Oscillations and chaos in the dynamics of a perennial grass

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ECOLOGICAL models describe the conditions required for chaotic population dynamics[1-7], but there are few studies with which to test these predictions[4,8-10], and none for perennial plants. In a five-year experiment, a perennial grass exhibited numerous traits associated with chaotic dynamics. Biomass oscillations were greater on more productive soils, with plots on the richest soils exhibiting a 6,000-fold crash. Curves relating the biomass one year to that in the previous year had the peaks and steep slopes associated with chaos, and the dependence of plant biomass on productivity became fuzzy over time. These dynamics resulted from the time-delayed inhibitory effect of plant litter on subsequent growth. A model incorporating litter inhibition predicts oscillations and chaos as productivity increases.

When ecologists sample populations, the resulting relationships are often blurred. This variance may result from sampling error and environmental variation or from deterministic processes that yield oscillations or chaos[8-11]. Although it is difficult to distinguish between noise and chaos[9,10], chaotic dynamics have several distinguishing features[8-11]. In models such as the discrete logistic, populations maintain a stable density when their regulatory force is small relative to the time delay with which it acts. At higher intensities of the regulatory force, populations exhibit sustained oscillations. At even higher intensities, these periodic orbits give way to aperiodic dynamics called chaos[1-3,11]. These dynamics can be described using a graph, called a one-dimensional map, of N_{t+1} (population size at time $t+1$) versus N_t. The slope of this curve at the equilibrium line ($N_t = N_{t+1}$) becomes steeper as the regulatory force increases. When sampling noise is superimposed, the one-dimensional map should be increasingly well defined as chaos is approached[8]. Moreover, bifurcations and chaos mean that a wide range of population sizes become associated with the same intensity of the regulatory force[3], thus leading to a fuzzy dependence of population size on the regulatory force[8].

All of these characteristics were displayed by monocultures of *Agrostis scabra* planted at two different initial densities on 10 different soil mixtures. Populations growing on unproductive,

low-nitrogen soils maintained fairly stable above-ground biomasses, those on richer soil oscillated more, and those on the richest soil exhibited a 6,000-fold crash (Fig. 1). None of the other four species growing in this garden exhibited a crash in 1988, suggesting that it was not caused by environmental conditions.

When data from each of the 10 soil mixtures were analysed separately, graphs of B_{t+1} (biomass at time $t+1$) versus B_t had clear, steeply peaked curves for high nitrogen soils (Fig. 2a, b), but had shallow slopes at the equilibrium line and little or no pattern for low-nitrogen soils (Fig. 2c). For the five lowest-nitrogen soil mixtures, none of the slopes differed significantly from zero, but three were significantly negative ($P < 0.05$) for the five richest mixtures. Observed slopes were significantly negatively correlated with soil nitrogen (Fig. 2c). The two most nitrogen-rich soil mixtures had slopes of -3.1 and -3.6. By comparison, two different forms of the discrete logistic model become chaotic at slopes more negative than -1.57 or -1.69 (ref. 3) and a model of plant-litter dynamics becomes chaotic at -2 (legend to Fig. 2).

In 1986 (Fig. 3a) and 1987, biomass of *Agrostis* was very linearly dependent on soil total nitrogen (1986: $R^2 = 0.92$, $N = 60$, $P < 0.001$; 1987: $R^2 = 0.84$, with high and low seed densities combined for each year) and was independent of the initial seeding density. This relationship was considerably weaker in 1988 ($R^2 = 0.04$) and 1989 ($R^2 = 0.01$). By 1990, the initially tight linear dependence had been replaced by a wedge of data points ($R^2 = 0.32$, $N = 60$, $P < 0.001$), and plots planted at high and low seed densities had diverged (Fig. 3b). This is consistent with the tendency for bifurcations and chaos to cloud the relationship between population size and the intensity of the regulatory force, and to magnify small initial differences.
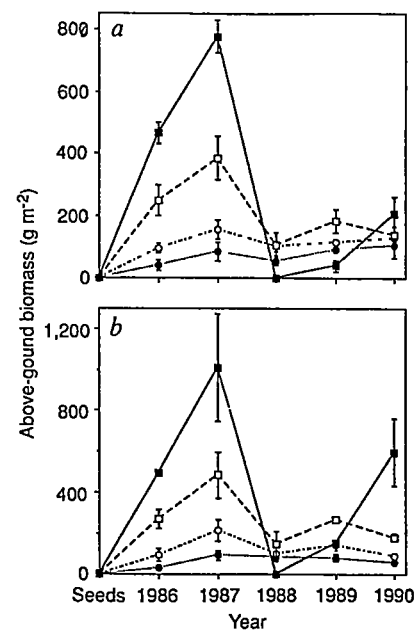

FIG. 1 Above-ground living biomass (mean, s.e.) of *Agrostis* in high seed density monocultures (a) and low seed density monocultures (b). Soil mixtures divided into four groups: N1, three soil mixtures with lowest total soil N (●); N2, three next richer mixtures (O); N3, three next richer mixtures (□); N4, richest mixture (■).

