Increasing evidence for chaotic dynamics in the soil-plant-atmosphere system: a motivation for future research

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Abstract

This paper reviews the background and current development of nonlinear dynamics and chaos as it applies to the soil-plant-atmosphere system (SPAS). We build the case that such processes are likely common in the SPAS and offer the possibility that the phenomena constituting chaotic dynamics are the underlying biophysical basis for sustainability of natural ecological and agricultural systems. Recent experiments that illuminate this viewpoint are described, along with data analysis methodology. It is concluded that a fuller understanding will require interdisciplinary research devoted to an improved understanding of complex system behaviour.

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1. Introduction

The coupled and interacting system composed of the plant, root, soil, microbes and surrounding atmosphere, which is vital to agriculture, is fascinating in its complexity [1-3, 52]. The anticipated climate change during the present century adds urgency to our search for improved understanding of complex natural and agricultural soil-plant-atmosphere systems (SPAS) [4, 70].

Innovative agricultural developments of the past and current centuries led to impressive production increases along with increased sensitivity to future environmental variables [46, 47]. The concepts of
complexity and chaos are being invoked in the soil and related agricultural and microbiological sciences literature. Chaotic dynamics is now an active area of research in mathematics, fluid mechanics [51], biochemistry [44], population biology [9], soil physics and many areas of ecology [6, 11, 52].

Having the ability to solve systems of coupled nonlinear differential equations easily and rapidly led to the rediscovery, during the 1960s, of a phenomenon called “deterministic chaos.” In 1963, the meteorologist E.N. Lorenz [7], using numerical analysis, rediscovered the original findings of the mathematician Poincaré, who came upon a seemingly disordered mathematical phenomenon [5]. Studies [6] indicated that sufficiently complex time-dependent models (at least 3 coupled, nonlinear, ordinary differential equations) display chaos by being highly sensitive to initial conditions. Because at each time step of a numerical solution the previous step serves as an initial condition, the phenomenon of ultra-high sensitivity must occur throughout the solution process. In fact, this is what led Lorenz [7, 8] to his seminal numerical experiments. The end result is that a mathematical model displaying chaos does not produce a unique solution associated with any particular initial condition. Instead, many possible solutions are predicted that diverge from each other as time increases, with no necessary involvement of stochastic processes. (Actually, stochastic processes appear to hide chaos [25].) Ultimately, the solution set becomes spread throughout the entire solution domain as illustrated beautifully by Strogatz [5, Pl. 2].

Chaos theory was first brought into the biological sciences by Robert May, a physicist who was drawn into the complexities of population biology. In a ground-breaking review article [9], he worked with a simple formula derived from an elementary form of the logistic equation. If $N$ represents a population size, and $t$ is time, then the logistic equation is given by:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{C}\right),$$

where $r$ is the growth rate (assumed constant), and $C$ is the carrying capacity of the local environment. Such a single nonlinear equation does not exhibit chaotic behaviour, but an algebraic relationship related to it, called an iterated map, does. The so-called logistic map studied by May [9] can be written as:

$$N_{n+1} = rN_n \left(1 - N_n\right).$$

Such an expression is mainly a “pattern generator” and is not a meaningful representation of population dynamics, and this was the spirit that May followed [10]. To see the pattern that develops, one picks an initial value $N_0$ and iterates the logistic map $n$ times ($n= 1, 2, 3$ and on) for different values of $r$. If values of $N$ are plotted against values of $r$, an amazing pattern develops for $r >$ about 3 [11]. For example, for $r$ between ~3.45 and 3.54, the population will approach permanent oscillations among four values. At $r \sim 3.57$, the onset of chaos is developed. Most $N$ values for $r > 3.57$ exhibit chaotic behaviour, but there are still certain isolated ranges of $r$ that show non-chaotic behaviour, which are sometimes called islands of stability. It was this complex pattern that May and many others tried to understand - mainly a mathematics problem [12].

In the 1980s-90s, the main point was that simple, nonlinear, deterministic expressions can display extremely complex behaviour, something not fully appreciated previously. However, the association with soil-related agricultural, geochemical, and biological systems stimulated the interest of many researchers, and soon continuous and mass-conserving mathematical models of soil and biological systems were developed that fully displayed chaotic dynamics for certain parameter sets [44-47]. For example, the
book [44] provides an introduction to the analysis of chaos and chaos theory as it relates to agricultural science, and also contains applications of the theory to real agricultural systems.

