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A FUNCTIONAL, FACTORIAL APPROACH TO PLANT ECOLOGY

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Plant ecology is concerned with interrelations of plants and their environments. This paper proposes a scheme for considering the qualitative aspects of these interrelations with some rigor and completeness. It also makes such interrelations amenable to quantitative treatment.

The proposed scheme is based on the theory that specific environmental factors exist and that they determine the characteristics of vegetation. This theory, implicit in plant ecological literature, can be elaborated to explain some of the empirically determined propositions and concepts of plant ecology.

The concept "interrelations" used by ecologists can be interpreted as the concept "function" used in quantitative science. The two ideas are basically one. Therefore, this paper approaches plant ecology as the study of the mathematical functions which relate vegetation to its environment. More precisely, these mathematical functions relate the specific properties or characteristics of vegetation to the groups of factors which we conveniently call "vegetation determining factors."

The methods and scheme suggested here may appear to contradict the holocoenotic belief exemplified by Cain's (1944: 19) statement: ". . . the complex interrelations among the environmental factors, and between them and the organism, with its complex physiological and morphological interrelations, are such as to defy solution in exact terms of causation. Ecological problems not only may be difficult of solution because of the interaction of factors and responses, but they may really be insoluble in a mathematical sense." However, the approach proposed here stresses only that the establishment of quantita-

tive functional interrelations in plant ecology is possible, provided one restricts the study to causation between vegetation and environmental factors (groups of factors determining vegetation) and deliberately omits the causes of variations in the environmental factors themselves. Causes of variations in the environmental factors are considered to be parts of such sciences as climatology, geology, geomorphology, pedology, anthropology, human history, organic evolution, and historical plant geography; they are left outside this treatment of plant ecology. In an etymological sense these sciences are ecological, but they are not considered plant ecology—which is the subject of this paper.

Solution of quantitative interrelations of vegetation and environment can be developed along the line Jenny (1930, 1941, 1946) used for the examination of soils in relation to environment. The basic thought of this paper and many specific ideas in it stem directly from the approach to soils used by Jenny. The writer very gratefully acknowledges this primary debt, the active encouragement Dr. Jenny has given to expansion of his own ideas, and his help on this manuscript. Discussions among Drs. H. Jenny, R. L. Crocker, and N. C. W. Beadle in 1949, which considered some of this paper's points, were attended briefly by the writer who appropriated the mutual conclusion identifying the flora as the independent aspect of the plant cover; vegetation as its dependent aspect. I wish to thank all three men for criticisms and opportunity for discussion. However, they should not be blamed for the following presentation, and it is not implied that they agree with it.

THE FACTORIAL EQUATION

Jenny (1941) relates any soil property, s , to the factors of soil formation as follows:

$$s = f(cl, p, r, o, t). \quad (1)$$

This simply states in abbreviated form that a soil property s is a function of, f , or conditioned by, the five groups of factors represented by the symbols in parentheses. The factors were given these meanings by Jenny:

cl = air climate (regional climate)

p = parent material from which the soil originated

r = topography or relief; referring to slope, exposure, and certain ground water conditions

o = biota or organisms

t = duration of soil formation or time.

These five soil forming factors are evidently the same factors which determine vegetation. . . . This statement is the crux of our argument. A wealth of plant geographical observation has demonstrated that vegetation is distributed in accordance with regional climatic patterns, changes as soil parent material changes, differs on opposing slopes, varies with the geographical differences between floras, and develops with time. The reader is referred for documentation to the classical works by Schimper, Warming, Clements, and to the texts by Weaver and Clements, Braun-Blanquet, Lundegårdh, Oosting, Daubenmire. Most of these books demonstrate in more or less explicit form by their organization the groups of habitat factors on which vegetation depends.

Since the five groups of factors of soil formation are the same factors which condition vegetation, it is permissible to write:

$$v = f(cl, p, r, o, t), \quad (2)$$

where v represents any property of vegetation that can be expressed in quantitative terms, such as weight per unit area.

Jenny designates the factors cl , p , r , o , and t the independent variables, in the mathematical sense. This designation

has caused confusion since, as is well known, some of these factors are not always independent of each other. What Jenny implies is that they may be found in nature under such a great variety of combinations that the effects of one of them on soil can be studied independently of variations among the others.

For example, a given type of rock, say granite, occurs in various climates; thus climate may be considered independent of rock type in its effects on vegetation and soil. Different slopes may be made of one type of rock; thus slope angle may be independent of the geological substratum in its effects. Low or high rainfall may occur in different areas along a given isotherm; therefore, it is possible to evaluate the influence of variable moisture on soil and vegetation at the same mean annual temperature. In other words, among the many different combinations of particular values of cl , p , r , o , and t found in nature it is often possible to select suitable combinations to evaluate the factorial equation. Illustrations of the method are given in subsequent pages.

Not only are specific properties of vegetation, v , related to the five environmental factors, but also entire plant communities, V , are conditioned in the same way. Therefore:

$$V = f(cl, p, r, o, t). \quad (3)$$

A plant community, designated by V and defined as a distinctive organized grouping of the plants living together in a circumscribed area, is a unit of vegetation. Such units have usually been described physiognomically or floristically. Both methods are qualitative, not quantitative, and do not produce a singular, characterizing number. A plant community is usually not summed up in a single number. Therefore, the functional relation of a plant community to its environment cannot yet be described quantitatively, mathematically. However, the dependence of a plant community on its five factors

can be stated in a factorial, qualitative way.

Besides being the factors of soil formation and the factors determining vegetation, these five—climate, soil parent material, topography or relief, organisms, and time—seem also to be factors which fix the character of any ecosystem or geographic landscape. Therefore they may be called ecosystem or landscape factors. They have areal extent and within this area form a unit which has been variously named an ecosystem (Tansley 1935: 299), coenose, biogeocoenose (Sukachev 1944), landscape, natural area (Cain 1947), environment, habitat (Munns 1950: 41), site (Munns 1950: 75) (note that these last three terms *do* include organisms found on the locality considered). None of these terms has prescribed limits of areal extent; and since, with the exception of parent material, there are few sharp breaks in the environmental factors, but instead they vary continuously, the size and extent of the kind of unit geographical area considered here is determined by the purpose and methods of a study.

The equation, $V = f(cl, p, r, o, t)$, has been printed by Tüxen (1931/32: 183) in abbreviated form.¹ Its use is implicit in ecological work at least from Schimper's time to the present. This paper proposes it as one explicit, fundamental, and logical starting point in relating a plant community to its environment. The equation may provide a unified and complete approach to plant ecology, obviously not to plant sociology since the latter's aims are different. Posing the equation is only a beginning.

¹ Tüxen (*loc. cit.*) actually wrote, "Vegetation = f (Climate, Soil, Man), in which simplified scheme the rock, relief, and moisture which are of first importance for soil formation are reckoned to the factor soil and on the other hand the influence of animals in addition to man (in long-cultivated lands at least) may be neglected as vanishingly small. In one large geographic area, natural and climatically uniform, . . . vegetation = f (Soil)."

DEFINITIONS OF TERMS OF THE EQUATION

A principal value of the fundamental equation is in pointing out the need for and in helping to define terms and concepts which are basic to plant ecology. The six concepts represented by the symbols V and v , cl , p , r , o , and t enter the fundamental equation and must be defined.

In accord with equations (2) and (3) in our definitions vegetation itself is dependent; it is dependent on the factors that determine it. A particular plant community is selected from the available flora by the environment of a particular locale, to paraphrase Crocker and Wood (1947), who refer the basic idea to Darwin. The other terms of the equations—the vegetation determining variables—are controlling and are treated as independent factors; that is, each environmental factor is defined so it is independent of the other terms of the equations. Actually, these determining factors are groups of variables classed under the headings climate, relief, etc., as a matter of convenience and logic. The following definitions may be bases for discussion.