METHODS. *Agrostis* monocultures were seeded in May 1986 to have 3,000 (high seed density) or 600 (low seed density) seedlings m⁻², with four high and two low seed density 0.75 m ×0.75 m replicates each in 10 soil mixtures at Cedar Creek Natural History Area, Minnesota, USA. Soils created, watered and fertilized as in ref. 19. Mass of germinated seed in spring 1986 ('Seeds', above) and living biomass in late July each year from samples from different plot subsections each year.

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FIG. 2 a, b, B_{t+1} (living biomass in year $t+1$) versus B_t for two richest soil mixtures (a, 1,116 mg N per kg soil; b, 1,550 mg N per kg soil). The 24 data points represent four annual intervals in each of six replicates. Curves were fitted using nonlinear regression ($y = ax - bx^2 - e^{-cx}$, with $y \geqslant 0$). Equilibrium line, $B(t)=B(t+1)$, is dashed. c, Slopes (at equilibrium line) of lines tangent to B_{t+1} versus B_t curves fitted to data from each of 10 soil mixtures. Slopes steeper than -2 give chaos for the model described below. d, Bifurcation diagram for a model of plant inhibition by litter. This illustrates the probability of different population biomasses for soils with different total soil nitrogen levels. The model is:

$$B_{t+1} = cN[e^{(a-bL_t)}]/[1+e^{(a-bL_t)}]$$

$$L_{t+1} = L_t^2/(L_t + d) + ckN[e^{(a-bL_t)}]/[1+e^{(a-bL_t)}]$$

where B is living biomass, L is litter mass, N is total soil nitrogen, t is time (year), and constants a, b, c, $d > 0$, and $0 < k < 1$. B attains its N-determined equilibrium (cN) in a single year in the absence of litter but is reduced below this by litter. Litter decay is determined by d. Litter production is k times living biomass. Results shown are for $a = 5$, $b = 0.1$, $c = 0.5$, $d = 100$ and $k = 0.4$, with the model solved at 1,500 different values of N. At each value, results of the first 1,000 years were not used, and those for the next 200 years were graphed against N. This model can be expressed in a simpler, dimensionless form: $X_{t+1} = X_t^2/(1 + X_t) + \alpha/(1 + e^{\beta X_t - \gamma})$ and $Y_{t+1} = \alpha/(1 + e^{\beta X_t - \gamma})$, where X (litter) is L/d, Y (plant biomass) is kB/d, α is ckN/d, β is db, and γ is a. This model illustrates the qualitative effects of a time-delayed litter

$B(t)$. (g m^{-2})

Total soil nitrogen (mg N per kg soil)
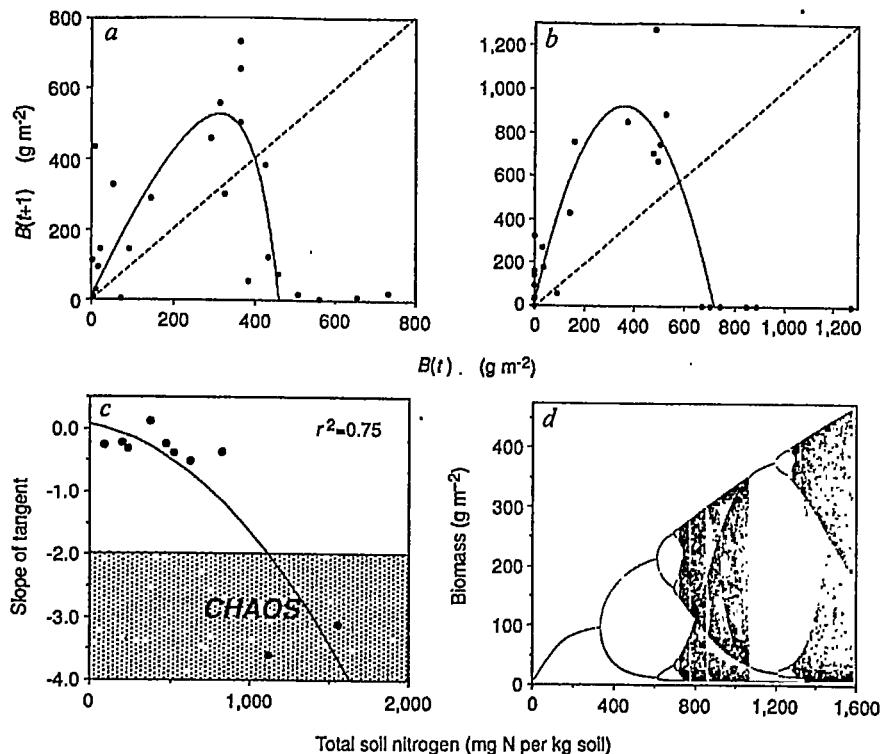
feedback on plant dynamics, but is not intended as a description of the dynamics of *Agrostis*.

