Nonlinear Dynamics in the Ultradian Rhythm of *Desmodium motorium**

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Z. Naturforsch. **50 a,** 1113–1116 (1995); received August 16, 1995

The dynamics of the lateral leaflet movement of *Desmodium motorium* is studied. Simple periodic, quasiperiodic and aperiodic time series are observed. The long-scale dynamics may either be uniform or composed of several prototypic oscillations (one of them reminiscent of homoclinic chaos). Diffusively coupled nonlinear oscillators may account for the variety of ultradian rhythms.

1. Introduction

Autonomous ultradian oscillations can be observed in higher plants. The lateral leaflet movement rhythm of *Desmodium motorium* (syn. *Desmodium gyrans* (L.f.) Merr., *Codariocalyx motorius* (Houtt.) Ohashi) has been described long ago [1, 2] and is well documented [3, 4, 5, 6]. *Desmodium motorium* belongs to the Fabaceae and is found in south east Asia and northern Australia. The leaves consist of a larger terminal and one or two (or none) lateral leaflets. Whereas the terminal leaflet moves up and down in a circadian fashion (period length about 24 hours), the lateral leaflets show an ultradian rhythm. Both movements are produced by small joints (pulvini) between the lamina and the stalk of the leaflets. The period length of the ultradian rhythm is in the minute range and depends strongly on the environmental temperature ($Q_{10} \approx 2$). The mechanism and the significance of this rhythm is still unknown (for recent work see [4, 5, 6, 7]).

2. Materials and Methods

Desmodium motorium was grown in a greenhouse under natural light conditions supplemented with fluorescence tube light (Osram L65W/25S) from 6:00 to 18:00 during the short days of the year (temperature: 24-28 °C, relative humidity: approx. 80%). They were cut from the plants and mounted in plastic photometric cuvettes filled with deionized water. A polystyrol insulated box with 3 Osram L40W/15-1 fluorescence tubes on the top of an acrylglass cover housed the 20 leaflets during observation. Temperature was recorded parallel to the lateral leaflet movement and did not change by more than 2 °C. The tip of the leaflet was marked with a tiny piece of styropore. Against a dark background a videocamera recorded the movements of each of these white spots and the data of vertical and horizonal movements were stored on disk for subsequent analysis. The video-computer-recording-system and the analysis method were described in [8].

3. Results

The lateral leaflets of *Desmodium motorium* in deionized water showed autonomous oscillatory movements. About 5 to 10% of the leaflets showed a uniform pattern during the time of recording. Inspection of these uniform patterns revealed that the individual dynamics of each leaflet varied qualitatively. Figure 1a is an example of a simple periodic oscillation of a lateral leaflet of *Desmodium* plotted as the time series of one spatial coordinate. The period length of this oscillation is approximately four minutes. In this case, the "downward" movement is faster than the "upward" movement. A phase space projection in two spatial coordinates is plotted in Figure 1b. The result is a limit cycle with a comparatively narrow distribution of loops during the course of time. During a recording period of twenty hours we observed a shift of the mean value of the oscillation in one spatial coordinate and slight modulations of the amplitude.

* Paper presented at the 5th Annual Meeting of ENDADYN, Grenoble, October 10 - 13, 1994.

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0932-0784 / 95 / 1200-1113 $ 06.00 © – Verlag der Zeitschrift für Naturforschung, D-72072 Tübingen

