

# From out of the blue

George Sugihara

NEARLY 2,000 years after accounts in the Book of Exodus of the locust plagues that God brought down upon the Egyptians, Chinese bureaucrats of the T'ang Dynasty (618–907 BC) began organizing one of the most ambitious entomological data-collection projects in history. As annual reports from district officials have been faithfully recorded to the present day, a remarkable time series was constructed<sup>1</sup> for the degree of locust infestation in the form of a severity index (1–10 based on density and spatial extent, a sort of non-logarithmic Richter scale) (Fig. 1). The original aim, which has yet to be completely fulfilled, was to use this information to help forecast locust outbreaks.

Little did the T'ang officials realize that, 1,300 years later, these data as well as their country's politics would be found

giving rise to an apparent paradox: observations for natural populations, such as those in refs 2 and 3, are redshifted, whereas theoretical models produce blue spectra.

This paradox has its roots in the debate between the so-called 'climate' and 'biotic' schools of population regulation that has polarized thinking among ecologists since the early part of this century. Although many economic entomologists favoured the view that external climatic factors dominated populations, others (especially those studying longer-lived and larger creatures such as birds and mammals) held that internal biotic mechanisms such as competition and predation are paramount. This debate has been reborn in various guises: density-independence versus density-dependence; nonequilibrium versus equilibrium; null models versus

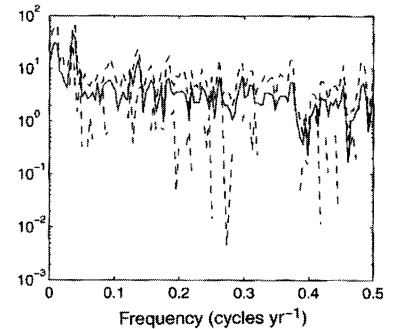


FIG. 2 The power spectrum for the migratory locust time series showing a shift towards the red. A moving window of 256 years was used to estimate the spectrum, and the error envelope (dashed line) corresponds to the 95% confidence interval.

wet periods, which promote nymphal survival. Moreover, climate variables themselves are often redshifted on this timescale (with interdecadal bumps).

So although redshifted observations align with the climate school, the blue-shifted output of classical autonomous population models align with the biotic school. Chaos in these simple models is achieved when self-regulation has run amok (that is, when the time-delayed birth/death response is fast, causing the system to overshoot and undershoot a target equilibrium to an extreme that becomes aperiodic<sup>6</sup>).

Indeed, the blueshift that Cohen observes should tend to be true of one-dimensional, unimodal maps in general, where there is anticorrelation between values at successive time steps. Thus, low values tend to be followed by highs and vice versa, giving rise to short-term anti-correlation or maximal power at the Nyquist frequency. In the chaotic regime, these correlations will fall off with the Lyapunov horizon, giving rise to an apparent blueshift. To achieve the intermittency that would push the spectra for these models towards red, they would need to be sensitively tuned to specific pathological values. Chaos with red spectra can arise more readily in higher dimensional models. So the full story behind the ragged ups and downs that many populations in nature exhibit is not likely to be explained as examples of simple chaos from classical difference equation models (that is, stationary, unimodal single-species maps). ▶

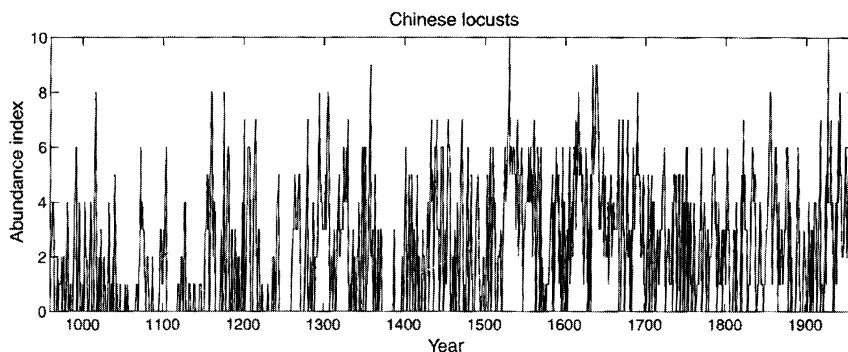


FIG. 1 A 1,000-year record (957–1956) of locust (*Locusta migratoria*) abundance in China, reproduced from ref. 1. This is an excerpt of the original 1,300-year total abundance record for all census regions combined.

to be shifted to the red (Fig. 2). That is to say, in common with many other population data on wild stocks, for instance those of Diamond and May<sup>2</sup>, and Pimm and Redfearn<sup>3</sup>, this ancient record of locust booms and busts possesses a redshifted power spectrum. This means that population variability appears to increase at the longer timescales. Thus, two population values a century apart will on average differ more than two population values a decade apart, and so on. And so what?