Properties of vegetation

Vegetation is defined here as the more or less organized plant cover of a region. It has many definable and measurable properties.

The following v -properties of vegetation can be quantitatively expressed, are therefore suitable for functional relationships, and will illustrate what is meant by a dependent property of vegetation: Autecological (referring to individual plants or plant species) properties include abundance, cover, production or weight per unit area, frequency, site index, constants of the age class distribution curve. Synecological (plant community) properties include abundance, cover of both living and dead vegetation, production or weight per

unit area, constancy, proportions of life forms, number of species in the community, properties of the microclimate (see below) such as relative light values.

The factor climate

Elements of climate are usually listed as amount, kind and periodicity of precipitation, range of temperature, mean temperature, humidity, wind, cloudiness, duration and quality of light, etc. Thornthwaite (1948) has pointed out that climate fundamentally consists of a heat and a moisture factor. Numerical indices of these two factors, including indices of their seasonal distribution, may suffice to classify most regional climates as they influence vegetation.

For purposes of this paper's argument the climate of any site at a given time may be considered as existing on several different levels of relative area. Most extensive is regional climate; local or topographic climates are found within a regional climate; and microclimates or phytoclimates occur within plant cover types.

The regional climate, *cl* of the equations, is defined here as the "standard condition" which the weather station net measures. Regional climate is a spatial and temporal average over an area. According to our basic formulation, regional climate within this area is not a function of the environment operative within the area. Thus regional climate is by definition independent of relief, soil parent material, organisms, and time. This is evidently a pragmatic, convenient definition only. Deviations from the regional climate are here named topographic and phytoclimates, corresponding to the conventional and poorly defined terms local and microclimates.

The local (or topographic) climate is defined as topographically determined. Frost pockets and insolation differences between north and south facing slopes are examples. Since this level of climate

is not usually measured directly but is a function of topography, which is an independent variable determining vegetation, topographic climate is discussed under topography. Such discussion is not intended to minimize its importance.

The microclimate we define as a function of the vegetation, including lack of vegetation, on the site. This level has usually been identified with the plant climate, phytoclimate. Microclimate is, therefore, a strictly dependent variable. As such it may be treated as a property of vegetation. Variations in the vegetative cover are accompanied by variations in microclimates. Thus, microclimate may be considered just as is vegetation a function of the independent variables regional climate (as defined above), soil parent material, relief or topography, biota, and time. Microclimate is not defined here as the climate at an arbitrary small height above the ground. This height depends on the kind of vegetation. Inside a forest the light, air movement, etc., are conditioned by the tall tree canopy; in a grassland the absolute height of vegetation which influences climate is only a few decimeters—but both modifications of the regional climate are defined as microclimate in this paper since both modifications are dependent on vegetation.

Essentially, then, climate as an independent variable is regional climate. Regional climate is to be contrasted with microclimate which is a dependent variable.

The factor soil parent material

Jenny (1941) devotes a number of pages to the question, "What is soil parent material?" The answer is not simple. It is by no means certain that the part of the regolith underlying the soil is that soil's parent material. Jenny mentions pseudoprofiles whose horizontal differentiation is a result of geological stratification and not of soil genesis.

Indeed, Whiteside and Marshall (1944: 14) point out, "Soil parent materials have seldom, if ever, been adequately defined." Adequate definition must include "chemical composition, mineralogical constitution, texture, and structure of the rock" (Jenny 1941: 56). For functional purposes the properties of the soil parent material should have quantitative, single-value statement. This is often difficult.

In short, Jenny's (1941: 52) definition of the soil parent material as the state of the soil system at soil formation time zero will be used here. The properties mentioned, then, are those of the parent rock or geological deposit at the beginning of soil formation.

The factor relief

Topography or relief has several independent aspects: those depths to ground water which are not conditioned by vegetative succession or soil formation; slope properties as degree, shape, length, and direction or exposure; and duration and depth of snow cover not conditioned by plant succession. These are independent variables and are quantitatively measurable.

But slope angle itself may not always be a factor entirely independent of vegetation. Slope, soil, and vegetation in parts of southern Idaho (Bailey 1939) are said to have all developed concurrently, for the slopes now are too steep to stand without a vegetative cover. These slopes are now steeper than the angle of repose of the unconsolidated rock at present found in their profiles. Present slope is dependent on present vegetation and soil. However, slope angle of repose as ordinarily defined by geologists (Van Burkalow 1945) is entirely independent of vegetation. We can accept the geologists' definition and say degree of slope is defined as of zero time of plant succession and soil formation. In this sense degree of slope is an independent variable.

The factor organisms

Organisms may be classified as flora, fauna, and microorganisms. The flora factor is designated o_f , the fauna factor o_z , the civilized man part of the fauna factor o_n , and the microorganisms factor o_m .

Flora factor.—The plant cover has both independent and dependent aspects. The plant cover is both a cause and an effect. We need a way to logically separate the two aspects since habitually causes are considered as independent factors and effects as dependent.

Classically the dependent aspects of the plant cover have been called "vegetation." Vegetation is dependent on the environmental factors. But the flora is not necessarily dependent on specific environmental factors. Depending on a landscape's history one of several different floras could occur there. That is, two regions with the same climate, soil parent material, relief, and time of plant succession may have two different floras. The flora behaves as an independent variable, independent of cl , p , r , t of a given ecosystem. Therefore, in this paper the flora will be considered as one of the independent conditioning factors which determine vegetation.

By flora is meant the totality of plant species present in an area. A floral list is, as Jenny (1941: 203) pointed out, a good first approximation to the plant biotic factor operative in a given area.

Most plant species are effective in conditioning the vegetation of an area only if they produce disseminules and disperse them. Although a plant may be a member of the flora, if it cannot spread and reproduce, it can have no effect on vegetation beyond its own immediate, established periphery. Long-lived plants may be relicts which take no active, dynamic part in a plant community but merely exist passively, without reproducing. Therefore, the flora factor is defined here as the summation of different kinds of viable plant dis-

seminules reaching the area in question.

While historical plant geography, or floristics, tells us what species occur in an area—what its flora is, the autecological peculiarities of each species determine its disseminule production (Salisbury 1942) and dispersal capacity. Thus, both historical plant geography and autecology define the totality of plant disseminules present.

Fauna factor.—The fauna, as a species list, may be independent of the environmental factors. But some aspects of animal populations are not independent. Animal nutrition is notably dependent on the plant cover. Pocket gophers seem to be more abundant in overgrazed mountain meadows (Hall 1946: 444). Seral communities in general may be more densely populated by rodents and some insects than climax communities. Such quantitative characteristics would seem to be dependent features of rodents. Accordingly, as with plant life we shall differentiate the animal life of an area into dependent and independent (fauna) factors.

Human factor.—Civilized man is the most important independent animal factor influencing vegetation. We would include primitive man under o_z . Where, as in the history of Europe, there has been no sharp temporal boundary between primitive and civilized man, such a distinction may not be valid. But the contrast in America between Indian and white cultures is probably sufficiently great. We have, unfortunately, only limited data on the use of fire by American Indians. As to modern man, by cutting of forests, grazing domestic livestock, and controlling predators of wildlife he has changed even wildland landscapes. As animals independent of cl , o , r , p , and t , men may have cattle or sheep graze an area, may have them graze heavily or lightly, and may even change the flora by plant introductions—range reseeding of exotics for example.

Applied plant ecology is concerned with the effects of the factor o_h on

vegetation. When o_h equals zero, we shall define the vegetation as natural. For applied plant ecology the study of natural vegetation would seemingly form the necessary prior basis.

