of perennial dicot herbs and low shrubs that rather abruptly and concurrently find moisture-temperature relations adequate. They are added to the major species of the drier grassland. For the most part the three species which abruptly drop out at this same point are low plants that cannot endure shading by the dense and luxurious meadow-steppe. This fourth subdivision of our steppe transect is conveniently referred to as the "*Festuca–Symphoricarpos albus* association." The ecotone here involves the addition of a *group* of species of equal synecologic significance in the wetter climate, and the disappearance of *several* species that are apparently unable to maintain themselves on deep silt-loams, with gentle relief, in the cooler climate. But the climatic distinction, while quantitatively definable, is no more pronounced than the two nodes described previously, where the vegetation discontinuity involved much less of a biologic break. Thus, multispecific and monospecific floristic discontinuities may have equal ecologic validity, provided, of course,

they are related to positions on environmental gradients, a requirement that eliminates the vast number of patterns of minor species that seem to bear no clear relation with other characters of their ecosystems.

The abruptness of the transition from steppe to forest in eastern Washington is marked by the dominance of a single tree, *Pinus ponderosa*. A little farther along the climatic gradient *Pseudotsuga menziesii* appears, and as it is competitively superior to *Pinus,* it marks a second clearly defined forest belt. The data for the two forest stands in Table 1 include only the species found in the steppe, as the purpose here is to allow the reader to observe the degree of abruptness of declining coverage of steppe species in the sequence of undisturbed forests beyond the steppe border.

Recognition of these four steppe zones seems thoroughly justified from the standpoint of synecology. Their limits can be stated quantitatively in terms of either climax vegetation or climatic data. That single-species differences comprise the major floristic distinction at two of the ecotones seems to me no reason for depreciating the ecologic significance of these discontinuities, especially since these are important dominants. Furthermore, the zones so defined extend both north and south of the transect (where other stands have been studied in equal detail), with the *Artemisia-Agropyron* and *Artemisia-Festuca* associations extending into Oregon, then reappearing beyond a mountain barrier in southern Idaho. The *Agropyron-Festuca* association and the *Festuca–Symphoricarpos* association extend into the Grangeville region of central Idaho. Such steppe subdivisions are thus not local arbitrary subdivisions of the landscape, distinguished by mere fortuitous species distributions. They represent ecosystem types with consistent environmental differences, furnishing the basis for mapping mutually exclusive bioclimatic areas, and allowing one to relate climate to vegetation structure in rather precise terms.

Goodall (*10*, p. 308) states that "so far evidence of continuous variation in vegetation has generally indicated that each species behaves independently of the others, so that a succession of optima for the various species is passed as one traverses the environmental gradient." And indeed for a few of the species in Table 1 (chiefly *Chrysotham-*

nus, Potentilla, and perhaps *Symphoricarpos*) it would be possible to smooth the data and select some appropriate ratio of ordinate to abscissa to demonstrate normal curves of changing dominance across the climatic gradient. Then for perhaps six of the plants (*Achillea, Erigeron, Iris, Plantago, Poa cusickii, P. secunda*) decidedly skewed curves might be justified. For *Astragalus spaldingii* the curve would have an inverse flexure. Thus only 3 percent of the species show changes in dominance that resemble the swarms of independently staggered, bell-shaped curves that have been offered in support of a vegetation continuum. The normal curves that we might make out of the data for a few of the species are far less striking than the rather abrupt and sometimes coincident changes in dominance, particularly among the dominants, that reveal obvious discontinua.

Now it is perfectly clear to me that this transect could be sampled so as to get types of data providing none but bell-shaped curves of variation in coverage. All one would have to do is sample the landscape randomly, or at least practice less rigorous stratification with regard to soils, slope exposure, or disturbance. For example, one can find *Festuca idahoensis* in the *Artemisia-Agropyron* zone, but only on steep north-facing slopes where precipitation transfer over an unusually high ridge top, combined with abnormal protection from sun and wind, provides highly specialized conditions with respect to microclimate and soil. Conversely, the *Artemisia-Agropyron* association extends into the *Artemisia-Festuca* zone, but only on the upper parts of slopes that face so steeply to the south as to exclude the *Festuca* by virtue of specialized microclimate and soil conditions. This situation, or some ecologically similar variant, prevails at all the zonal ecotones, resulting in peninsular interfingering or island-like inclusions of one type in the zone of another; yet the boundaries of the stands remain surprisingly sharp, and the defining characters hold for all extrazonal stands. If one restricted his attention to the upper parts of south-facing slopes of about 20 to 40 percent, he would encounter the same discontinuities along this climatic gradient, but with the positions of the geographic limits shifted considerably eastward; and vice versa for steep north-facing slopes. The microclimatic islands in which each

