

On a state factor model of ecosystems

Therefore, speak I to them in parables; because they seeing see not. (Matthew 13: 13)

The study of terrestrial ecosystems is an area of intellectual inquiry that is fundamental to our very concept of nature. Like all modern sciences, the ecosystem sciences are concerned with a quantitative understanding of various properties and processes and the controls on these features. Yet, the facts or knowledge that a science can acquire and the very questions that it asks depend on the concepts, models, and theories that it collectively possesses (Kuhn 1962). From this perspective, models function as the parables of science.

The concepts and theories of ecosystems have, like those of other natural sciences, evolved greatly since the scientific renaissance of the nineteenth century and the subsequent coining of the term "ecosystem" by Alfred Tansley (1935). Many, if not most, of these ecosystem models have evolved from the field of ecology (Golley 1993). Yet, there is another perspective of ecosystems, and a model to study them, that evolved apart from ecology but coincident with the development of the science of pedology in the late nineteenth and early twentieth centuries. For the purposes of this article, we call this perspective the *state factor model*. This model is now being used, either implicitly or explicitly, in a growing number of ecosystem studies (e.g., Pastor et al. 1984, Schimel et al. 1985). In this article, we review the structure and attributes of this model, briefly identify its origin, trace its evolution, and illustrate its use during the twentieth century, with

the goal of bringing it to a wider audience in the ecological community.

Structure of the state factor model

The earth's surface, although it varies greatly from place to place, is essentially a continuum in both space and time (Figure 1). Ecosystems, therefore, are arguably human constructs that break the continuum into manageable and differing segments for study. The size of the ecosystem chosen for study is also somewhat arbitrary (Likens 1992), but it will possess certain characteristics: it is open with respect to its surroundings and is capable of exchanging matter and energy with the surrounding environment. Moreover, its properties at any time—that is, the state of the system—depend to a great degree on the characteristics of the surroundings.

What variables determine the state of an ecosystem at any time, t ? From comparisons with other sciences, the main factors can be grouped into the following categories: initial state of the system, external conditions, and age of the system. Over a century of field observation has revealed a set of independent variables that, for most ecosystems, can be shown to define or control the ecosystem's state (i.e., its properties, or dependent variables) at any given time. Expressed in general mathematical form, the equation is

$$\text{ecosystem properties} = f(\text{climate, organisms, topography, parent material, time, humans, ...})$$

All state factors share several general properties (Jenny 1958). First, they are independent of the system being studied (i.e., the system does not affect the state factors). This will be true only if the system being stud-

ied is small in relation to its surroundings. For ecological studies dealing with landscape segments, such as sites or plots, such a restriction is unimportant. Second, the state factors may, in many locations of the earth or for certain periods of geological time, vary independently of one another. This independence of one state factor relative to the others creates the possibility that through judicious system (i.e., site) selection, the influence of a single factor on ecosystem properties may be observed and quantified in nature. There are, of course, many site comparisons for which it can be shown that not all of the state factors are independent of one another. For example, it is well known that climate varies through long expanses of geological time. Consequently, differences between ecosystems of different ages may in part reflect differences in climatic histories.

The ecosystem properties equation defines an ecosystem. Following Jenny (1941), ecosystems can be defined as those portions of the earth's terrestrial surface whose properties vary in response to variations in the state factors. Therefore, a difference in state factor assemblages (no matter how small) between two locations on the earth's surface results in two differing ecosystems. Theoretically, therefore, the earth is composed of an infinite number of ecosystems.

The terms describing the state factors have been in use for more than a century, and their meanings have varied greatly over this time. In this article, we use the current definitions of the state factors, which are consistent with formulations of the model during the past half century (Amundson and Jenny 1991, Jenny 1941, 1958). A discussion of the way in which these definitions and concepts differ from those of the nineteenth and early twentieth cen-