Microorganisms factor.—Microorganisms living in the soil influence soil formation and soil properties. Through these activities they also influence the vegetation growing on the site. Therefore, conclusions on the functional nature of soil microorganisms may apply not only to their effects on soil but also on vegetation.

Jenny (1941: 199–200) concluded that the soil microflora may be considered a constant independent factor in soil formation because it is potentially about the same throughout the world. That is, in the course of many decades all soils are repeatedly inoculated by all kinds of microorganisms. Potential microfloras, o_m , seemingly are identical. This rather startling postulate of Jenny's has been supported by Feher and Frank (1947): "The most common species of soil bacteria appear to be worldwide in their distribution, the same species occurring in the different soil types and geographical areas of the world. They are probably absolutely ubiquitous." It does not follow that all soils have identical microbial populations. On the contrary, the number of each microbial species living in soils varies from soil to soil, because growth is a dependent variable. Too, parasite numbers differ between soils—but parasites by definition are dependent. Also dependent are the relations between groups of microorganisms in the soil. Differences between soils and vegetations on two different sites cannot be caused by the variations in microorganism populations found in the soils of the two sites because the microorganism differences depend—as do the soil and vegetation differences—on the environmental factors operative on the two sites.

Tentatively we can adhere to Jenny's postulate that the independent aspect

of the microorganism factor, o_m , is the same for all soils and all vegetations.

The factor time

Vegetation changes with time. In any natural plant cover time changes may occur at 5 definable levels (Iaroshenko 1946): 1) seasonal, evidenced as aspeption; 2) annual, related to the variations of meteorological and biotic factors; 3) successional, or the time series of plant communities on some specific locality; 4) historical, or the alternation of types of plant communities in some specific region during a series of geological epochs; 5) genetics of plant communities, or the evolution of various phytocoenoses from an earlier vegetation. Diurnal changes in the plant cover may be added, but these influence neither vegetation nor flora as commonly considered.

The last two of Iaroshenko's items are historical changes in the flora, on a geological time scale. They seem to involve times of an order of magnitude at least greater than 1,000 years. On the other hand, succession as defined above seems to stabilize most vegetation within periods of less than 1,000 years. Thus, succession and the "historical" factors are definably different, and the amounts of time necessary for each process differ by a factor whose lower limit approximates 10. The first two aspects of time changes show periods with orders of magnitude of one and less than 20 years, respectively. This paper is not concerned with these rapid fluctuations in vegetation due to seasonal or annual variations. It is concerned with plant succession, for this is an effect of time evidenced by changes which are contemporaneously observable yet are not so rapid as to be classed as oscillations. Also, plant succession seems to go in a definite and determinable direction in a given ecosystem and produces a plateau of little change, stabilized vegetation. Definite and determinable direction, relative end stage, etc., are not

characteristics of the other time changes in the earth's plant cover named by Iaroshenko.

In other words, there are various kinds of change in vegetation with time. If all such changes are called "succession," important differences are obscured. Succession is defined here as a particular kind of change in vegetation with time. It is a progressive process with a marked time zero.² The historical changes in vegetation have no such well-marked time zero unless caused by introduction of a single, dominant new organism, such as the chestnut-blight, into the ecosystem.

Professor Herbert L. Mason in lectures on changes in the plant cover refers to its ontogeny those changes we here name succession and to its phylogeny those changes we here name historical. The splitting of time changes in the plant cover into two levels was recognized by Braun-Blanquet (1932: 336) who named the historical aspect "secular succession," and the other "present-day" (called "actual succession" by Lüdi 1932: 535, "recent succession" by Etter 1947). Sukachev (1944) uses the terms "syngensis" and "cenogenesis" for recent and secular succession, respectively.

Finally, succession as here defined produces changes directly in *vegetation*; the historical factors produce changes directly in the *flora* and only secondarily in vegetation. We have found it necessary to use the flora as one of the environmental factors determining vegetation. Only *through* changes in the

² Time zero in primary succession may be taken as the first occurrence of plant disseminules in the bare area; for secondary succession as the first occurrence of plant disseminules in the area bared, wholly or partially, by whatever catastrophe destroyed or markedly changed the vegetation. The same time zero probably should be used for studies of soil changes with time. In general, a new time zero must be chosen whenever one of the environmental factors changes suddenly and with great effect on the vegetation or soil.

independent determining factors—the flora, climate, soil parent material, relief, or human activity—do the historical factors affect vegetation. Successional change as here defined is a time change unique to vegetation, *i.e.*, to plant communities. This certainly doesn't preclude use, including definition, of the term by zoologists.

The definition of succession used here is not intended to minimize the effects of historical changes in climate on vegetation. But such effects can only be evaluated after we know the effects on vegetation of regional differences in climate.

"Soil or edaphic factor"

It will be noted that, contrary to expectation, the factor soil is not contained in equations (2) and (3) although obviously soil and vegetation always mutually influence each other. Strictly speaking, in nature one cannot separate the effects of one from the effects of the other since the same set of conditioning factors pertains to both soil and vegetation. Both soil and vegetation vary with time and both are determined by *cl*, *p*, *r*, and *o*. Both vegetation and soil are dependent variables. They depend

for their nature on the very same thing, the nature of the ecosystem or landscape.

Dokuchaiev and Hilgard, pioneers of Russian and American soil science, stated the dependence of soil on the landscape factors. Schimper similarly was a pioneer plant ecologist and pointed out the dependence of vegetation on factors of the environment. We can conclude the landscape or ecosystem is a plexus of a set of environmental factors which determine *both* vegetation and soil. Data so far show that on a given rock in a given landscape with a common flora a particular vegetation develops, so does a particular soil. Table I gives an example. This example illustrates a case of parallel development of soil and vegetation in a particular ecosystem. Causation between soil and vegetation is not implied.

Ecologists may profit by working with the concept of parent material rather than soil, for only the parent material of a soil is independent of the other landscape or ecosystem properties which determine both vegetation and soil. Soil properties such as acidity, organic matter content, depth, etc., are not independent factors but are determined by the same set of landscape factors which determine such properties of

TABLE I. *Parallelism between plant succession and soil development in the limestone Alps of the Engadine, Switzerland. After Braun-Blanquet and Jenny (Jenny 1941: 218)*

Development of vegetation			Development of soil				
Stage	Plant association	Relative production of organic matter, per cent	pH	Total acidity, milli-equivalents per 100 g.	Organic matter of surface soil, per cent	Thickness of humus layer, centimeters	General description of soils
Initial	Firmetum	40	7.2 ± 0.04	0	0-30	0-5	Disintegrated and slightly weathered limestone rock
Transitional	Elynetum, Festucetum	100	6.1 ± 1.07	1.3	20-50	10-30	Rendzina* profile, leaching of lime, humus accumulation
Climax	Curvuletum	60	4.8 ± 0.03	7.2	20-60	10-100	Alpine humus soil, leached profile, acid humus

* Since 1944 the Zürich pedologists headed by Pallmann have differentiated rendzina soils (developed from soft, clay-rich limestones) from Humuskarbonat soils (developed from hard limestones, poor in silica and clay). Cf. Leuenberger (1950).

vegetation as species list, weight production, cover, physiognomy, etc.

"Competition factor"

Competition is obviously a factor in determining where and when a particular plant or plant community occurs (Braun-Blanquet 1932: 82). But it is not an independent factor. Plant competition occurs only in the presence of vegetation—a tautology of course. A floristic list for the vegetation, defining o_f , is a measure of the competition factor. It expresses potential intra- and interspecific competition. Since competition cannot be construed as a factor determining vegetation independent of the five ecosystem factors, it is not to be found in equations (2) and (3).