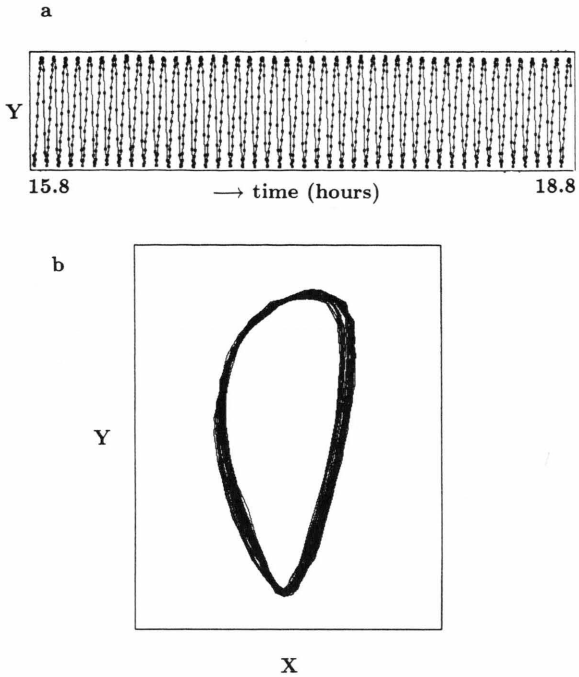

Fig. 1. Time series (a) and phase plot (b) of periodic oscillations of *Desmodium* lateral leaflets. The horizontal (x) and vertical (y) positions of the tip of the leaflets were recorded by a computer-video-digitizing system.

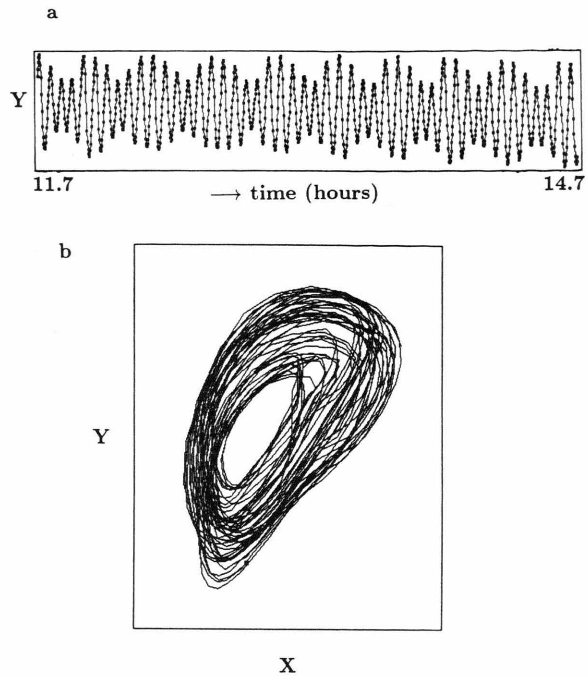

Fig. 2. Time series (a) and phase plot (b) of quasiperiodic oscillations.

However, these irregularities did not seem to effect the basic limit cycle behavior significantly.

In contrast, Fig. 2a is an example of a periodically modulated periodic oscillation. The low-frequency modulation has a period length of about twenty minutes and the time series is quasiperiodic. The phase space projection in Fig. 2b reveals the shape of the underlying two-torus. The toroidal structure is further confirmed by plotting minima of the time series in a next-amplitude plot (not shown). Whether the observed oscillation is truely quasiperiodic or rather a locked mode on a two-torus with high periodicity cannot be distinguished from the experimental data. As in the case of the limit cycle there are shifts of the mean value of the oscillation during the course of twenty hours.

Figure 3a is a time series with no detectable regularity yet with uniform texture. The period length of the oscillations is in the range of the limit cycle oscillations in Fig. 1, its variations are irregular, however. The amplitude also shows large irregular variations. The phase space projection in Fig. 3b is a complicated bundle with no apparent order. A Poincaré cross-section consists of a broad, noisy distribution of points. Taking into account that shifts of the mean value occur in all recordings, the irregular behavior was found to be stable for more than 16 hours. Among the leaflets with uniform patterns the three dynamic prototypes presented were approximately evenly distributed.

The majority of leaflets did not show a uniform pattern of oscillation during the recording. Rather, combinations of different prototypic patterns were observed. Each qualitative pattern lasted for a couple of hours. The switching between patterns often was abrupt. Sometimes slow shifts preceded the switching. For example, the first part of Fig. 4 shows a simple periodic oscillation with decreasing amplitude. The time series then spontaneously (as far as external conditions are concerned) switches to an aperiodic mode composed of small and large amplitude peaks. Even though we cannot exclude the influence of external noise or low-frequency changes of environmental conditions on the recorded lateral leaflet movement, we did not observe any connection between the switchings in different leaflet preparations in the same observation chamber. It should also be noted that leaflets from a single plant differed with respect to their qualitative dynamics.