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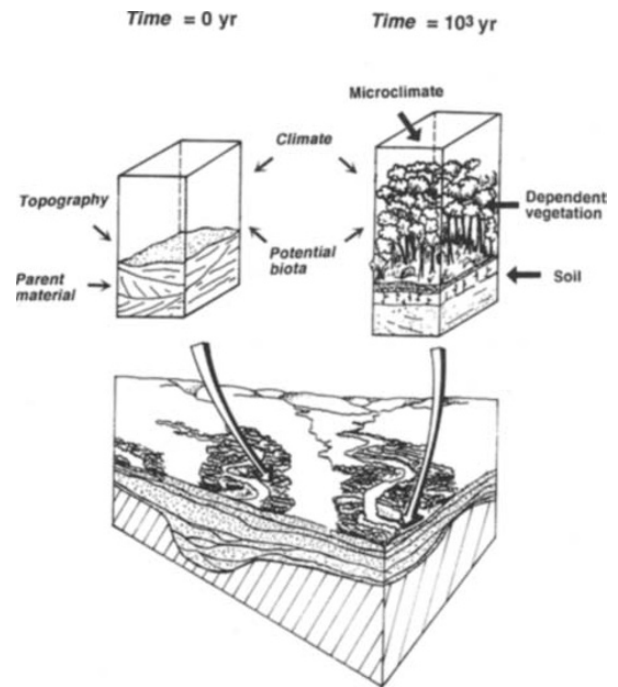
studies can be found in Jenny (1941, 1989).

- The state factor *climate* (*cl*) is the climate (e.g., rainfall, temperature, and humidity) surrounding the ecosystem. It is often consistent with the concept of regional climate. The climate within an ecosystem (which is a property of that ecosystem) is referred to as microclimate or dependent climate (*cl'*). This dependent climate is related to the regional climate but is also conditioned by the other state factors that are affecting the ecosystem.

- The biotic factor, sometimes called *organisms* (*o*), is defined as the potential biota of the system. From a practical standpoint, the biotic factor is the microbial, plant, and animal gene flux that enters the system from the surroundings. The vegetation (*v*) and animals (*a*) that actually survive or reproduce in the system are dependent ecosystem properties. These living organisms may not directly reflect the potential biota because they depend on the constellation of all the state factors. For example, plants that grow at a site can be a function of climate (Amundson et al. 1989), topography (Elgabaly 1953), parent material (Pastor et al. 1984), and ecosystem age (Burges 1960, Van Cleve et al. 1991). Given the ease with which seeds and animals are dispersed, it is difficult to compare natural ecosystems that differ only in their biotic factors. Sites separated by biotic barriers, such as mountain ranges and oceans, may be used for these comparisons. In addition, the invasion of introduced species into otherwise undisturbed island ecosystems offers an opportunity to observe the initial phases of a change in the biotic factor (Vitousek and Walker 1989).

- The state factor *topography* (*t*) is made up of a number of subvariables that correspond to the physical configuration of an ecosystem at $t = 0$ (the beginning of the system's development or the beginning of an observation period). These subvariables include the site's topographic position on a hillslope complex, the aspect of the slope, and the proximity of the system to a shallow groundwater table.

Figure 1. Two terrestrial ecosystems at different stages of development. State factors are identified in italic type, and important ecosystem components are indicated by roman type. The sediment in the system on the recent fluvial deposit ($t = 0$; upper left) is defined as the parent material. The system has had insufficient time for establishment of flora and fauna, even though a biotic source (potential biota) exists. In the ecosystem on the stabilized river terrace (time = 10^3 years; upper right), pedogenic processes have formed a soil. These two ecosystems are but the most recent members of a long temporal continuum of systems, many of which are buried in the sediments illustrated in the lower part of the figure. A rich vegetation, reflecting controls imposed by the system's state factor assemblage, has also evolved. The microclimate within this ecosystem is no longer the same as that of the regional climate, as in the young ecosystem, but is instead a function of the system's age, biotic factors, and other state factors. After Retallack 1983.



- The state factor *parent material* (*p*) is defined as the initial state (at $t = 0$) of the sediment, rock, or soil component of the ecosystem. For an ecosystem developing on fresh alluvium or on a recent volcanic flow, the parent material is the geological material itself. For an ecosystem that is reforming on a site that has been burned or clear-cut, the parent material is the soil that is present at the time at which the new flora begin to reinhabit the site.

