

become less depleted in deuterium in summer due to greater evapotranspiration associated with higher temperatures and lower humidity. It is therefore concluded that the D/H ratio of cellulose in the wood of *P. radiata* changes with temperature due to the temperature effects on one or more of the biochemical reactions leading to cellulose. Taking into account the isotopic variations of the atmospheric precipitation we obtain a temperature coefficient for the C-H hydrogens of cellulose of -5% per $^{\circ}\text{C}$.

Most probably this change reflects the air temperature since it is the biochemical pathways leading to the synthesis of the sucrose in the leaves which lead to the formation of the C-H bonds. The sucrose is translocated to the trunk where it is converted to cellulose. If it is indeed a temperature effect on the biochemical steps leading to the synthesis of sucrose, then the effect described in this communication should be found to occur generally in C-3 plants. The temperature coefficient of this biochemical thermometer could enable past temperature measurements to be measured to better than 0.1°C which should be more than adequate for studying past climate changes.

The other isotopes both in cellulose and in the other compounds in wood are being studied and will be reported elsewhere.

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Stability of Lotka-Volterra systems

NONLINEAR systems are very often studied in terms of simple mathematical models. The Lotka-Volterra equations provide such a model and have been used to study physical, chemical, ecological and social systems¹. An important question in the analysis of these equations is the stability of the equilibrium values of the interacting variables. Most work with Lotka-Volterra models has considered only neighbourhood stability against small perturbations away from equilibrium. The question of global stability when large perturbations from equilibrium are involved has only been analysed in a few special cases². We establish here that for the general Lotka-Volterra models local stability ensures global stability (asymptotic stability in the large). This result provides justification for the work that has been and is being done^{2,3} on linearised versions of the Lotka-Volterra models.

Our emphasis here will be on ecological systems: we consider a set of interacting biological species, but that does not restrict the analysis. If N_i is the biomass (or population) of species i , it changes with time t according to the generalised Lotka-Volterra equations

$$dN_i/dt = N_i \left(b_i + \sum_j a_{ij} N_j \right)$$

Here b_i are growth rates in the absence of interactions, and a_{ii} and a_{ij} ($i \neq j$) are intraspecies and interspecies interaction coefficients, respectively. We make no assumption about the

elements a_{ij} , except that they are real. Equilibrium values of the biomass, N_i^* , are defined by $dN_i/dt = 0$, or

$$b_i = - \sum_j a_{ij} N_j^*$$

We consider 'feasible' models, where all $N_i^* > 0$.

A local stability analysis is carried out by introducing small perturbations $y_i = (N_i - N_i^*)$, and obtaining a linear system $dy/dt = Ay$. Here y is the vector of y_i , and the 'community matrix' A has elements $(a_{ij}N_j^*)$. This system is stable, or equivalently the matrix A is stable, if all of the eigenvalues of A have negative real parts. The stability of A guarantees the local stability of the system about the equilibrium values N_i^* .

To examine global stability, we first introduce variables x_i through the substitution $N_i = N_i^* \exp(x_i)$. The x_i then obey the equation

$$dx_i/dt = \sum_j a_{ij} N_j^* [\exp(x_j) - 1]$$

Let x be the vector of x_i . Consider the function⁴

$$V(x) = \sum_i [\exp(x_i) - x_i - 1]$$

Observe that $V(x)$ is positive definite, continuously differentiable, and that $V(x) \rightarrow \infty$ as $|x| \rightarrow \infty$. The time derivative is

$$dV(x)/dt = \sum_{i,j} [\exp(x_i) - 1] a_{ij} N_j^* [\exp(x_j) - 1]$$

Now, if the derivative dV/dt is negative definite, the function $V(x)$ would be a Lyapunov function for the system, and would ensure global stability about the equilibria N_i^* .

The conventional way of writing quadratic forms is in terms of a symmetric matrix. So we define a symmetric matrix $B = (A + A')/2$, where the prime indicates the transposed matrix. Then we rewrite dV/dt as a quadratic form with the elements of B , b_{ij} , as

$$dV/dt = \sum_{i,j} [\exp(x_i) - 1] b_{ij} [\exp(x_j) - 1]$$

Now if B is a negative definite matrix, dV/dt is negative definite, and V is a Lyapunov function.