VEGETATION FUNCTIONS AND SEQUENCES

By holding³ all environmental factors but one the same throughout a series of ecosystems, variations in vegetation caused by that one factor may be studied. Five possible types of functions, using v values, can be obtained. Also, five types of sequences, using V values, occur (Jenny 1946). These functions and sequences are listed and named in Table II. Climofunctions can obviously be split into hydro- and thermofunctions; similarly biofunctions can be divided into floro-, zoo-, and homofunctions with corresponding se-

³ No experimental approach is implied. Plant ecology is primarily a field study and to allow only one environmental factor to vary, areas (ecosystems or landscapes) must be chosen where this occurs naturally. Such methodology is discussed by Jenny (1930, 1941, 1946). In other words, in any one function or sequence, four of the five groups of environmental factors do not effectively vary; in a mathematical sense they are "constant" even though they are factors with a pronounced annual, or even diurnal, periodicity such as temperature; they are the same throughout the sequence. If the forms of functions which express effects of the environmental factors were known, statistical methods of eliminating variables could be used.

quences. Further subdivision of these principal functions can well wait on at least preliminary solution of those named or demonstration that these are inadequate. Functions involving microorganisms are purposely omitted altogether for reasons already stated. In each of the tabulated cases the chosen variable factor is enclosed in parentheses; the remaining four ecosystem factors which are the same throughout the function or sequence are written as subscripts.

The functions are to be understood as having the ordinary properties of most mathematical functions—continuity, differentiability, possibility of graphic portrayal, quantitative statement, etc. Usual mathematical methods may be applied both to individual functions and the general fundamental equation (2). The sequences on the other hand are qualitative series.

A mathematical approach is used in this paper because it offers a method of abstracting concepts from their verbal definitions, a universal notation, a logical system of manipulating concepts, and the ultimate opportunity to replace qualitative by quantitative data.

In each function or sequence, 4 of the 5 environmental factors are postulated to be the same throughout. But the ecologist is extremely fortunate who finds a series of landscapes where only one of the environmental factors varies⁴ and all others do not. However, absolute constancy of all factors but one need not be insisted on in order to study the effects of that one factor on vegetation. A property of vegetation or a plant community can be approximated as a function of only one independent factor, in Jenny's (1946) words, as the "result of the following two possibilities: 1) the one factor varies greatly while the

⁴ "Varies" in the sense that it has different values in the various landscapes. The factor may have a periodical march in any one landscape.

TABLE II. Possible kinds of vegetation functions and sequences

Functions (quantitative mathematical relationships)		Sequences (qualitative series)	
$v = f (cl)_{p, r, o, t}$	Climofunction	$V = f (cl)_{p, r, o, t}$	Climosequence
$v = f (p)_{cl, r, o, t}$	Lithofunction	$V = f (p)_{cl, r, o, t}$	Lithosequence
$v = f (r)_{cl, p, o, t}$	Topofunction	$V = f (r)_{cl, p, o, t}$	Toposequence
$v = f (o)_{cl, p, r, t}$	Biofunction	$V = f (o)_{cl, p, r, t}$	Biosequence
$v = f (t)_{cl, p, r, o}$	Chronofunction	$V = f (t)_{cl, p, r, o}$	Chronosequence

remaining ones vary, in comparison, but little. 2) save for the one function, the slopes of the others are nearly zero. In other words, some factors may vary considerably, yet be of relatively little importance in determining differences in soil [or vegetation] properties."

The reasoning behind Jenny's statement can be understood by totally differentiating our fundamental equation (2) giving:

$$dv = (\partial v / \partial cl) dcl + (\partial v / \partial p) dp + (\partial v / \partial r) dr + (\partial v / \partial o) do + (\partial v / \partial t) dt. \quad (4)$$

That is, to determine a change in a property of vegetation (dv) we must determine the changes in the five independent variables, the differentials $dcl, dp, dr, etc.$, in practice often replaced by $\Delta cl, \Delta p, \Delta r, etc.$, and in addition also determine the five rates of change of the vegetal property with the independent variables, the partial coefficients $\partial v / \partial cl, \partial v / \partial p, \partial v / \partial r, etc.$ A complete statement of a vegetal property function is:

$$v_2 - v_1 = \int_a^b (\partial v / \partial cl) dcl + \int_c^d (\partial v / \partial p) dp + \int_e^f (\partial v / \partial r) dr + \int_g^h (\partial v / \partial o) do + \int_i^j (\partial v / \partial t) dt. \quad (5)$$

It would be very difficult to solve this equation completely, but we can hope to approximate it or solve certain parts.

The differential equation (4) permits a complete statement of the problem of isolating the variables. To set up a change in vegetation, v , as a function of say, climate only, just v and cl can appear in the differential equation, *i.e.*, we must

be able to write:

$$dv = \frac{\partial v}{\partial cl} dcl \text{ or } v = F (cl)_{p, r, o, t}.$$

Evidently the four products $(\partial v / \partial p) dp, (\partial v / \partial r) dr, (\partial v / \partial o) do,$ and $(\partial v / \partial t) dt$ must equal zero. This can be accomplished in either of two ways. First, $dp, dr, do,$ and dt can all equal zero. This means these variables $p, r, o,$ and t do not change. Or, $\partial v / \partial p, \partial v / \partial r, \partial v / \partial o,$ and $\partial v / \partial t$ can all equal zero. This means that the rates of change of the property of vegetation with respect to these four independent variables are zero. Obviously any combination of the differentials equaling zero and the partial coefficients also equaling zero is possible, just so the respective products of partial coefficient and differentials all equal zero.

In words, the partials are simply the effects of the independent on the dependent variable; $\partial v / \partial cl$ is the effect of climate on vegetation. Rigorously, however, $\partial v / \partial cl$ is the rate of change of a property of vegetation, represented by v , with respect to a climatic measure, represented by cl , holding the factors climate in all its other aspects, soil parent material, relief, biota, and time in all their aspects constant. "The partial of v with respect to cl " is shorter and simpler; " $\partial v / \partial cl$ " is still better. Both of the latter are rigorous.

This differential nomenclature may appear forbidding. However, it is precise, logical, neat, space-saving, and lends itself readily to mathematical and logical manipulation. It appears useful.

Plant ecology is not concerned merely with investigating the effect of one factor on vegetation. It often wants to analyze why an observed difference between the vegetation on two sites

exists. We can use equation (5) as the basis for discussion. The difference $v_2 - v_1$ has been observed. The problem is why does this difference exist? Obviously the factors of the environment must be known. Cl , p , r , o , and t represent only groups of factors. Much analysis and definition must be done within these groups before a complete list of habitat factors for any given ecosystem can be drawn up. Given the habitat factors, do they differ between the investigated sites? In other words, do the differentials exist? Now, within what limits do the environmental factors exist; what are the limits of integration for each variable? Finally, what is the influence of each variable on the vegetation characteristic being investigated; what values have the partials? Information of the above three kinds for each determining factor is necessary for the solution of the problem presented by differences in vegetation on different sites.

Below are given a few examples of functions and sequences. Many others are of course known. Following each description of a sequence, such as the climosequence $V = f(Cl)_{p, r, o, t}$ is a short description of the factors which do not effectively vary in the sequence being discussed. In a climosequence the levels of p , r , o , and t would be stated.

Illustrations of climosequences

As pointed out in the discussion of climate, the variables moisture and temperature can influence vegetation independently.