- The state factor *time* (*t*) is defined as the elapsed time since the ecosystem began forming or since the assemblage of state factors of an ecosystem changed. For some ecosystems, this starting point, or $t = 0$, begins after a depositional event, such as fluvial sediment or volcanic ash deposition. In others, $t = 0$ might be considered the time at which a major disturbance or change in the configuration of the remaining state factors occurred. Climatic change, biotic influx, or human disturbance can all be of such magnitude that, from an investigative standpoint, one must consider them capable of resetting the "clock"—that is, starting the development of a new ecosystem.

In light of this definition, it is apparent that many of the earth's ecosystems have been influenced by multiple constellations of state factors and may be regarded as polygenetic—that is, as reflecting two or more contrasting periods of formation, each with a different constellation of state factors. Pedologists have long recognized that many soils older than the Holocene reflect conditions of past climates (Hilgard 1887). The fact that these soils do not entirely reflect the modern assemblage of state factors does not invalidate the use of the state factor model to investigate these soils or ecosystems. Instead, it opens the possibility that relict features in those ecosystems may be used to reconstruct past climates using climate and ecosystem relationships developed in Holocene environments (Retallack 1990).

- The state factor *humans* could conceptually be subsumed under the *biotic factor* (*o*; e.g., Jenny 1941) because, like all other biota, humans contain a genetic component (a genotype). However, unlike many other species, human populations possess a cultural component (Amundson and Jenny 1991, Jenny 1980) that

varies greatly from society to society irrespective of genotype. Culture is defined as the assemblage of technologies, ideas, and philosophies possessed by a group of individuals. Thus, to distinguish the purely physiological characteristics of humans from their sociological aspects, the state factor *cultural inheritance* (c ; the cultural assemblage of a population in a system at $t = 0$) has been defined as a distinctive state factor of ecosystem formation (Amundson and Jenny 1991).¹

It should be recognized that the collective culture of a human population at any time t may vary greatly from that at $t = 0$. These changes in the resulting culture (i.e., in the dependent variable c') reflect the influence of the constellation of the state factors of the ecosystem. This dependent variable varies in response to state factors. For example, the social structure of early nineteenth-century Great Plains indigenous populations varied with climate (Bamforth 1988), and the agricultural practices (and associated technologies) of migrating Polynesian populations varied in response to the characteristics of the islands being settled (Kirch 1982).

This list of state factors is not exhaustive, and the equation on page 536 is written to allow the addition of other factors of local importance, as the ellipses indicate. Some additional factors include fire, coastal salt spray, and dust (Jenny 1980).

The key to using the state factor model quantitatively lies in being able to numerically represent the properties of both the ecosystem and the state factors. If numerical relationships can be constructed, then various univariant functions describing the relationship between ecosystem properties (e) and state factors can be derived from field observations:

$$\text{climofunctions: } e = f(c)_{c, \theta, r, p, t, c, \dots}$$

$$\text{biofunctions: } e = f(\theta)_{c, \theta, r, p, t, c, \dots}$$

¹The full human state factor (b) therefore contains genetic (θ_g) and cultural components: $b = (\theta_g, c)$. For most ecosystem studies, the role of culture is of interest, and it is stressed here. In this article, cultural inheritance is designated simply as c (in contrast to our earlier use of the symbol c_1), and dependent culture is designated as c' (compared with our earlier use of c ; Amundson and Jenny 1991).

$$\text{topofunctions: } e = f(r)_{c, \theta, r, p, t, c, \dots}$$

$$\text{lithofunctions: } e = f(p)_{c, \theta, r, p, t, c, \dots}$$

$$\text{chronofunctions: } e = f(t)_{c, \theta, r, p, t, c, \dots}$$

$$\text{anthropofunctions: } e = f(c)_{c, \theta, r, p, t, c, \dots}$$

The design and quantification of univariant functions have been the primary field application of the state factor model for studying soils and ecosystems (Jenny 1941, 1961, 1980). The effect of a given factor on an ecosystem property can be evaluated by holding the other factors invariant between sites. This principle can be best understood by considering the differential form of the equation that describes the difference in properties between ecosystems (Jenny 1941):

$$de = (\partial e / \partial c) dc_{c, \theta, r, p, t, c, \dots} + (\partial e / \partial \theta) d\theta_{c, \theta, r, p, t, c, \dots} + (\partial e / \partial r) dr_{c, \theta, r, p, t, c, \dots} + (\partial e / \partial p) dp_{c, \theta, r, p, t, c, \dots} + (\partial e / \partial t) dt_{c, \theta, r, p, t, c, \dots} + (\partial e / \partial c) dc_{c, \theta, r, p, t, c, \dots} + \dots$$