association finds adequate compensation for worsening climate get smaller and smaller until they are only a few meters in diameter. But random sampling of the landscape that ignored the boundaries of these islands, and fused data from steep slopes with those from gentle slopes where vegetation bears a clear relation to macroclimate, would artificially blend one type into another and appear to demonstrate a continuum.

Goodall (10, p. 511) suggests that an objective test can be made of the concept of relatively homogeneous stands separated by usually narrow belts of conspicuous intergradation, "provided the samples are small compared with the size of the individual stands postulated." A restriction in size might indeed reduce the proportion of objectively determined samples that would straddle obvious ecotones. But this only raises another difficulty, for aggregation among the individuals representing most species places a restriction on the smallness of sample. If plots are too small, those falling in what might be considered one association bear scarcely more relation to each other than those representing different associations. Even small samples must be stratified to avoid the ecotone problem. In my steppe mosaic the aquatic *Scirpus* can grow within a meter of the xerophytic *Artemisia rigida,* yet a square meter is inadequate as a sample of the two communities involved by almost anyone's standards. If both species were recorded for the same plot, then the record would form a bridge suggesting a blending of two ecosystems that are extremely contrasted. A recording of 10-percent coverage by the *Artemisia* would carry an implication that 10 percent is distributed over the sample, whereas it is restricted to a corner opposite *Scirpus.* Where would one collect soil samples in an attempt to relate this unit of floristic "information" to the edaphotope? The data from plots of this nature are an artifact of the method of objectively sampling the landscape.

If two methods of analysis support different conclusions, one must ask whether they are equally valid. As I see it, no sample is valid unless it is drawn from an area of maximum homogeneity (11). If one uses field methods such that the stands delimited are of maximum homogeneity, then applies ordinary scientific procedure in testing vegetational relationships with
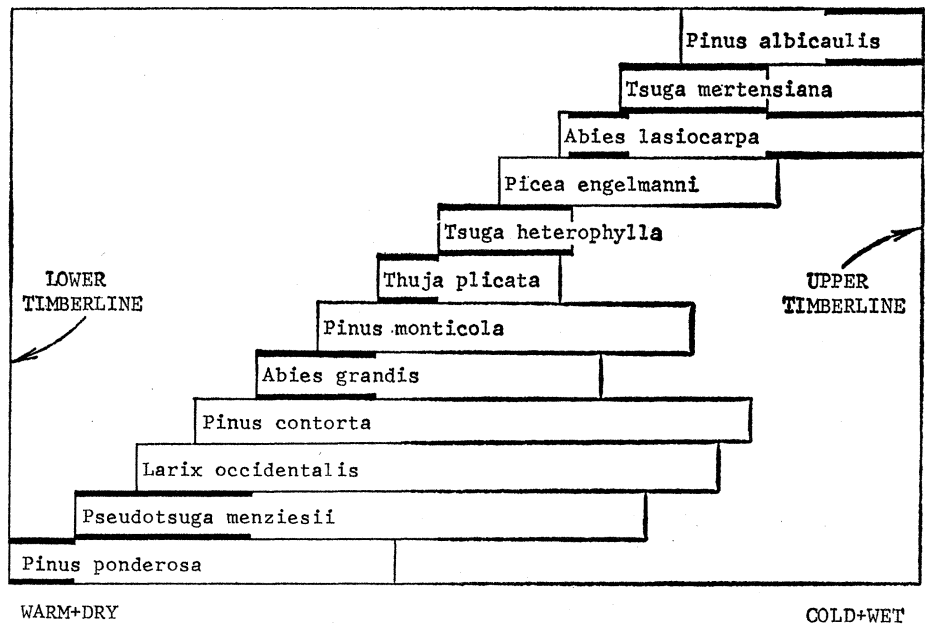
Fig. 2. Coniferous trees in the area centered on eastern Washington and northern Idaho, arranged vertically to show the usual order in which the species are encountered with increasing altitude. The horizontal bars designate upper and lower limits of the species relative to the climatic gradient. That portion of a species' altitudinal range in which it can maintain a self-reproducing population in the face of intense competition is indicated by the heavy lines.

one factor-complex at a time, any weak tendencies toward bell-shaped trends in species abundance are overshadowed by definite discontinuities.