The Great Plains area contains excellent examples of moisture sequences. Along an isotherm, say 11°C (52°F) annual temperature, the vegetation changes with increasing precipitation from shortgrass, to midgrasses, to tall bunchgrasses, and finally in the easternmost and wettest part to tall bluestem sod. This sequence is illustrated by Jenny (1941: 210, Fig. 104). The moisture boundaries of these communi-

ties are approximately 17 inches precipitation a year for shortgrass, 17–21 inches for the midgrasses, 21–27 inches for tall bunchgrass, and 27–38 inches for bluestem sod. Most ecologists would probably say that these changes in vegetation are related to the precipitation differences. Then the influence of the other environmental factors must be nil or these factors must not vary. The former alternative seems more improbable than the latter. Therefore we find some justification for saying that the factors other than precipitation are relatively constant throughout the sequence: $T = 11^\circ\text{C}$ as mentioned, p = loess and other windblown materials, r = undulating, o_f = one Great Plains flora for the whole area, o_s = no overgrazing, t = the same for all the grassland types and approximating a few thousand years since the latest major climatic change, the postglacial xerothermic period.

In the same region Weaver's (1924) data on three years' (1920–1922) average annual production of virgin grasslands show a striking increase in yield with increasing moisture (Fig. 1). The other environmental factors are the same throughout, or their differences are too small to be effective, evidently. They are listed below:

T (Temperature) = $10\text{--}12^\circ\text{C}$ mean annual; potential evapo-transpiration, calculated by Thornthwaite's method (1948), is 68.5 cm of water per year for Burlington, 77.5 Phillipsburg, and 74.0 Lincoln

p , r , and o as above

t = unknown but of no influence. Plant communities corresponding to Weaver's three have been described as climax in these areas. The climax is stable; it is the stable stage of a sere. Thus there are no successional changes in climax vegetation. The effect of time, according to our definition, is nil in the climax; $\frac{\partial v}{\partial t}$ in the climax approaches zero.

For the stations listed in Figure 1, temperature is not exactly the same throughout. However, yields of prairie hay are not significantly correlated with

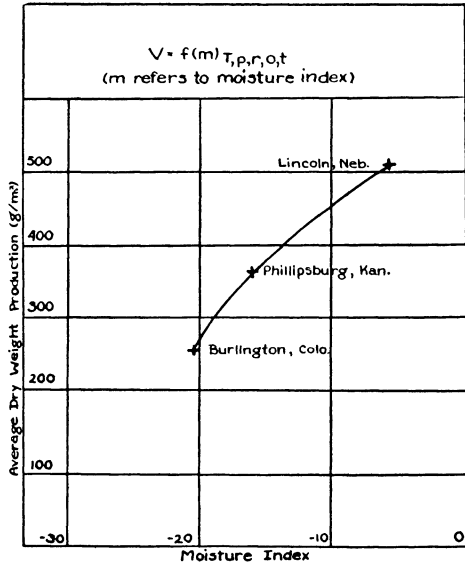


FIG. 1. Average dry weight production of virgin grasslands in the Great Plains correlated with moisture, other environmental factors not effectively varying. Production data from Weaver (1924), included approximately 50 meter square quadrats per year per site. Moisture indices calculated by Thornthwaite's method (1948). Mean annual precipitations are Burlington 420 mm, Phillipsburg 570 mm, and Lincoln 690 mm. A curve of constantly decreasing slope is more reasonable than a straight line; i.e., $dv/dm = k/m$ or $v = a + b \ln m$.

mean annual temperatures (Jenny 1941: 213, Fig. 105); the partial derivative $\partial v/\partial T$ therefore approximates zero. In other words, the temperature variation from 10 to 12° C which occurs among Weaver's three stations probably does not materially influence vegetation weights and can therefore be neglected.

Moisture sequences caused by rain shadow effects can be readily found. Vegetation and moisture across the north-south extending Pahvant Plateau of Central Utah are diagrammed in Figure 2. The two plant communities, sagebrush and shadscale, are determined by differences in moisture (Billings 1949). They exhibit a true moisture sequence because the determining factors other than precipitation are nearly the same at both places:

$T = 9.2^\circ \text{ C}$ (Richfield) to 11.0° C (Fillmore) mean annual; 62.8 cm of water per year (R.) to 69.7 (F.) potential evapo-transpiration. This difference we assume to be negligible
 $p =$ alluvium from red sandstones and shales
 $r =$ gently sloping alluvial fans
 $o_f =$ a Great Basin flora. No floristic barriers, to the dominants at least, exist
 $o_z =$ grazed moderately
 $o_h =$ not burned, plowed, overgrazed, etc.; substantially natural conditions
 $t =$ long enough so $\partial V/\partial t$ is negligible.

A temperature sequence is shown by the plant communities at St. George and Frisco in southwestern Utah. The *Larrea tridentata* community at St. George contrasts with the *Artemisia nova-Atriplex confertifolia* community to the north at Frisco. In St. George potential evapo-transpiration (Thornthwaite's measure of temperature effectiveness, 1948) is 87.7 cm of water per year, in Frisco 66.5 cm. Mean annual temperatures are 15.2° C (St. G.), and 10.0° C (F.).

The black sagebrush-shadscale community is the characteristic representative of the northern desert shrub zone which is in all respects save temperature regime comparable with the creosote bush community farther south. Other communities of the northern desert shrub zone are unduly influenced by saline ground water and soil (pure shadscale, greasewood), by overgrazing (little rabbitbrush), or by the wetter climate

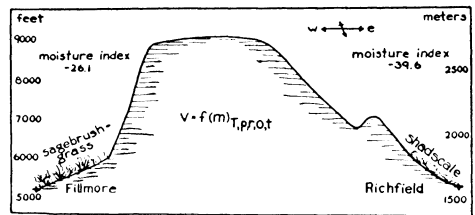


FIG. 2. An east-west transect across the Pahvant Plateau in central Utah showing a moisture sequence of plant communities. Seasonal distribution of precipitation is the same at both Fillmore and Richfield; mean annual precipitations are: F. = 367 mm and R. = 212 mm (U. S. Weather Bureau). Moisture indices were calculated by Thornthwaite's method (1948).

or rockier soil of benchlands (pinyon-juniper), and are therefore not suitable for comparison.

The factors other than temperature are the same at St. George and Frisco or their differences are too small to be effective:

- m (moisture) = 208 mm (F.), and 218 mm (St. G.) mean annual precipitation, with very similar distributions. Thornthwaite's moisture index ranges only from -41.2 (F.) to -45.0 (St. G.)
- p = alluvium from tertiary extrusives of chemically intermediate or mineralogically mixed composition (Butler *et al.* 1920)
- r = alluvial fans, bajadas; the playas and lower mountain slopes have different vegetation
- o_f = a southern Great Basin flora; the Pine Valley mountains north of St. George have probably not been a barrier to the dominants
- o_s = protected from overgrazing
- t = long enough so stable vegetation has developed; $\partial V/\partial t$ is negligible.

Illustrations of lithosequences

In these sequences vegetation is related to soil parent material; cl , r , o , and t must remain constant or if they do differ, then ineffectively.

Tüxen and Diemont (1937) describe a "Klimaxgruppe" of plant communities from northwestern Germany. These are lithosequences of stable communities which differ because of variations in soil parent materials. On Cretaceous limestone occurs the Querceto-Carpinetum primuletosum, on calcareous loess the Querceto sessiliflorae-Betuletum typicum. Tüxen and Diemont say (p. 81), "Similar examples of a strong mosaic of terminal communities on level surfaces with old soils and within the same climatic region, which are conditioned only by alternations of soil parent material, are to be found everywhere in northwest Germany, what is more, also in northwest and central Europe. Neither soil formation nor development of vegetation in our region can by their effects on [micro-] climates fully equalize the effects of the petrographic properties of the 3 principal groups of soil parent material rocks: limestone, silicate rocks,

and quartz sand." In this example, of the five factors cl , p , r , o , and t , only p varies effectively.