The total change in properties between ecosystems (de) can be evaluated with respect to a single factor in one of two ways. First, the range, or total variation, in the other factors between systems can be kept negligible through clever site selection. For a study in which the effect of climate is to be evaluated, for example, $d\theta$, dr , dp , dt , and dc all equal 0, or nearly so. A second way to hold other factors constant emerges from considering the second equation. Even if total variation in some factor is not held constant between sites ($d\text{factor} \neq 0$), then the effect of the factor may still be unimportant, so long as $\partial e / \partial \text{factor} = 0$ for the sites of interest. For example, in soil studies, the effect of climate on soil organic carbon storage can be evaluated by choosing sites that vary greatly in climate but have similar slopes, parent materials, and biotic factors. However, the age of the soil (i.e., the age of the deposits on which the soils form) may be difficult to hold constant across a broad climatic gradient. Although the age of the soils may vary considerably, if they are all more than several thousand years old they may be near steady state with respect to organic carbon storage (Schlesinger 1990), making variations in carbon storage between sites

due to variations in the time factor negligible. The existence of steady state (or, more generally, the insensitivity of an ecosystem property to any factor) cannot be assumed; it must be verified through empirical observation for each ecosystem property of interest.

Development of the state factor model

The state factor model is not well known in ecology (Golley 1993), although methodological approaches such as comparative ecosystem analysis (Duarte 1991, Peters et al. 1991) appear to be closely related to it. The relative obscurity of the state factor model in ecology is probably related to a historical lack of communication between the field in which it developed (the earth sciences) and the field in which most ecosystems researchers are trained (the biological sciences; Golley 1993). Golley (1993) noted that important concepts related to ecosystem studies were developed by Russian earth scientists but concluded that these concepts had little impact on present ecosystem thought.

Although the early Russian ideas remained unknown to the English-speaking world for some time, these concepts did eventually reach the West through a circuitous pathway and have become part of mainstream pedological thought for much of the second half of the twentieth century. These ideas, as modified and redefined by others (Jenny 1941, 1958, 1961), serve as the initial framework for the state factor model described here.

The origin of the state factor model is commonly traced to Vasilii Dokuchaev, who is widely recognized as being among the originators, if not the founder, of modern pedology (Krupenikov 1993, Vucnich 1970). Dokuchaev was born in Russia in 1846, the son of a priest. On beginning a fellowship at the Theological Seminary in St. Petersburg, his attentions turned to natural science, and he eventually obtained his doctorate in geology, becoming curator of the geological laboratory at St. Petersburg University in 1872 (Joffe 1936). An important event for Dokuchaev was his

selection, in 1876, by the Free Economic Society to organize the first systematic study of the Russian chernozem (prairie soil), with specific instructions to explain its structure, origin, and evolution (Dokuchaev 1883, Krupenikov 1993, Vil'yams 1936). The participants in Dokuchaev's study sought advice from scientists of a broad range of disciplines, using the most advanced chemical and physical analyses available to them for their investigations.

Within a short time, Dokuchaev perceived soil to be an "independent natural body" (Vil'yams 1936) that is amenable to explanation by natural laws. As early as 1880, he wrote (Dokuchaev 1880):

Like any other individual body in nature, any other organism, soil has also its specific origin, its chemical composition and physical attributes, its individual structure, its habitude, its specificity in geographical distribution. As has been explained in other papers, every normally located surface soil bearing vegetation has to be regarded as a function of the:

- (a) Local maternal rock variety
- (b) Age of the land (in particular the time since it became surface land)
- (c) Climate
- (d) Vegetation

...By issuing from these assumptions, the distribution of soil cannot any more be regarded as an absolutely casual phenomenon. The geography of soils, just like the distribution of other organisms, conforms to definite laws....