Let us turn to a different aspect of the problem, one that is well illustrated in the forests just east of these steppes.

Importance of Stability

Upon leaving the Washington steppes and entering the Bitterroot mountains one encounters the coniferous tree species that characterize the mountain landscape in a highly predictable order (Fig. 2). First, at lower timberline, is our most drought-resistant tree, *Pinus ponderosa.* Then under slightly cooler and more moist conditions we encounter *Pseudotsuga,* then in turn *Larix, Pinus contorta,* and so forth. In this diagram I have attempted to show only relative lower and upper limits of the principal tree species along the moisture-temperature gradient. It is evident that no two species have the same ecologic amplitudes. Although the diagram does not so indicate, when one first encounters a species it is a minor constituent of the entire landscape, for at the lower margin of its range it finds only highly specialized habitats suitable. Progressing into the mountains it occupies a variety of sites and be-

comes generally conspicuous. Then at still higher altitudes it again becomes narrowly confined to some habitat of compensation. Thus we can generalize that the tree *flora* is a continuum, in that each species has a distinctive range and is best represented in the landscape near the middle (climatic optimum) of its range.

What I have said about the trees applies equally well to the shrubs and herbs that form the forest undergrowth, and to the steppe flora as well. Certainly if one takes into account only *species distribution* and *relative abundance over the landscape,* vegetation is a continuum lacking nodes useful for establishing natural subdivisions. But in dealing with the plant components of ecosystems must we restrict our attention to *species distribution* and *relative abundance,* as is usually done in continuum-oriented research? These are such elementary floristic concepts that they are fully as much a part of taxonomy as of synecology. In synecology we must come to grips with matters of more fundamental biologic importance, especially population structure and dynamics.

Referring again to Fig. 2, along most of the climatic gradient represented here several species are in contact with each other, each of them competing for a place in the sun. In nearly all cases,
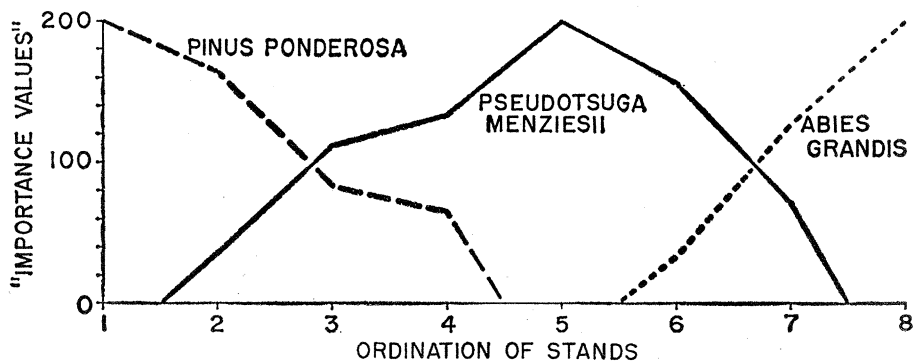
Fig. 3. Graphic portrayal of "importance values" in Table 2. Groups of stands are arranged in order of increasing moisture availability, the stands within each group being arranged according to increasing proportions of shade-tolerant species. Because of their very low values, *Larix* and *Pinus contorta* are omitted.

population structure in homogeneous stands of these montane forests shows that one tree species is clearly superior to all others, with the superiority shifting from one species to another along the climatic gradient. To illustrate, Table 2 contains complete tallies of all trees by species and size on six homogeneous areas, each 15 × 25 meters. Stand 1, which I would interpret as being "near-climax" (*12*), shows by its population structure that, of the three species present, *Thuja* is superior in the capacity to reproduce on this site after intense competition has developed. From this one might predict the future outcome of competition here to be a pure stand of this species. Indeed, we can find nearby areas visited by fire less recently where all seral trees have been

eliminated, and so verify this prediction. Thus stand 2 is composed of old *Thuja* trees about a meter in diameter, the only other tree species being *Abies grandis,* which is represented by seedlings resulting from seeds that are annually blown in from contiguous habitats and are unable to survive much past germination here.