Illustrations of toposequences

Toposequences due to slope exposure differences are clearly evident in arid mountains. Shreve's (1915) example is classic. In the Santa Catalina Mountains of southern Arizona at several topographic levels vegetation is strikingly different on north and south slopes of ridges. The situation is diagrammed in Figure 3. At 8,000 ft altitude yellow pine forest on the south exposures contrasts with fir on the north, at 6,100 ft evergreen oaks with yellow pine, at 4,200 ft desert vegetation with evergreen oaks.

The pertinent area of the mountain can be described as follows:

- cl = the same within each topographic level, such as 8,000, 6,100, and 4,200 ft
- p = gneiss throughout
- r = the same except for the single topographic factor, exposure; at least Shreve makes no differentiation of vegetation in relation to degree, length, or shape of slopes
- o = probably one flora throughout; certainly in each altitudinal (climatic) zone within which the vegetation contrasts on north and south slopes, the flora is the same clear around the mountain; the north slope flora does not differ from the south slope flora, only vegetations differ
- t = such that essentially stability has been attained throughout, at least in the dominants; $\partial V/\partial t$ approaching zero and therefore negligible.

At other elevations there may be no differences between the vegetation of

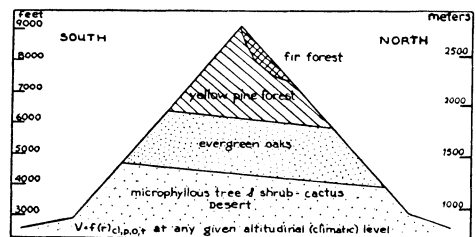


FIG. 3. Differences in vegetation on contrasted exposures in the Santa Catalina Mountains of southern Arizona (from Shreve 1915: 12).

north and south slopes. Thus, below 3,900 ft is desert, at 4,700 to 5,800 ft is evergreen oak, at 6,300 to 7,300 ft is yellow pine forest on both north and south exposures. At elevations within these altitudinal limits regional (average of the altitudinal) climate determines type of vegetation; in the exposure ecotones local climate is decisive and is a function of slope exposure.

Tüxen and Diemont (1937) designate as "Klimaxschwarm" the group of stable communities differentiated by slope exposure from the *Fagetum boreoatlanticum* in the Harz mountains. "Mapping of vegetation has shown that the distribution of these communities (and their soil profiles) is regularly related to the different slope exposures so that the *Fagetum dryopteridetosum* occurs on north and northeast slopes, the *Fagetum festucetosum* in general on summits and gently sloping northwest to north slopes, the *Fagetum luzuletosum* on northwest and southeast slopes (*Calamagrostis-Poa Chaixii* Fazies) and on the gently sloping west and southwest slopes (*Luzula-Deschampsia* Fazies), and finally the *Querceto-Betuletum* on the steep south to southwest slopes." This toposequence is diagrammed in Figure 4. Throughout the sequence *cl*, *p*, *t*, and *o* do not vary effectively.

Depth and duration of the winter snow cover have been used in Swedish Lapland to explain distributions of vegetation (Du Rietz 1950). Deep snow insulates ground vegetation against extreme cold and drying; a long-continued snow cover shortens the growing season.

In the lower Alpine zone, a *Vaccinium myrtillus* community is found in sheltered spots where snow is not removed by the wind; a *Loiseleuria-Diapensia* community occupies exposed spots where the snow is blown away by the wind; a *Salicetum herbaceae* occurs where the growing season is drastically shortened by heavy snow accumulation. Areas including these three plant communities

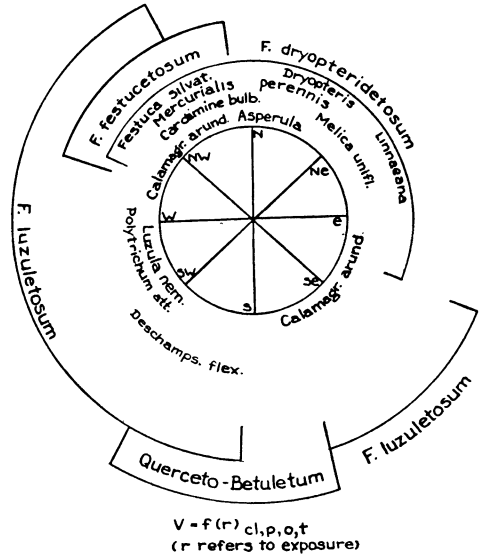


FIG. 4. Dependence of the subassociations and facies of the *Fagetum boreoatlanticum* in the Harz mountains on various directions of slope exposure (from Tüxen and Diemont 1937).

may be selected in such a manner that *cl*, *p*, *o*, and *t* do not vary effectively. Variations in wind, associated with relief, are responsible for the differences in snow accumulation within this climatically fairly uniform region. Snow accumulation is thus a function of relief. Therefore, these three communities form a toposequence.

Illustrations of biosequences

Some sequences of plant communities are associated with differences in floras. That is, a floresequence is due to a significant difference in the floristic factor.

A flora is composed of individual species, each with its individual distribution. Species distributions may show gaps or discontinuities due not only to the phylogenetic and geological history of the species but also to physical barriers to migration or to lags in that migration caused by past climatic changes, such as a glacial or xerothermic period. As already noted, migration of species is generally an historical process on a

geological, not successional, time scale. Succession is treated in the next section under chronosequences. The results of plant migrations are areas with different floras, producing florosequences. In accord with the definition of the floristic factor given previously, local discontinuities in the environmental factors which may determine a species' local existence do not directly determine the limits of a flora, for existence is a dependent feature of vegetation; disseminule distribution is independent of such environmental discontinuities over contiguous areas.

Differences in vegetation due to the differences in floras caused by migration or isolation have been qualitatively described. Ramaley (1931) ascribed the present northern limit of *Quercus gambelii* in the foothills east of Denver, Colorado, to historical, not climatic factors. The alpine and subalpine vegetation of the Uinta mountains in Utah differs from that of the adjacent Wasatch mountains by having in its flora some 72 species not found in the latter range, including such prominent alpine and subalpine species as *Elyna* (*Kobresia*) *bellardi*, *Trollius albiflorus*, *Papaver radiculatum*, *Sedum rhodanthum*, *Kalmia microphylla*, etc. The floristic differentiation probably results from Pleistocene glaciation with its attendant plant migrations and exterminations. Although the Uinta mountains are more massive, higher, and less dissected than the Wasatch mountains, alpine and subalpine landscapes which are similar with respect to the factors cl , p , r , o_z , and t can be found in both ranges. Since the alpine floras of these ranges differ, their alpine plant communities are distinctive and are members of a florosequence.

The essential problem in establishing florosequences is to correlate differences in species ranges with differences in vegetation communities, the factors cl , p , r , and t being constant or ineffectively varying.

Homosequences are common. Samp-

son (1919) described several "weed stages" in the subalpine zone of the Wasatch Plateau of central Utah. These stages resulted from various degrees of overgrazing by domestic stock, mostly sheep. They are steps in an intensity-of-grazing sequence. Ellison (1947) has pointed out that on the Wasatch Plateau today a vegetation sequence occurs which is related to the class of stock grazed—sheep producing a narrow-leaved grassland, cattle a plant community of broadleaved forbs.

In these grazing sequences, if the plant communities were not stable, natural plant succession would play a role in determining them. This would involve the factor time. But the plant communities named are stable under the given levels of o_h . Thus, Sampson's "weed stages" and Ellison's grass *vs.* forb communities are the result of predominance of the factor o_h above all other environmental factors. The influence of grazing herds is continuous, and the partial $\partial V/\partial o_h$ overshadows the partial $\partial V/\partial t$ (natural plant succession). The natural plant successions have not been worked out thoroughly enough in a quantitative way to separate precisely the changes in vegetation into what is natural and what man-caused.