Vil'yams (1936) stated that these factors were recognized by Dokuchaev's predecessors, but he credits Dokuchaev with considering their combined effect and evaluating each independently. Dokuchaev clearly recognized that his theory of soil formation had implications for the natural world (i.e., terrestrial ecosystems) as a whole (Dokuchaev 1898):

It is my undaunted opinion, that the concepts of modern soil knowledge, as developed in Russia, should be placed in the center of the basis on which we construct

our new understanding of nature as a whole. I believe that our soil knowledge should become the very springboard from which our teachings on the relationship between "living" and "dead" nature derive their impetus for the grasping of the idea of the relationship between man and the rest of the world, i.e., its organic, as well as mineral part.

According to Krupenikov (1993), Dokuchaev commented, in the following year, that the "time is not far when in its own right and because of its great importance for humanity, it (i.e., the science of the study of terrestrial systems as a whole) will occupy an independent and fully respected place."

The dissemination of Russian pedological thought to the western world, particularly the United States, was hindered by a language barrier. In 1908, the Russian scientist N. M. Tulaikov wrote, in a review of soil science in the United States (Tulaikov 1908):

I wish to express my regret that the success in the understanding and the application of fundamental principles of scientific "soil-knowledge" as emphasized in the contributions of Russian soil scientists, remain still to a great extent unknown to the foreign reader interested in this realm of science. We have not yet gained such a position among the circle of European and other scientists, to be read in our own native tongue, therefore, we remain completely unknown, notwithstanding that in many fields we should deserve a different attitude toward us.

Eugene W. Hilgard, the eminent American soil scientist, urged the Russians to publish abstracts in either French or German, which would "assist to the distribution of Russian contributions from the border of Russia to the Bay of San Francisco" (Tulaikov 1908). It was the eventual German publication of Russian pedological ideas that led to the passage of Russian pedological thought to American science. With help from the German scientist Hermann Streme, Konstantin D. Glinka, a student of Dokuchaev and an important contributor to Russian pedology in his own right, wrote *Die Typen*

der Bodenbildung in 1914 (Simonson 1997, Tandarich and Sprecher 1994). By 1917, this book was translated into English by the American soil scientist Curtis F. Marbut, the director of the Division of Soil Survey, US Department of Agriculture (USDA). According to Joffe (1936), Marbut's introduction to Russian pedological theory inspired him to transform many aspects of the US soil classification system and the way in which soils were studied in the United States.

The infusion of the Russian concepts of soils and nature into ecology began as early as 1930, with the publication of Charles Shaw's discussion of factors of soil formation (Shaw 1930). However, the primary breakthrough was Hans Jenny's reformulation and further quantification of the state factor concept and the publication of these integrated ideas as a book in 1941 (Jenny 1941). As noted elsewhere (Amundson 1994b), this publication provided a detailed definition of both soil and the "larger system," as well as a method to quantitatively and numerically link soil and larger system properties to state factors.

The concept of the larger system immediately suggested ecosystem to Jenny and his students. In 1951, Jack Major published the first paper (Major 1951) explicitly linking the factorial model to ecosystem analysis by focusing on the relationship of state factors to vegetation. A subsequent paper by Jenny (1958) further discussed the significance and interpretation of the biotic factor, and in later publications he explicitly expanded the model to ecosystemwide applications (Jenny 1961, 1980). The present status of the factorial model in ecology and ecosystem science has been discussed recently by Phillips (1989) and Vitousek (1994).

The state factor model as a historical science

The state factor model of ecosystems shares elements of concepts used by other branches of the historical sciences, of which geology is a notable example (Frodeman 1995). A historical science is one in which the object of understanding—in this case, ecosystems—involves a knowledge of both place and time (Frodeman