On page 610 of this issue<sup>4</sup>, Joel Cohen presents a new dilemma in population modelling that pits this observation against classical theory. As Cohen points out, the ubiquity of such a  $1/f$  signature, or shift in power to the low frequencies, is at odds with his simple analysis of prevailing autonomous population models (some of which are used in resource management). Cohen shows how these models tend to have blueshifted power spectra in the chaotic regime (more variation in the higher frequencies; adjacent generations tend to be more different than distant ones),

biogeographical pattern; physics of transport versus real population growth; noise versus chaos. It is a practical problem for resource managers on a daily basis. For example, whether or not commercial fishing can be sustained depends critically on whether specific fish populations are behaving in a predominantly density-dependent or density-independent manner<sup>5</sup>, and the form of the density dependence is especially crucial.

Insofar as the Chinese locust data measure the action of locusts, and not the sociological trends of census takers, the redshift reported here and the many cases of short-term redshifted population data surveyed elsewhere<sup>3</sup> seem to be in step with the views of the climate school (though as Diamond and May point out<sup>2</sup>, with short-term measurements it is difficult to discount other sources of 'nonstationarity', such as human disturbance, as the cause of the redshift). Indeed the only published analysis<sup>1</sup> of the locust data suggests a significant correlation between outbreaks and climatic factors, especially

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This leaves us with at least three alternatives: first, that natural population fluctuations are not chaotic and/or are nonstationary; second, that the models are fundamentally flawed; or, third, that environmental forcing needs to be incorporated. Such forcing can easily push a stable map into the chaotic regime<sup>7-9</sup>, and Steele<sup>10</sup> has suggested that environmental forcing (red noise) superimposed on models containing multiple stable states may

lead to the kind of intermittency that could produce a redshift. Whatever the case, Cohen's article poses a dilemma that should stimulate some lively discussion around what remains one of the classic unresolved issues in ecology. □

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## PLANT BIOLOGY

## At the roots of nutrition

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PLANTS grow and develop while remaining rooted in one place. Therefore, identification of the molecular mechanisms through which plants accumulate the often sparse soil macronutrients essential for growth has been a central aim in plant biology. Two papers in this issue add further to our knowledge of such mechanisms. Harrison and van Buuren (page 626<sup>1</sup>) report the first cloning of a mycorrhizal phosphate-

(patch) clamp and molecular cloning studies having provided first insights into the biophysical uptake mechanisms and molecular structures of key plant transporters for the essential 'NPK' macronutrients (nitrogen, phosphorus and potassium). These include low-affinity<sup>3</sup> and high-affinity nitrate-uptake transporters<sup>4</sup> and high-affinity ammonium transporters<sup>5</sup>. Furthermore, low-affinity K<sup>+</sup> uptake channels<sup>6-8</sup> and high-affinity K<sup>+</sup> transporters<sup>9,10</sup> have been characterized in cell biological, biophysical and molecular terms. But the molecular mechanisms for phosphate uptake have remained unknown.

Harrison and van Buuren<sup>1</sup> describe the isolation of a complementary DNA encoding a high-affinity phosphate-uptake transporter from vesicular arbuscular (VA) mycorrhizal fungi. The family of VA mycorrhizal fungi form symbiotic associations with most higher plants, including agricultural crops. This association greatly increases plant phosphate uptake (see figure), growth and crop yields<sup>11</sup>, the fungus getting carbon in return. The phosphate transporter, from VA *Glomus versiforme* mycorrhizae, named GvPT, was cloned by homology to the PHO84 phosphate transporter from yeast<sup>12</sup>. The GvPT sequence encodes a membrane protein, which complements a yeast mutant defective in high-affinity phosphate uptake. GvPT also has a high affinity for phosphate ( $K_m$  value of about 18  $\mu\text{M}$ ) required for nutrient accumulation. The transporter appears to be expressed predominantly in the external hyphae of the mycorrhizae; VA fungi have extended hyphae that can reach into undepleted soil regions and are crucial for transfer of phosphate and other minerals from the soil to the host plants<sup>11</sup>.