Many other sequences of vegetation due to man's activity are well known. These include secondary seres in forests, grasslands, arable land, etc. In such seres separation of the partials $\partial V/\partial t$ (natural plant succession) and $\partial V/\partial o_h$ (civilized man's continuing influence) is certainly not easy, but it appears to be a necessary step in planned land management.

Illustrations of chronosequences

By means of dated photographs Ives (1941) traced the development of a burned spruce-fir forest in Colorado to brush, through an aspen stand, and back to spruce-fir. In this well-dated case the single landscape studied has had one essentially constant set of cl , p , r , and o

throughout the sequence, which is therefore an excellent chronosequence, however qualitative in its description of the vegetation concerned.

Unfortunately succession has not always been studied by making consecutive observations on one area. Instead inferential methods have been used. The present reaction against the use of deductive reasoning in plant ecology (Cain 1947) seems to be a reaction in part against exclusively inferential methods of investigating succession.

Besides this methodological problem there exists another difficulty in studying succession, the collecting of quantitative data on vegetation. Without quantitative data, it is impossible to establish chronofunctions. Without chronofunctions, as contrasted to chronosequences, predictions cannot be precise and details of the process of succession remain obscure. To be specific, what is the shape of succession-time curves? Cooper (1926: 403) almost 25 years ago said that succession "in rate, too, is more or less subject to rule, an initial increase, a medial maximum, and a long decrease in rapidity of change being characteristic." Most ecologists would probably concur. Data to illustrate the rule, however, are few. Moreover, it is not always clear what property of vegetation can be measured and plotted against time to yield a curve. The question of curve shape is not merely academic since if we know what type of equation describes a curve, very few points are necessary to approximate the constants of the curve. Given the curve's constants, predictions can be made—later to be checked against field data. Thus, theories and generalizations can be tested.

Of those successional data which meet both the above objectives of consecutive observations on one area and quantitative nature, some of Cooper's (1939) from permanent quadrats on the shores of Glacier Bay, Alaska, are graphed in Figure 5. In these chronofunctions v is the number of stems per unit area.

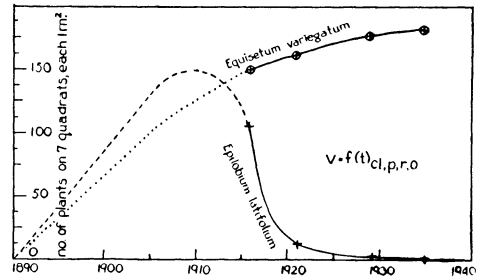


FIG. 5. Numbers of plants on seven 1 m² quadrats at Glacier Bay, Alaska, as a function of time (from Cooper 1939). Time zero is 1879 for two plots, 1892 for two plots and 1899 for three plots, with the average, 1891 (dates kindly supplied by Dr. D. B. Lawrence). The dotted lines are purely hypothetical.

Evidently *Equisetum variegatum* has been increasing in abundance. However, its rate of increase is decreasing. That is, the partial $\partial v/\partial t$ (slope) although positive is slowly approaching zero. Thus, the number of shoots of *Equisetum* may be approaching a maximum. On the other hand, the number of *Epilobium latifolium* shoots is decreasing to zero. The partial $\partial v/\partial t$ is negative and decreasing in absolute amount. Presumably *Epilobium* has passed a maximum. But there is a considerable gap in the data between time zero (deglaciation) and the first records. The quadrats were laid out in vegetation already in a pioneer stage. Thus, it is unsafe to speculate very much on the basis of the few available observations. The dotted lines are purely hypothetical.

Of course any seral species would show a maximum in its curve of abundance against time; the curve should have a hump. A seral species first increases, then decreases in abundance. As it increases the slope, $\partial v/\partial t$, is positive; at the maximum $\partial v/\partial t$ is zero; as it decreases $\partial v/\partial t$ is negative; and finally as v approaches zero so may $\partial v/\partial t$ also. Species of stable vegetation, however, should show only one branch of this humped curve. They increase, probably asymptotically, to their mean stable abundance. For such species $\partial v/\partial t$ re-

mains positive, but approaches zero. The data quoted have all covered too short a period of time to exhibit the complete hypothesized curve for any species. *Equisetum* at Glacier Bay may be on the ascending branch, *Epilobium* on the descending. The hypothetical curves were drawn on this basis.

The two cases cited above are concerned with primary succession. Secondary succession is being recorded by permanent quadrats in the subalpine zone of the Wasatch Plateau in Utah by the U. S. Forest Service. This secondary succession was induced at the turn of the century as a result of destruction of the plant cover by grazing and subsequent protection. Data from these quadrats extend over a 30 year period and show humped curves for certain species. *Achillea lanulosa*, notably a seral species and almost the only perennial one on these quadrats when they were established around 1916, shows this hump. Interestingly enough, it appears that *Agropyron trachycaulum* does also. Early in the period of study of this area Sampson (1919) concluded that *Agropyron* was climax. His argument was based largely on the comparative physiology, as judged from their growth forms, of the dominant species. Ellison (1947), on the basis of the quadrat record available after 20 additional years and by analogy with long-protected natural areas that he found, believed *Agropyron* was not climax over much of the area. The criterion mentioned above of deciding when a species is seral and when a member of stable vegetation supports Ellison's thesis.

The Wasatch Plateau records are complicated by yearly climatic irregularities and, as Ellison (1943) has said, by continued accelerated soil erosion. However, accelerated soil erosion is probably not an independent factor in mountain secondary plant succession. Abundant data show that a well-developed vegetative cover lessens runoff

and soil erosion on slopes. Therefore, any denuded site on a slope will be eroded at an accelerated rate. And so no change in such secondary vegetation can be assigned to soil erosion as such. Erosion is not an independent factor. As already pointed out, in a given ecosystem changes of vegetation and soil cannot be separated.

Many quantitative successional data employ a relative time scale, only. This is notably true of the work of Braun-Blanquet and Jenny in the Swiss National Park (*cf.* table I) where pH of the soil is a function of relative time. The quantitative functional relationship, $pH = f(\text{time})$, could not be evaluated.

PARALLELISM OF SOIL FORMATION AND PLANT SUCCESSION

Both soil and vegetation are functions of five groups of factors. A vegetation and a soil property can be correlated only in the special case where four of the five groups of determining factors are constant in effects. Thus, in general no soil property can be universally correlated with a property of vegetation (Jenny 1941: 267-9). In general vegetation is not a function of soil; soil is not a function of vegetation. Both the soil and vegetation of a particular landscape are functions of the factors of that landscape, that site, that ecosystem, that environment—whichever term is preferred. Soil will be a function of o_f , the flora which is an independent ecosystem factor, when cl , p , r , t , and the other aspects of o are constant or ineffectively varying. But then vegetation will also be a function of o_f .