Based on a series of experimental chemostat studies, Kot et al. [13] were among the first to develop an early mathematical treatment of coupled nonlinear microbial processes, with a food source and a number of competing microbes. The three Kot et al. equations are given by

$$\frac{dS}{dt} = D(S^*_i - S) - \mu_1 \left( \frac{SC}{K_1 + S} \right)$$  
$$\frac{dC}{dt} = \mu_1 \left( \frac{SC}{K_1 + S} \right) - DC - \frac{\mu_2}{Y_2} \left( \frac{CP}{K_2 + C} \right)$$  
$$\frac{dP}{dt} = \mu_2 \left( \frac{CP}{K_2 + C} \right) - DP$$

In this nonlinear and coupled system, $t$ is time, $D$ is the chemostat dilution rate, $S$, $C$ and $P$ are concentrations of substrate, substrate consumer (also prey), and microbial predator, respectively, and the other symbols represent constants associated with Monod chemical kinetics [14]. (Substrate flows in ($DS_i$) and out ($DS$), $C$ feeds on $S$ and $P$ feeds on $C$, both following Monod kinetics.)

When one considers the complexity of the SPAS, including the rhizosphere, one realizes that many equation systems analogous to the Kot et al. set may be developed. Note that the rhizosphere plays an important role in nutrient cycling, and is strongly influenced by root exudate quantity and composition, as microbial species differ in their ability to metabolize, and compete for, different carbon sources [48]. For such complex systems, a set of 10, 20 or more variables are not precluded. Moreover, if spatial or temporal (or both) dependence is included, the ordinary differential equations (ODEs) become partial differential equations (PDEs). Although many scientists have already investigated the development of chaos from the solution of ODEs and PDEs, we are at the very beginning of understanding how to detect deterministic chaos from experimental investigations and to access its practical implications in SPAS studies.

### 2. Is chaos real?

Since the discovery of deterministic chaos was associated with unexpected and strange solutions to ODEs and PDEs, the initial response of some was to think that this phenomenon might be just a “mathematical phenomenon.” However, in the area of fluid mechanics and other mechanical/electrical systems it rapidly became apparent that chaos was physically real, and in fact was at least the initiating phenomenon behind fluid turbulence [15]. Of more direct interest to the SPAS, research involving unsaturated water flow in porous media and fractured rock indicated the occurrence of chaotic dynamics, which tied into the previously existing fluid mechanics literature [16-18]. In ecology and the life sciences, however, definitive experiments were difficult to achieve, and in 1999 Zimmer [19] made the case that after many years of searching for chaos in the real world, ecologists came up mostly empty-handed. He acknowledged the early demonstration by Costantino et al. [20] of chaotic dynamics in captive flour beetles, but captive beetles are not the real-world, and noise-free, detailed, real-world data are difficult to obtain. Other examples of dynamic systems that display nonlinear deterministic chaotic behaviour with aperiodic and apparently random variability include atmospheric [7, 8, 56], geologic [60], geochemical [58], and geophysical [61, 62] processes, avalanches resulting from the perturbation of sand piles of various sizes [63], falling of water droplets [64], river discharge and precipitation [65], oxygen isotope concentrations [57], viscous fingering in porous media [66], oscillatory fluid release during hydro-fracturing in geo-pressured zones in actively subsiding basins [58], thermal convection in porous media at large Rayleigh numbers [67], instabilities at fluid interfaces [70], and nonlinear dynamics of soil moisture at climate scales [70]. So we would have to conclude that chaos is real, but as complexity increases in
environmental and living systems, such as those found in the SPAS, does chaos dominate or does it interact with or merge with something else? These are wide open questions that will be fun trying to answer.