In slightly drier areas we find stands, such as stand 3, in which *Abies grandis* seems the only tree capable of self-reproduction. Again, on comparable sites that have had a longer history since disturbance, we can find stands in which all seral trees have been eliminated, such as stand 4. In a still drier climatic belt *Pseudotsuga,* according to data for stands 5 and 6, can eliminate all competitors that may be able to in-

vade an area devastated by fire or logging.

An extremely important principle is illustrated by the data for these six stands. A tree which is climax in one habitat type is usually seral in one or more contiguous habitat types, so that in disturbed stands we have unstable mixtures of species which, in the absence of further interference, sort themselves out into pure stands. Similar population analyses of many old, undisturbed forests in these same mountains show that in more than 95 percent of the stands population structure points clearly to one species as capable of displacing all others.

Now if only one tree species is the climax dominant on most habitats, Fig. 2 can be made more informative by shading in those segments of the species' moisture-temperature range where each attains this state of preeminence. (Note that a few taxa are such poor competitors that they never can replace themselves where contested.) In a belt along lower timberline, *Pinus ponderosa* retains climax status for lack of any other tree competitor, but immediately as environment in the foothills becomes moist enough for *Pseudotsuga,* the pine occurs only as a temporary occupant of burned or logged sites, where population structure shows that it is invariably replaced, in time, by *Pseudotsuga. Larix* and *Pinus contorta* are additional seral species on *Pseudotsuga* sites; nowhere in our region can they reproduce successfully under competition from another tree.

Then farther back in the mountains, as the water balance continues to change in the same direction, a point is reached where *Abies grandis* can establish seedlings. Here *Pseudotsuga* is at once reduced to a seral role, along with *Pinus ponderosa, P. contorta,* and *Larix.* Since some species, such as *Larix,* are always seral, and others play seral roles on several sites in addition to a climax role on one, Fig. 2 as a whole shows that a wide variety of mixtures can result from chance dissemination, while most habitats are becoming reforested naturally. But if it is possible through population analyses to classify practically the entire climatic gradient according to tree species that are competitively superior in different segments of that gradient, we are provided here with a synecologically very important basis for recognizing discontinuities along the moisture-temperature gradient which anyone can verify by objective means. The ecotones

Table 2. Population analyses for trees in areas 15 × 25 meters, each in a different homogeneous stand of forest that has never been logged or evidently grazed by livestock. Data represent the number of trees in each category.

Tree flora	Diameter at breast height (decimeters)									
	0–0.5	0.5–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8+
Stand 1—Near-climax										
Thuja plicata	38	1	3		4	1	4		1	2
Abies grandis	82								1	1
Pseudotsuga menziesii										1
Stand 2—Climax										
Thuja plicata	1					1	1	1		5
Abies grandis	172*									
Stand 3—Near-climax										
Abies grandis	37	4	12	7	2	2				
Pseudotsuga menziesii				1	1					
Pinus contorta			2	2	1					
Pinus ponderosa					1					
Stand 4—Climax										
Abies grandis	50	2	6	5	6	2	1	1	1	
Stand 5—Near-climax										
Pseudotsuga menziesii	2	11	29	20	1	4	1		1	
Larix occidentalis						4	1			
Pinus ponderosa			1					1		
Stand 6—Climax										
Pseudotsuga menziesii	107	4	8	2	8	9	2			

* Current-year seedlings, from seeds produced in abundance in contiguous habitat.

established on this basis are nearly always narrow—surprisingly so. According to this diagram, eight types of forest are recognizable on the basis of the dynamic relations among the trees. Most of these eight types are then susceptible of subdivision on the basis of distinctive types of herbaceous and shrubby undergrowth.

Although population analyses reveal the existence of clear vegetational discontinuities along the climatic gradient, one can take the same quantitative data and use other methods of summarizing them to obtain a series of normal curves that can be presented as proof of a continuum. Table 3 contains the population data for eight stands of trees. Horizontal breaks divide the stands into groups in each of which the same species seems transcendent. Thus each group represents a habitat type with equivalent climax potentialities (for the tree layer) throughout. In ordination methodology all species are usually considered of equal significance, and all the larger individuals too—small trees being ignored—are considered of equal importance regardless of size. In accordance with this procedure, in the right-hand section of Table 2 trees less than 1 decimeter in diameter have been ignored, the others summed, then relative density and relative dominance (as basal area) have been calculated. In the last column on the right the sums of relative density and relative dominance are referred to as "importance values." These values can be used to plot the changing "relative importance" of the species along the climatic gradient, as has been done in Fig. 3.