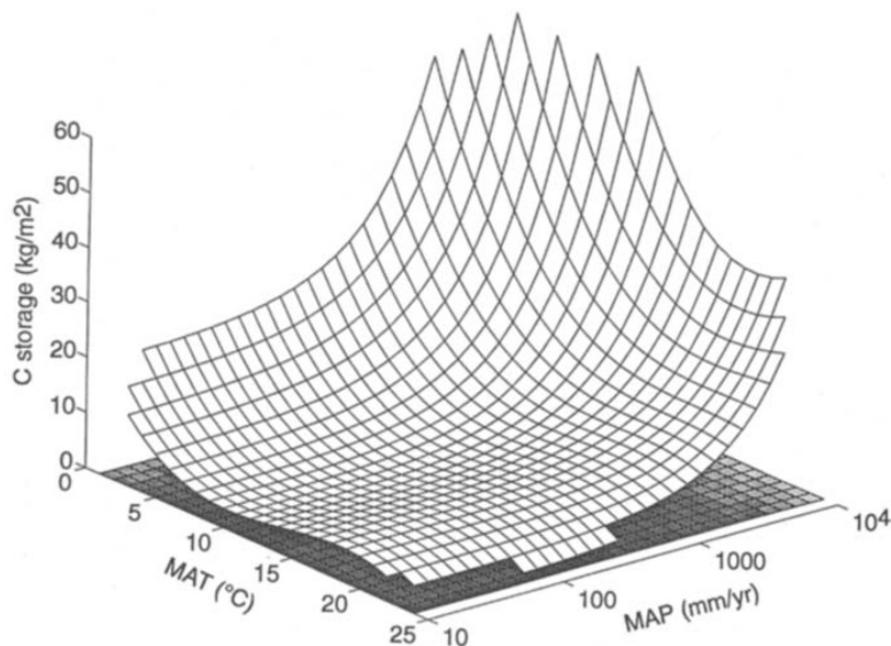


Figure 2. A schematic representation of global soil carbon in relation to mean annual temperature (MAT) and precipitation (MAP). The three-dimensional surface was generated by interpolating between the carbon storage to climate relationships given in Figure 1 of Post et al. 1982.

1995). One challenge common to all historical sciences is to define the object of study, to identify the set of characteristics that define it, and to determine how much change can occur before it is considered a new entity (Frodeman 1995).

In the historical sciences, as Stephen J. Gould has noted, “the results of history lie strewn around us, but we cannot, in principle, observe the processes that produced them. How then can we be scientific about the past?” (Gould 1983). It is common in the earth sciences to assemble the results of a given process in its different stages to determine the rate and direction in which the process proceeds (Gould 1983). The state factor model of ecosystems shares this premise but expands on it by suggesting that it is also possible to examine portions of the earth, all at the same stage of development but in a variety of different environments, to decipher quantitative relationships between ecosystem properties and the independent variables known as state factors. The state factor model is, therefore, one of several likely approaches to “comparative ecosystem analysis” (Cole et al. 1991), and its use in this context has been discussed and illustrated in a few recent

publications (e.g., Vitousek 1994, Vitousek and Matson 1991).

The state factor model (Jenny 1941), like many comparative ecosystem models (Peters et al. 1991), is nonmechanistic. Strictly speaking, the state factor model tells us nothing about how a system acquires its properties—it is phenomenological (Amundson and Jenny 1991). To address processes or mechanisms, one must resort to different types of models that address other aspects of the ecosystem. The dichotomy between state factor models (nonmechanistic) and process models (mechanistic) has been much discussed in the pedological literature (e.g., Hoosbeek and Bryant 1992) and in the history of science literature (e.g., Gale 1984), with the recognition that the two approaches are, in many cases, complementary and essential to a fuller understanding of natural phenomena (Amundson 1994a).

Finally, the state factor model differs from some other concepts of ecosystems in that it explicitly includes soil, water, and the atmosphere—all of which are subject to changes in response to any changes in the independent state factors—as integral components of ecosystems. In this sense, these components are

much more than abiotic factors that affect the living organisms of the system—they are dynamic ecosystem features that vary spatially and temporally across the globe.

The state factor model in the study of terrestrial ecosystems

The array of concepts and models for describing ecosystems is diverse (Likens 1992), and communication between divergent points of view has not been effective historically (Golley 1993, Pimm 1994). This Balkanization may be due to several factors, among them the tendency of practicing scientists as a group to be relatively unconcerned with the origin and implications of the models and theories that they use (Gale 1984, Kuhn 1962). But as many scientists have argued (Frodeman 1995, Gale 1984), a better awareness of the nature and origin of scientific reasoning will benefit not only the individual scientist, but also the scientific community as a whole.