3. How is chaos detected?

Chaos is relatively easy to detect from a numerical time-series solution of a nonlinear mathematical model. The original procedure is to plot the dependent variables of a coupled mathematical model against each other; so 3 variables, the minimum required for ODE-based chaos, would result in a 3-D plot. The domain of such a plot is commonly called “phase space” or “state space.” Each point in phase space represents the values taken on by the dependent variables at a particular instant of time, and the collection of points, showing how a solution evolves with time, is called a phase space trajectory. Starting from even slightly different “first” points (i.e., the initial conditions), phase space trajectories will fall on different parts of the phase space, as chaotic systems are sensitive to initial conditions. In phase space, steady state behaviour is represented by a single point (i.e., a fixed point), and 2D periodic behaviour results in a closed loop, like a circle or an ellipse [5]. Solutions with singularities may generate more complex “phase portraits,” but a plot involving chaotic dynamics results in a uniquely complex object.. An example, using a solution of the Kot et al. [13] system (see above) is shown in Fig. 1 The object that results is called a “strange attractor,” because many different nearby initial conditions will yield solution trajectories that will enter (be attracted to) the unique attractor space. It is called “strange” because classical solutions do not display this type of bounded behaviour that continues indefinitely. (Further description of strange attractors may be found in [24, 25, 42, 53, 54, 55].) Note that deterministic chaotic behaviour may not be evident in time series plots, but more discernible structure appears in the phase space plots.
If detecting strange attractors and studying their properties was the only way to detect chaos, then using experimental data to detect chaos would be difficult. One would need to identify the entire model and how the many parts interacted before collecting data. There are now several types of diagnostic criteria of chaos that can be applied to single data sets (Values vs. time.). They include Lyapunov exponents, correlation dimension, embedding dimension, etc. [25, 26, 42, 53-55]. One of the most important criteria is that the largest Lyapunov exponent be positive. If one developed two solutions with slightly different initial conditions, the separation of phase space trajectories could be expressed with the relationship, \[ \Delta_n \approx \Delta_0 e^{\lambda n} \], where \( \Delta_0 \) is the separation of the initial conditions, \( \Delta_n \) is the trajectory separation after \( n \) time steps in the numerical solution, and \( \lambda \) is the largest Lyapunov exponent. The “approximately equal” symbol is used because in an actual calculation there would be a Lyapunov exponent for each coordinate direction (at least 3 for chaos). It can be shown, and indeed is intuitive, that ultimately the one largest exponent will dominate the rate of separation of the two solutions [5], so phase-space dimensions >3 are less of a problem. If the exponent is zero, then the trajectory separations will not change with time; a negative exponent yields decreasing separations with time, but a positive Lyapunov exponent implies a separation that grows with time and is unbounded. The latter indicates that no matter how close together initially, the chaotic model solutions with a positive exponent will ultimately separate “exponentially” the phase space. The trajectory separation calculated in this way won’t go to infinity, it’s like racing on a circular track - the leader can lap other runners, but if one starts with say 100 initial conditions very close together, the exponentially fast effect will spread the advancing points of the trajectories all over the strange attractor, and the solutions will appear unrelated in the attractor or real domains. This overall effect is what is meant by extreme sensitivity to initial conditions, and it occurs all along a solution trajectory [5, 22, 25]. So a positive Lyapunov exponent is a clear indicator of chaotic behaviour [5], and a zero or negative value is characteristic of classical behaviour. Illustration of the phase space domain for the numerical solution of the Kot et al. model is given in Fig 1. One would expect that another phase space plot would result in a very similar, but slightly different form of the strange attractor.