In total, our results suggest that *Agrostis* biomass underwent oscillations of increasing amplitude, leading to chaos as productivity increased. A likely cause was the inhibition of growth by accumulated litter (the dead plant material produced at the end of a growing season). A dense litter layer mulches the soil surface and intercepts light, thus inhibiting growth until it decays[12-16]. By 1988, litter mass increased significantly with total soil nitrogen (linear correlation for 1988: $r = 0.84$; 1989: $r = 0.46$; 1990: $r = 0.54$; $N = 60$, $P < 0.01$ for all). In 1988, the six monocultures on the richest soil mixture had dense litter layers (mean: 381 g m^{-2} of litter) and little living biomass (mean: 0.1° g m^{-2}). By 1990, they averaged 153 g m^{-2} of litter and 335 g m^{-2} of living biomass. In the two highest nitrogen soil mixtures, there were significant negative correlations between litter biomass one year and plant biomass the next ($r = -0.66$ and $r = -0.48$; $P < 0.05$). Thus the dramatic decline in living biomass in the high-nitrogen plots from 1987 to 1988, and the suppression in 1989, may have been caused by accumulated litter.
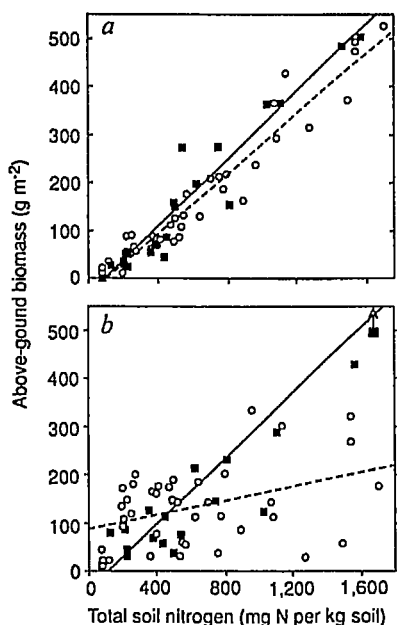
Oscillations and chaos have been hypothesized to be rare for perennial plants because regulatory forces, such as competition for nutrients or light, act without a significant time delay. Litter causes a one-year time delay between growth and inhibition of future growth. Because litter production is greater in more productive plots, the magnitude of this time-delayed inhibitory force should increase with productivity. A simple model of plant–litter interactions exhibits bifurcations and chaos as soil nitrogen increases (Fig. 2d). Its two-point cycle, for instance, represents oscillation between a year of low litter and high living biomass, and a year of high litter and thus low living biomass.

Our results suggest that terrestrial plants may exhibit chaotic dynamics caused by a previously unsuspected mechanism, the inhibition of growth by accumulated litter. Other studies have reported litter inhibition of survival and growth, especially for herbaceous plants[12-18]. Such litter feedback could cause population oscillations and possibly chaos in productive habitats. Because litter is deposited where it is produced, however, such litter-driven chaotic dynamics may mainly occur at small spatial scales. Chaos may not be detectable on larger spatial scales if local dynamics are asynchronous or weakly coupled[10]. Moreover, unlike *Agrostis*, some plant species have robust shoots that can penetrate a deep litter layer[12]. Such species should not

FIG. 3 a, Dependence of above-ground living biomass on total soil nitrogen in 1986, the first year of the experiment, for low seed density plots (■) and high seed density plots (O). b, Similar results in 1990.

display chaotic dynamics by the mechanism described here and may displace species like *Agrostis* from productive habitats. Furthermore, both fire and grazing reduce litter mass[17,18], and should decrease the likelihood of chaotic dynamics in native grasslands. Native species that evolved with fire and grazing may be more likely to be inhibited by litter and displaced from habitats after fertilization, fire suppression, or cessation of grazing or mowing. Further work is needed to determine the generality of the patterns we report, to elucidate the role of chaotic dynamics versus stochastic factors in contributing to the fuzziness of patterns observed in nature, and to study the role of litter inhibition in structuring plant communities. □

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