The state factor model is a unique and useful means of studying nature: both conceptually and quantitatively. It is particularly useful for experimental design in comparative ecosystem studies, because it forces the investigator to explicitly determine the variation in the complete array of factors that affect the systems being examined. For many scientists, the usefulness of a model is the most critical criterion for general acceptance. Nearly 75 years of data collection and analysis attest to the applicability of the state factor model to the study of soils. As an example of its utility in this application, we show how it can be applied to an ecosystem problem of immediate concern: the role of terrestrial ecosystems in the global carbon cycle.

It is well documented that the largest terrestrial reservoir of carbon resides in soil organic matter (Schlesinger 1991). There have been two approaches to quantifying and organizing the global soil carbon pool: taxonomic (e.g., Bohn 1976) and ecological (i.e., based on a state factor approach; Post et al. 1982). Both give similar estimates of soil carbon pools (Kern 1994), but the taxonomic approach has no predictive value, whereas the ecological approach has

been the basis for estimates of the effects of both past and future climate changes on the global storage of terrestrial soil (and plant) carbon.

The taxonomic approach relies on the determination of the areal extent and average carbon content of the major soil taxonomic groups of the world (e.g., soil orders or suborders of the USDA system or mapping units of the Food and Agricultural Organization world soil map). The USDA soil classification scheme is deliberately nonscientific in the sense that taxa are established for practical purposes of land management and are not defined or determined by their direct relationship to state factors or to soil processes. The concepts used in the definition of soil taxa in the USDA system are outlined by Smith (1965, p. 19): "Properties selected as differentiae should be soil properties. The use of theories acts to limit the possibility of acquiring new knowledge. The use of non-soil properties, such as the bedrock or the climate, tends to focus our attention on the climate or the geology rather than on the soil." Although post-factum arguments have been raised to highlight the relationship of defined taxa to state factors or processes (Cline and Johnson 1963), it remains inherently impossible to predict what new soil taxa and, therefore, soil carbon might develop in response to a climate or environmental change because, as Smith (1965, p. 22) notes, "At least one step of reasoning is necessary to develop genetic interpretations from the definitions of the (soil taxonomic) classes."

The ecosystem approach provides an entirely different basis for estimating and organizing global soil carbon reservoirs. The basis for this method is the observation that broad ecological life zones (Holdridge 1947) are distributed in relation to variations in climate, a state factor. Based on the general observation that plant communities and soil organic carbon covary in response to climate variations, Post et al. (1982) tabulated the areal extent of the world's major life zones and calculated the average soil organic carbon content of each life zone to assemble what might be the most widely quoted estimate of the global soil carbon pool.