4. Review of results of recent experiments.

During the past 8 years, at least 3 well-controlled laboratory experiments were performed that indicated both chaotic dynamics and classic dynamics in microbial systems under specific conditions. Becks et al. [21] demonstrated chaos in a microbial food web in a chemostat. The web was composed of a food source, 2 bacteria that consumed the food with different efficiencies (a rod and a coccus), and a ciliate predator that consumed both bacteria but preferred the rod over the coccus by a factor of 4. The variable driving the system was the food supply that was varied by changing the dilution rate. The 4 coupled dependent variables were concentrations of substrate and the 3 microbes. For a fixed set of dilution rates, the 3 microbe concentrations were measured at a selected set of time intervals. At high dilution rates typical steady-state behaviour was observed; in a midrange of rates chaotic dynamics occurred and at lower rates something looking more like periodic behaviour was observed. Each set of data constituted a time series (concentrations as a function of time), and chaos was identified by using a computerized version of the analytical procedure developed by Rosenstein et al. [22] for calculating the largest Lyapunov exponent (TISEAN package [27]). In the chaotic data range, which averaged a dilution rate of about 0.5 d\(^{-1}\), the dominating Lyapunov exponents had statistically significant values of about 0.18 d\(^{-1}\). Since the experiments typically ran for 50 days, this would imply an increase of a small initial separation by a factor of about \( \exp(9) = 8000 \), if the strange attractor were sufficiently large. Standard plots of the chaotic data as functions of time showed irregular, non-periodic behaviour. A particularly
interesting run was one where a dilution rate of 0.5 d⁻¹ was increased to 0.75, and the observed behaviour went from apparently chaotic to classical steady state with a Lyapunov exponent of negative 0.25.

A 2nd experiment was reported by Graham et al. [28], who observed chaotic dynamics in a controlled laboratory environment with a much more complicated community, using biological nitrification. In this study, the aerobic bioreactors were filled initially with a mixture of wastewater from a treatment plant and simulated wastewater, involving a mixture of many microbes. The main variables recorded as a time series were total bacteria, ammonia-oxidizing bacteria (AOB), nitrite-oxidizing bacteria (NOB), and protozoa, along with effluent concentrations of nitrate, nitrite and total ammonia. (The microbe “group” variables were called “guilds”.) Once again the method of Rosenstein et al. [22] was used to calculate Lyapunov exponents, which fell in the range of roughly 0.05 to 0.2 d⁻¹. Additional approaches to analysis were discussed, and it was suggested that “nitrification is prone to chaotic behaviour because of a fragile AOB-NOB mutualism” (interaction).

Beninca et al. [29] conducted a laboratory experiment over a period of 6.3 years, which demonstrated chaotic dynamics in a plankton community in a water sample obtained from the Baltic Sea. Fig 2 schematically illustrates complex interactions between a suite of multiple organisms and nutrients, which were studied in this experiment. This experiment was housed in a cylindrical mesocosm that was 45 cm in diameter, 74 cm high and filled with 90 l of water with a 10 cm sediment layer at the bottom. The “predictability” of each data set was shown to decrease with time (essentially lost after 15 - 30 days), consistent with positive Lyapunov exponents averaging about 0.058 per day. While small, these numbers are significantly above zero because of the large amount of data collected. They were calculated based on

![Fig. 2. A schematic of a conceived food web structure of the Beninca et al. [29] experiment (Reproduced with permission through Rightslink®).](image)

2 methods: attractor reconstruction using time-delay plots, and direct calculation of the Lyapunov exponents [22, 30]. It is apparent that when dealing with exponential divergence of trajectories in phase space, the dominant and positive Lyapunov exponent does not have to be large for the phenomenon of chaos to occur rapidly.
5. Chaos and fractals.

Because of the pervasive heterogeneity of natural environmental and agricultural systems, property measurement has always been fundamental in hydrology, hydrogeology, atmospheric and soil sciences. In recent years, several scientists have converged on the suspicion that heterogeneous property distributions, while highly irregular, are not simply random. There may be a “hidden” internal structure that is fractal in nature [31-34]. Investigations of strange attractors in phase space showed that they are a type of fractal. So what could give rise to fractals, mainly stochastic fractals? As described in Strogatz [5], “fractals” are complex geometric shapes with fine structure at arbitrarily small scales.” The popular idea of a fractal is that some type of geometrical structure is repeated over and over at different scales, as in a Koch curve [5]. Such a curve has endless structure, so one can conceive of its “dimension” as being somewhere between 1 (a smooth line) and 2 (a plane surface) [35]. However, these idealized, rigidly self-similar, structures do not seem applicable to the type of heterogeneity found in the SPAS. Most past applications have dealt with “stochastic fractals,” where a statistical property, not a geometrical property, holds at different scales. A stochastic fractal pair that has found wide-spread application in subsurface hydrology are fractional Brownian motion (fBm) and fractional Gaussian noise (fGn) [36]. FBM is a non-stationary stochastic process (a set of points with a mean and variance that are not constant along the set - like hydraulic conductivity values as a function of position), but the set of differences between neighbouring points is stationary and follows a Gaussian distribution. This stationary set of fBm increments is fGn, and the statistical scaling law (called self-affinity rather than self-similarity) specifies how the mean and variance of fGn varies with the distance over which the increments are calculated [36].