This exercise demonstrates strikingly how, by ignoring population structure and dynamics, and by confining attention to floristics and relative abundance, with all species treated as having the same synecologic significance wherever they occur, a floristic continuum can be demonstrated. Goodall (10, p. 302) says that to divide a continuous variable (such as vegetation) "into discrete classes, and use class membership in place of position in a series, necessarily involves a loss of information." In our comparison above, it would seem that it is the continuum approach that obscures fundamental competitive relations of paramount importance.

The data in Table 3 can be used to demonstrate a misinterpretation that may arise when a continuum is hypothesized on the basis of the individualistic moisture requirements of trees without regard for differences in their population structure. Such an approach would align stands 6, 7, and 8 in this order, grading from the one having the greatest proportion of relatively xerophytic trees (especially *Pinus ponderosa*) to the one that is a pure stand of *Abies*. But such an alignment suggests degrees of xerophytism among the stands that do not exist. The presence of the *Pinus* in stands trending toward pure domination by *Abies* means only that when the area was last deforested by fire, one or more trees of *Pinus* happened to be within dissemination distance. *Pinus ponderosa* can invade sites much more moist than it can then retain in the face of competition, and in fact makes its best growth on such sites (13). Thus the varying proportions of *Pinus* and *Abies* indicate not varying degrees of environmental dryness, but varying stages in the displacement of *Pinus* by *Abies*. While there must certainly be a gradient of average moisture conditions across the *Abies grandis* belt (from its dry edge next the *Pseudotsuga* belt, to its wet edge next the *Thuja* belt), seral stands with abundant *Pinus ponderosa* are well represented along even the wet edge, whereas pure stands of self-reproducing *Abies* can be found within a few meters of the dry edge. The climax type of community exhibits ecologic amplitude as clearly as does any species.

Table 3. Population analyses of trees in eight homogeneous stands of forest that have never been logged or evidently grazed by livestock. Data represent the number of trees in each category. Each stand was 15 × 25 meters or larger, with data reduced to this basis. Derived statistics are based only on trees over 1 decimeter at breast height. Relative density and relative dominance (as basal area) each add up to 100 for a stand, and their sum is always 200 for a stand.

Tree flora	Diameter at breast height (decimeters)									Derivations		
	0–0.5	0.5–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	Relative density	Relative dominance	"Importance value"
Stand 1												
Pinus ponderosa	15	4		1	2	2	1			100	100	200
Stand 2												
Pinus ponderosa			4	11	6	3	1			86.2	77.8	164
Pseudotsuga menziesii	25	8		1	1	1	1			13.8	22.2	36
Stand 3												
Pinus ponderosa	1	1			1				3	11.8	72.8	85
Pseudotsuga menziesii	69	39	29							85.3	26.3	112
Larix occidentalis			1							2.9	0.9	4
Stand 4												
Pinus ponderosa		0.7	0.3	1.3	0.7		0.3			41.9	24.5	66
Pseudotsuga menziesii	1	0.7		1.0	0.3	1.0	0.3	1		58.1	75.5	134
Stand 5												
Pseudotsuga menziesii	107	4	8	2	8	9	2			100	100	200
Stand 6												
Pinus ponderosa	4									0	0	0
Pseudotsuga menziesii	42		7	6	5					72.0	85.3	157
Pinus contorta	5			1						4.0	4.7	9
Abies grandis	56	3	6							24.0	10.1	34
Stand 7												
Pseudotsuga menziesii				1		1	4			24.0	49.1	73
Abies grandis	330	1	7	8	2	1		1		76.0	50.9	127
Stand 8												
Abies grandis	50	2	6	5	6	2	1	1	1	100.0	100.0	200

Discussion and Conclusion

The data I have used to demonstrate discontinuities represent vegetation in essentially pristine and stable condition. It is generally recognized that such vegetation consists of types that are more distinctive than derivatives subsequent to grazing or burning (14). This principle of landscape convergence attendant upon disturbance is clearly illustrated in both steppe and forest in my study area. Continued heavy grazing by livestock in the drier (*Artemisia-Agropyron, Artemisia-Festuca,* and *Agropyron-Festuca*) zones fosters communities in which the introduced *Bromus tectorum* everywhere becomes the major dominant, regardless of soil texture, depth, salinity, macroclimate, or microclimate. But starting abruptly with the *Festuca-Symphoricarpos* zone and continuing upward through the forests even as far as the lowermost *Abies lasiocarpa* forests, excessive livestock grazing converts most of the landscape into communities in which *Poa pratensis* is the outstanding dominant. Thus if my data had included grazed stands in each zone, the discontinuities would have been weakened in proportion to the degree of disturbance represented, and if none but heavily grazed vegetation were available for study, one would expect to find only the discontinuity where *Bromus* and *Poa* swards meet.