We now have fresh challenges. For example, further research will be needed to characterize the mechanisms of phosphate transfer from mycorrhizae to roots, to identify plant (non-fungal) phosphate uptake transporters, and to determine the effects of transgenic manipulation of GvPT on phosphate nutrition. On the practical side, further characterization

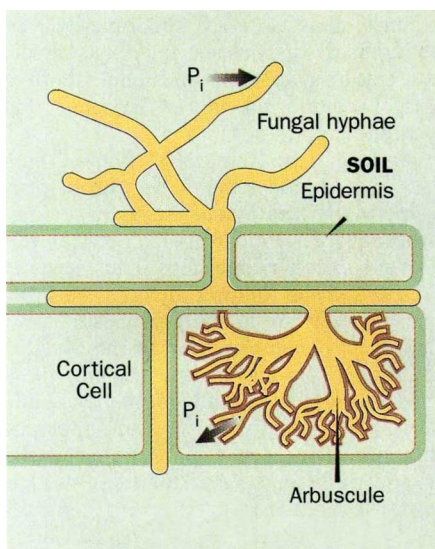
may allow investigation of the use of GvPT/PHO84 homologues for biological removal of leached phosphate.

Nitrogen is a macronutrient that often limits plant growth and crop yields. Leguminous plants have built-in symbiotic factories, root nodules, which contain nitrogen-fixing bacteroids inside organelles (symbiosomes) of the root cells. The bacteroids produce excess ammonia (NH<sub>3</sub>) which accumulates in the symbiosome space. Symbiosomes are surrounded by a specialized organellar membrane, the peribacteroid membrane, but the mechanisms for NH<sub>3</sub> or ammonium ion (NH<sub>4</sub><sup>+</sup>) uptake across this membrane into the root cytosol have remained unknown.

Tyerman *et al.*<sup>2</sup> address this question in a first patch-clamp analysis of the peribacteroid membrane. They report a prominent, non-selective monovalent cation current in the peribacteroid membrane that is activated by negative potentials on the plant cytosol side of the membrane. As the transporters are most permeable to ammonium, the negative potential would cause NH<sub>4</sub><sup>+</sup> uptake into plants. The cation transporter has a low affinity for NH<sub>4</sub><sup>+</sup> uptake ( $K_m$  of about 37.5 mM), which correlates with estimated NH<sub>4</sub><sup>+</sup> levels of about 20 mM in the symbiosome space.

Reversal potentials for the NH<sub>4</sub><sup>+</sup> uptake currents shifted in a strictly Nernstian manner at a symbiosome NH<sub>4</sub><sup>+</sup> concentration of between 3 and 150 mM. This shows that the ammonium uptake pathway is passive, which is the thermodynamic definition of a channel. The passive ammonium uptake channels differ from the plant high-affinity H<sup>+</sup>-coupled NH<sub>4</sub><sup>+</sup> transporters, which show a  $K_m$  of about 10  $\mu\text{M}$  (ref. 5).

To approximate the conductance and density of the underlying cation channels, the authors have pursued fluctuation analyses (which can be compared to analysing the noise of uniform raindrops falling on a tent roof to estimate the size and density of drops). This analysis showed that the ammonium channels have unusual, 'non-Lorentzian' properties, pointing to the existence of multiple states, cooperativity among channels or



Symbiosis in plant nutrition. A vesicular arbuscular mycorrhizal fungus invades root cortical cells and facilitates phosphate (P<sub>i</sub>) uptake from soil.

uptake transporter proposed to function in plant phosphate nutrition; and Tyerman *et al.* (page 629<sup>2</sup>) describe the identification of a mechanism for nitrogen accumulation from nitrogen-fixing root nodules.

Macronutrients are usually added to fertilizers, because their limited availability in soils is responsible for reduced plant growth. But some consequent environmental problems, such as large energy use for fertilizer production and groundwater contamination caused by leaching of fertilizers, have added impetus to the quest to identify associated nutrient transporters. A great deal of progress has been made, voltage

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