One must remember that phase or state space is not the space of the real world, so how fractals in phase space might translate into observable fractal structure in real space is not clear. Nevertheless, it is conceivable that a geometric fractal structure in phase space somehow implies a stochastic fractal structure in the real space of sediment properties (irregular but non-random), and a recent data analysis that also brings in the concept of geologic facies supports this possibility [37]. Overall, it seems striking that chaotic dynamics and fractals are related conceptually in a natural way.

6. Is a chaotic system sustainable?

The strange attractor shown in Fig 1 defines a global domain of stability. An infinite set of initial conditions near the attractor initiate trajectories that end up in that stable domain, and environmental disturbances unrelated to the on-going process (noise) simply shift the system behaviour to another part of the attractor - provided the disturbance is not too large. Once on the attractor, the lifetime of the trajectory is unbounded as long as outside influences do not change beyond a certain limit. In a global sense, this does not sound like unstable behaviour.

The classical solutions to ODEs and PDEs that we classify as transient, steady state or periodic are seldom seen in a “healthy” natural system. When talking about changes in populations of organisms, things that continually increase (like the human population today) or continually decrease (like the historically large number of animals now heading for extinction) are not an indicator of stability - just a warning of the opposite. The classical steady state, wherein a variable is steady in time, is simply not seen in complex natural systems, nor is true periodic behaviour seen. What we observe is always irregular and a-periodic. The word “sustainable” is currently popular, but what is a “sustainable system”? We would like to suggest the possibility that within an ecological context, the phenomenon of chaos represents sustainability - something that is irregular, but has the capacity, whatever that is exactly, to continue indefinitely. So what if the future details can’t be predicted in detail? The objective is to stay on the sustainable state represented by the attractor. This would require the management of natural systems
to shift to the system level [47]. On such a level, activities that seem protective, such as preventing forest fires, can turn out to be damaging because the full system was not considered. Moreover, chaos is a phenomenon that involves what is called “emergent behaviour” - the creation of properties that are not evident below the level of the phenomenon. One such emergent process is called “synchronization” - how signals self-modify to be in time with each other. Strogatz in his popular book [42] explains how SYNC is widespread and discusses how chaotic cycles can become synchronized - so irregular, non-periodic signals can synchronize [43]. This is another nonlinear phenomenon that might occur in the SPAS and associated natural systems.

7. Concluding thoughts.

The purpose of this brief and limited review is to build the case that nonlinear dynamics and related complexity is probably ubiquitous in the SPAS and related natural environmental and agricultural systems. Early work was primarily theoretical, but it gave way in the recent decade to a series of experiments, three of which were reviewed herein, documenting chaos in laboratory studies involving increasing ecological complexity. This should be significant in lessening past concerns that chaos might not occur in “real” ecological systems. We think the present question is, “to what extent does it occur and what is the biophysical basis of the phenomenon”, but the studies are still needed? Because the field of nonlinear dynamics originated from mathematical analysis, and the individual variables studied were irregular, non-periodic functions of time, the originators used terms like “erratic,” “unstable,” or “unpredictable” - hence the name chaos. Could we be missing the main point here - that chaotic systems are stable on the system scale?

Another purpose of this review is to encourage interdisciplinary research in the SPAS - the system to which this conference is devoted. Clearly there is need and opportunity for future research. Complex systems do not respect disciplinary boundaries, and the natural system known as the SPAS is doubly important because that resource is central to the health of the Earth as well as to providing our food supply. Two recent theoretical papers have been published dealing with the rhizosphere [38], one devoted to competition between nitrifying and non-nitrifying bacteria [39] and the other devoted to the competition between native an injected microbes [40]. Chaotic behaviour is not mentioned explicitly in either paper, but we have verified that such behaviour can occur in the model involving nitrogen metabolism [41]. We are sure that other opportunities abound, and there is much to be understood from both numerical and especially experimental studies.

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