The theorem of Lyapunov⁵, states that a matrix A is stable (in the sense that the real parts of its eigenvalues are all negative), if, and only if, there exists a positive definite matrix C such that $(CA + A'C)$ is negative definite. We choose $C = I/2$ where I is the unit matrix. With this choice, our earlier matrices A and B are related by $B = (CA + A'C)$. Thus the theorem states that local stability (stability of our matrix A) occurs if, and only if, B is negative definite. And the negative definiteness of B makes $V(x)$ a Lyapunov function, ensuring global stability.

Thus for the general Lotka-Volterra systems, local stability implies global stability, and vice versa. This result is a happy consequence of the general form $dN_i/dt = N_i F_i(N)$ and the linearity of the F_i . This result does not apply to situations where the 'community matrix' A is critical, that is, has eigenvalues with vanishing real parts. The special cases mentioned earlier for which global stability has been studied follow from the insertion of specific assumptions about the interaction coefficients. The implications for any specific system must of course be considered within the definite limitations of the Lotka-Volterra model as a representation of reality.

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Recovery process of the sensitive plant

THERE is a long history of study of the unusual behaviour of the 'sensitive plant', *Mimosa pudica* L., stretching back to the *Enquiries into Plants*, written by Theophrastus in about 300 BC. A large literature has built up, much of which can be traced from the papers of Pickard¹, Sinyukhin and Gorchakov², and Weintraub³. In spite of this, very little work seems to have been done on the detailed kinematics of the recovery of the plant following a collapse. We report here the results of a study of the recovery of the primary petiole after seismonastic stimulation, that is, after collapse induced by a blow.

Plants used in this study were all grown from seed obtained from commercial seedhouses. The temperature was kept in the range $21 \pm 3^\circ\text{C}$ by suitable thermostatic controls. The lighting was supplied exclusively by a battery of eight 35-W fluorescent tubes mounted horizontally 24 cm above the plant pots. The sequence used was about 12 h light followed by 12 h darkness, the dark period being from 1700 to 0500. Plants were investigated at various ages in the range 1–18 months. They were grown in John Innes number 2 mixture, germinated in closed polythene containers and then transplanted into 2-inch pots.

Preliminary films of the collapse and recovery of plants taken 'end-on' to various primary petioles showed that the motions of the latter were always planar, although the motions of the secondary pinnae were more complex and sometimes gave an illusion of non-planar motion of the primary petiole. It was therefore convenient to place the plant in front of a vertical screen covered with 1-mm graph paper and orientate it so that the plane of motion of the primary petiole on which attention was to be focused was roughly parallel to the screen. A Sankyo CME 660 Super-8 cine camera was mounted so that its optical axis was roughly normal to the screen and passed close to the primary pulvinus connecting the stem of the plant to the primary petiole of interest. Preliminary experiments showed that the collapse takes a couple of seconds, whereas the recovery can take an hour or more. The camera was therefore run at its normal speed of 18 frames s^{-1} while the plant was being stimulated and collapsing, but thereafter only one frame was used every 5 s to obtain time-lapsed film of the recovery. As a check on the timing a stopwatch calibrated in 0.1-s intervals was mounted near the plant and filmed with it.

Since in most cases the primary petiole is approximately straight at all times the angle θ which it makes with the horizontal provides a quantitative measure of its geometrical condition. The graph paper on the screen was of assistance in measuring this angle. Any error in its measurement due to the direction of observation not being quite normal to the plane of motion would be small and would not affect either the general form of the θ -time curves or the periods of any oscillations contained in these.