While a soil may exist without vegetation as a special case, judging from current definitions soil formation seems to be impossible without vegetation. Jenny (1941: 17) defines soil in terms of his fundamental equation (1) in which the flora explicitly enters. Presence of a flora means vegetation is also present (v at t_0 is disseminules). Some Russian

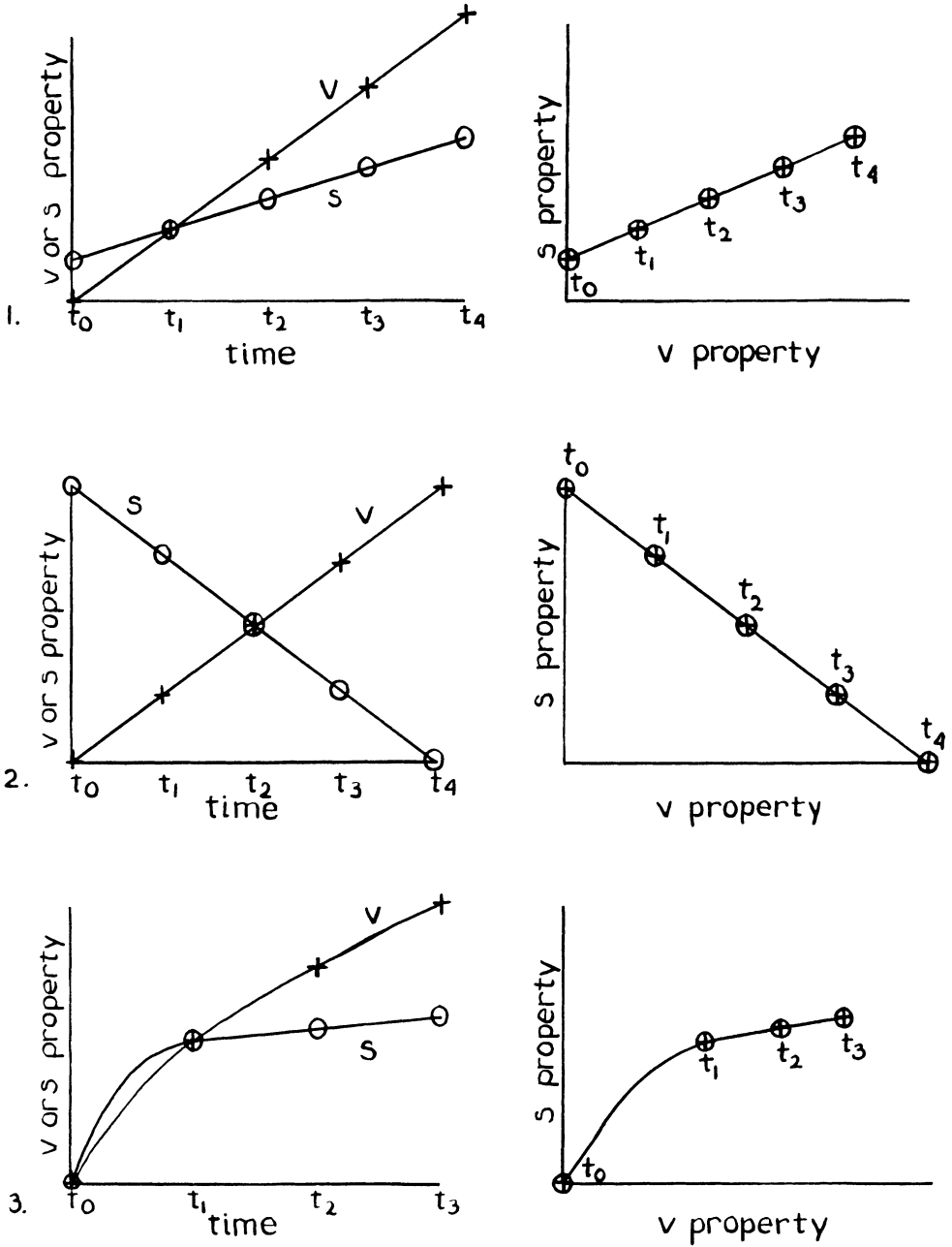


FIG. 6. Illustrating for a given ecosystem with cl , p , r , and o constant. 1—Soil formation and vegetation succession both progressing with time in the same direction, differing only in rate, standard error of estimate of the equation $s = \varphi(v)$ is zero. 2—Soil formation and vegetation succession progressing with time with slopes equal but one positive (v) and the other negative (s); standard error of estimate of the equation $s = \varphi(v)$ is still zero. 3—Curvilinear development of soil and vegetation with time (the probable case); standard error of estimate of the equation $s = \varphi(v)$ is zero (v can represent weight of vegetation per unit area; s can be percentage nitrogen in the surface 20 cm of the soil).

pedologists (Vilensky 1937) simply define soil as the result of the interaction of mother rock and the biosphere. Pallmann (1948: 60) defines soil as "the polydisperse, loose layer of the solid earth's crust that arises through physical and chemical weathering of rock, humus formation, and various translocations of the products of weathering and humus formation." Humus comes only from vegetation. Finally, zero time of soil formation may also be considered zero time of plant succession. Under the definitions of soil quoted, the reverse is also true.

Thus we may conclude that in a given landscape, soil formation cannot be separated from vegetative succession. Both processes are related to the time sequence of events determined by the particular levels of cl , p , r , and o obtaining in the particular ecosystem. In a given ecosystem characterized by specific values of cl , p , r , and o , say cl_x , p_y , r_z , o_n , soil and vegetation develop simultaneously. A given soil property, s , changes with time, symbolized as:

$$s = f_s(t)_{cl_x, p_y, r_z, o_n} \quad (6)$$

A given property of vegetation, v , also changes with time in accordance with the formal equation:

$$v = f_v(t)_{cl_x, p_y, r_z, o_n} \quad (7)$$

The left hand curves of Figure 6 illustrate equations (6) and (7), *i.e.*, some possible functional relationships of soil formation and vegetation succession with time.

The right-hand curves of Figure 6 are plots of the equations obtained by eliminating t from equations (6) and (7) giving $s = \varphi(v)$, or $v = \psi(s)$. Note that in Figure 6, part 2 could be made to show not only perfect correlation between soil and vegetation development but also absolute coincidence in these developments by reversing the scale used to measure s .

In other words, in a specific ecosystem or landscape, soil and vegetation develop

together and in the same direction. The nature of their functional relations with time determines how nearly parallel they develop. Such parallelism between soil formation and plant succession was found by Braun-Blanquet and Jenny (*cf.* table I) in the alpine zone of the Alps and by Braun-Blanquet in the Mediterranean region (1933). Braun-Blanquet (*cf.* also his colleague Tüxen 1931/32: 183) made the generalization of parallel development of soil and vegetation on empirical grounds; theory agrees.

SUMMARY

Starting from the definition of plant ecology which says that vegetation is conditioned by five groups of factors, here taken to be climate, soil, topography, biota, and time, substitution of Jenny's soil forming factor equation and appropriate definition lead to a systematization of plant ecology expressible by the equation: V or $v = f(cl, p, r, o, t)$. V represents a plant community, v a property of vegetation; f is "a function of"; cl is regional climate; p is soil parent material; r is relief or topography; o is the biota; t is time.

Use of this fundamental equation makes possible closer and more accurate delimitation of the factors determining vegetation, provides a frame within which quantitative data on vegetation can be collected, offers methods of manipulating such quantitative data, and finally also offers methods of manipulating the symbols representing ecological abstractions.

Vegetation is dependent on the five mathematically independent groups of factors represented by cl , p , r , o , and t . These factors determine a particular kind of system, an ecosystem or natural landscape.

For the purposes of this paper the following definitions are used:

cl is regional climate; local or topographic climate is a function of relief; microclimate or

phytoclimate is a dependent property of vegetation

p is the state of the soil system at time zero

r has reference to degree, solar direction, length, and shape of slope, independent aspects of ground water and snow cover depth and duration

o can be subdivided into o_f , representing the flora or the summation of plant disseminules reaching the site; o_z or fauna, including o_h or the influences of man; and o_m or the effectively constant influence of microorganisms.

Sequences of plant communities or vegetal property functions can be recognized and named according to one factor which changes while the others do not change effectively. Thus, changes in vegetation can be ascribed to one cause.

From mathematically considering the equations: $s = f_s(cl, p, r, o, t)$, and $v = f_v(cl, p, r, o, t)$, we may conclude there are no universal correlations between vegetation and soil; in such a system soil is not determined by vegetation, vegetation is not determined by soil; vegetation and soil develop concomitantly.

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