This ecosystem approach has several advantages. First, it provides an

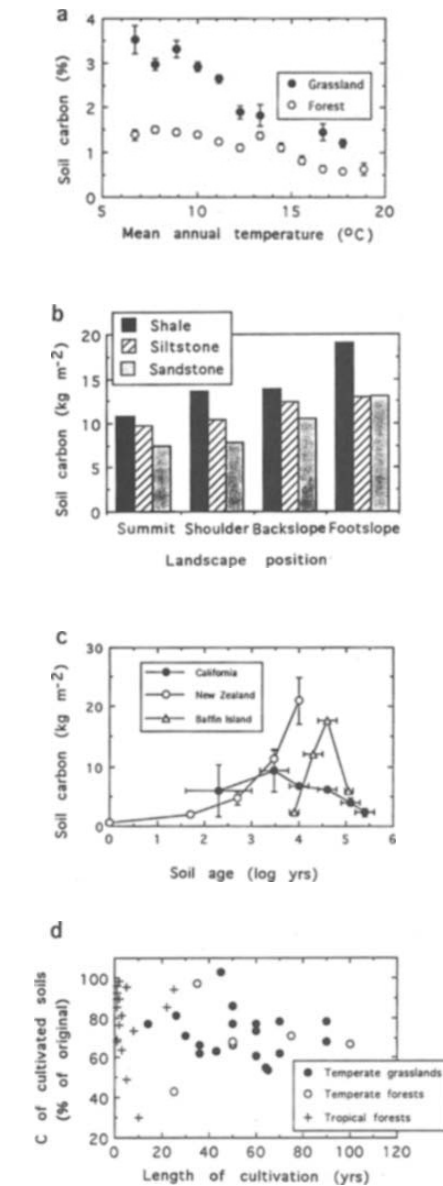


Figure 3. The effect of state factors, other than climate, on the organic carbon content of soils. (a) The relationship between organic carbon (in the upper 20 cm of soil) and mean annual temperature in the grassland–forest boundary in the Great Plains (data from Jenny 1930). The difference in carbon between the grassland and forest sites approximates a biosequence because the vegetative difference is most likely a function of fire (Brown 1985), which may be considered a state factor in its own right, rather than of differences in potential vegetation. (b) The relationship between soil organic carbon and hillslope position and parent material in the northern Great Plains (data from Aguilar et al. 1988). (c) The relationship between soil organic carbon and soil age (California data from Harden 1987; New Zealand data from Syers et al. 1970; Baffin Island data from Evans and Cameron 1979). (d) The relationship between length of cultivation and remaining soil carbon in some major biotic zones of the world (data compiled by Schlesinger [1986]). For data where nitrogen rather than carbon content was reported, a C:N ratio of 12 was assumed in the calculation of the carbon content. In all graphs except (d), explicit attempts were made to control variations in all state factors other than those being examined.

effective means to reconstruct past (or future) soil carbon storage based on ecological changes. For example, changes in global terrestrial carbon storage from the last glacial maximum to the present have been calculated by reconstructing glacial maximum vegetation patterns (either from paleoecological data [Adams et al. 1990] or from modeling [Prentice and Fung 1990]). In these approaches, soil carbon storage at the glacial maximum was calculated using the relationships between present-day soil carbon and ecosystem vegetation established by Post et al. (1982) and others.

Moreover, using the ecosystem approach to tabulate soil carbon provides an opportunity to explicitly link global soil storage directly to

climate, because both soil organic carbon and plant communities are functions of regional climate. Figure 2 uses data from Post et al. (1982) to illustrate the relationship of soil carbon to mean annual temperature and precipitation that can be derived from an "ecological life zone" or "Holdridge life zone" organization of carbon storage. This figure illustrates, at a global scale, what is well known from smaller, regional studies: Soil carbon increases with mean annual precipitation and decreases with mean annual temperature (Burke et al. 1989, Jenny 1930, 1941). Most important, as noted by Post et al. (1982), this analysis reveals the climatic regions that are most susceptible to large changes in soil carbon storage with small changes in climate (i.e., Figure 2 shows areas where carbon changes greatly with small changes in either temperature or precipitation). Figure 2 does not illustrate the large variability of soil carbon in any given climatic zone (generally at least 50% of the mean value in either direction; Post et al. 1982). Presumably, this variability results from the fact that

carbon storage does not depend on climate alone but results from the entire series of state factors (Figure 3): Variations in biota, topography and parent material, soil age, and humans within any given climatic region all probably contribute to the reported "noise" in the data (Post et al. 1982).

These applications of the state factor model in its broadest sense are, like all historical sciences and related methodologies, limited in their predictive value. To paraphrase Frodeman (1995), the present world may be too narrow a window to view the past or the future, and our modern analogues may not directly apply backward or forward in time. Nevertheless, historical approaches may, in many cases, represent our best, or even our only, means of scientifically addressing many ecosystem problems of immediate global concern. Not only their limitations, but also their strengths, should be both acknowledged and explored.

The state factor model of ecosystems possesses an elegance, outward simplicity, and potential breadth of application that makes it an appealing means of studying nature. Yet in actual practice, the selection of ecosystems to study the effect of one state factor or another is seldom a simple matter, and rigorous experimental design commonly involves the expertise and interaction of geomorphologists, ecologists, pedologists, climatologists, and many other specialists. This need for a multidisciplinary approach strikes at the heart of what ecosystems are conceived to be (Tansley 1935) and provides an opportunity for greater communication among disparate sciences that are now confronted with urgent problems and questions of a global and human dimension.

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