Detailed observations were made of numerous collapses and recoveries using the plants at various ages and at a variety of times of day. The collapse process, which was always complete within 2–3 s, showed no particularly surprising features (detailed quantitative study will be reported elsewhere). The recovery process on the other hand, which usually took about an hour for completion, showed some rather unexpected features. The curve of θ against time for the recovery could take any one of three different forms which showed strong similarities to the displacement-time curves for an unforced damped harmonic oscillator. The first two forms (Fig. 1a and b) are similar to the two possible types of behaviour of a heavily damped harmonic oscillator, and accounted for 10 and 30%

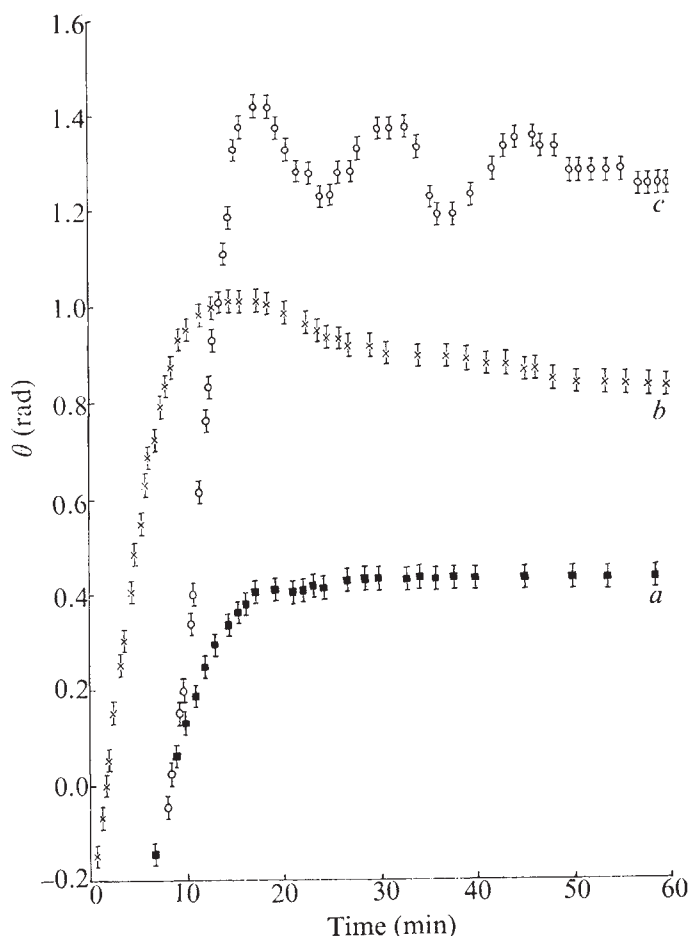


Fig. 1 Examples of the three types of recovery: a, heavily damped mode (undershooting type); b, heavily damped mode (overshooting type); c, lightly damped mode.

of the observed recoveries, respectively—referred to jointly as the heavily damped mode. The third form (Fig. 1c) is similar to the lightly damped harmonic oscillator curve. The period of oscillation was typically about 15 min. It accounted for the remaining 60% of observed recoveries. This similarity to the damped harmonic oscillator does not extend to the fine detail. In the lightly damped mode, for example, the successive displacement maxima and minima do not obey the log. dec. rule. In view of the complex internal structure of the primary pulvinus it is not surprising that the response should deviate somewhat from that of a damped harmonic oscillator: the surprise is that it should show any resemblance to it at all. In fact it seems quite likely that the system can be modelled by the usual spring-mass-dashpot system with some simple nonlinearities imposed—for example, anisotropic damping.

In addition to the main observation that a primary petiole behaves in a manner resembling a damped harmonic oscillator a number of other interesting facts emerged from our study. First, different primary petioles of the same plant can recover by way of different modes at the same time. Second, a given petiole at a given age always recovers by way of the same mode. If this mode happens to be the heavily damped one, however, its type may change. Third, on the first stimulation after a long rest period (say, at least 24 h) the final equilibrium position reached differs from that before stimulation, but immediate restimulation produces no further change in the equilibrium position. Finally, for a given petiole recovering by way of the lightly damped mode the period of oscillation is greater on second and subsequent stimulations than on the first after a long rest period. In a typical case we found that the initial period was about 15 min but that this increased by about 30%