It is my impression that nearly all studies supporting the continuum viewpoint have included many severely disturbed or seral stands, if they were not based on these exclusively. In Curtis's investigations (3) of forest remnants scattered over the intensively farmed landscapes of southern Wisconsin, he had to adopt standards that would permit inclusion of a stand of trees developed on an area that had been clear-cut only 26 years previously, and of which up to 10 percent of the total tree population had recently been selectively logged. Since stability in these forests requires several centuries, extremely labile vegetation made up much if not most of the data on which the forest continuum for southern Wisconsin was based. The Great Smoky Mountains of southeastern North America have been subjected to extensive and varied types of disturbance, listed by Whittaker (8), such as the catastrophic elimination of *Castanea dentata;* yet Whittaker used mechanically determined sampling points for compiling his lists, providing no evidence for degrees of stability and making no claim for homogeneity of

each sample. In Wales, Anderson (15) distributed 100 plots, each 3 × 3 meters, in a randomized pattern over a heavily grazed landscape, then, for reasons not fully clear to me, chose to leave out of consideration the second most important dominant (*Pteridium*), and demonstrated continuity that I feel sure could be equalled in eastern Washington if the plots were distributed over equal area, attention were confined to the heavily grazed lands, and *Poa pratensis* areas were ignored.

Many additional illustrations are available to show that continuum advocates have used disturbed vegetation mosaics in which seral mixtures can provide frequent bridging between otherwise reasonably distinct stable types, or in which degradation has proceeded to a relatively stable network of variation that is infinitely simpler than the mosaic which it replaced. Any argument that such intergrades are now the prevailing vegetation, and so must "objectively" be included, is more pragmatic than fundamental, for it ignores the synecologically significant phenomenon of the sharpening of ecotones by competitive elimination.

Finally, I would like to return to a point I made earlier—that even where undisturbed vegetation is sampled, methods of analysis or of subsequent data manipulation can completely determine the nature of the conclusions reached. This point is cogently illustrated by a comparison of two studies: Dahl (16) has presented the results of detailed analysis of vegetation in a transect across the gradual environmental gradient of a snowbed, which in his photograph shows discrete vegetational zones. By his methods of analysis he showed that "at certain points the frequency of a number of species changes simultaneously while the vegetation is comparatively uniform in between. This simultaneous change is probably due to the fact that plants live in communities where competition factors are of importance. The zonation of the transects is not based upon an arbitrary choice of one indicator species." Dahl believes that "an objective classification is possible, i.e., a classification largely independent of the observer." It is instructive to compare this with the report by Beschel and Webber (17) who also analyzed vegetation along a transect across a gradual environmental gradient, in this case from swamp to uplands in the forests of eastern Canada. These authors say that "this vegetation shows distinct belts of the dominants from the

air," but by the methods of analysis and data manipulation which they employed they "did not find a sufficiently sharp break along the transects within the swamp forests to warrant a separation into different communities." It would seem that with so many possible ways of analyzing vegetation, some leading to opposed conclusions, any method failing to reflect discontinuities that are apparent even from a photograph might be at least suspect.

It seems hardly debatable that the earth's *flora* presents a continuum, with the plant life of one area blending imperceptibly with that of contiguous areas, this including vegetation at all latitudes. In support of this, see the extensive compilation of floristic data by McIntosh (5) in support of this. But in order to reach the conclusion that *vegetation* (involving dominance parameters of flora) likewise is fundamentally a continuum, lacking nodes, it seems necessary to adopt methods that either (i) employ heterogeneous samples rather than samples based on rigorous ecologic stratification, or (ii) ignore the important influence of population dynamics in determining the discreteness of vegetation types. There is no denying that vegetation presents a continuous variable by virtue of ecotones; the argument hinges on the existence or absence of plateau-like areas exhibiting minor gradients separated by areas of steeper gradients, with the plateau-like areas being of sufficient similarity to warrant being designated as a class.

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