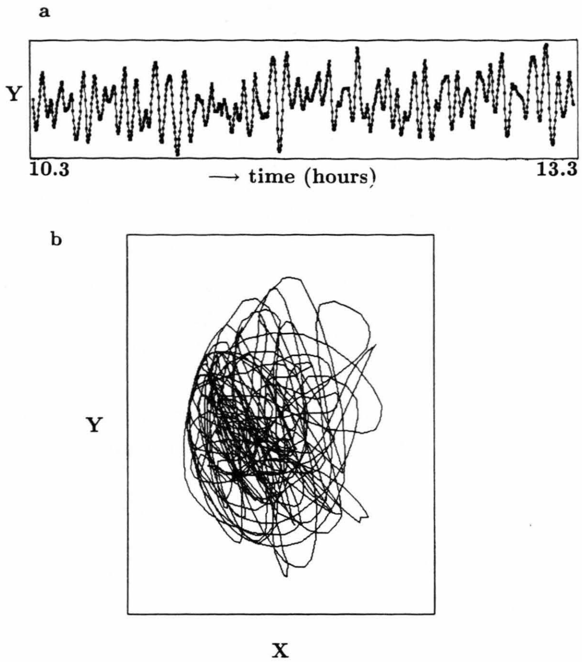

Fig. 3. Time series (a) and phase plot (b) of aperiodic oscillations.

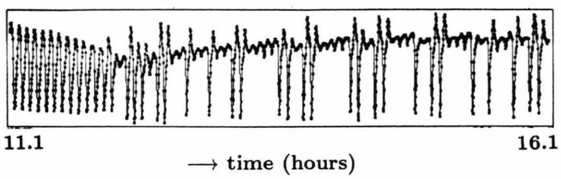

Fig. 4. Time series with dynamics switching from periodic to chaotic oscillations.

4. Discussion

The examples of the lateral leaflet movements of *Desmodium motorium* indicate widely known prototypes of nonlinear dynamics. We thus conclude that the mechanism governing the control of this movement is associated with a low-dimensional attractor of the underlying dynamical system. For a minimal mathematical description of the limit cycle behavior in Fig. 1 a nonlinear oscillator with only 2 variables is sufficient. In the case of the quasiperiodic oscillation in Fig. 2, either a nonlinear oscillator with an additional (linear) third variable or two coupled oscillators (with four variables) are required. The interpretation of the irregular behavior in Fig. 3 is not clear at present. Time series, phase space projection and Poincaré cross-section indicate a chaotic attractor with a dimension larger than 2. However, the limited time series does not allow a reliable quantitative evaluation of the spectrum of Lyapunov characteristic exponents so far. A possible alternative could be a hypertoroidal behavior with several interacting independent frequencies. Improvements of the stationarity of the time series are necessary to arrive at a decision.

Evidence for the presence of a low-dimensional chaotic attractor is found in the chaotic part of the time series in Figure 4. Subsequent small amplitude oscillations show a slow increase in amplitude followed by a small number of large spikes. This is indicative of a saddle focus with reinjection of trajectories. Such a structure allows for a homoclinic orbit and thus low-dimensional (Shil'nikov) chaos is possible (cf. [9] for an experimental observation).

Fostad has tried to simulate the movements of the pulvinus of the lateral leaflets by using 4 rings each consisting of 8 oscillatory units [10]. Each unit was described by a linearly damped harmonic oscillator. The coupled oscillator system exhibited periodic and quasiperiodic oscillations. However, the time series of the periodic, quasiperiodic and aperiodic oscillations presented here require a nonlinear modeling to account for the qualitative types of attractors including low-dimensional chaos and for the spontaneous switching between qualitatively different types of dynamics. It was demostrated recently that the bifurcation diagram of a ring of diffusively coupled (nonlinear) biochemical oscillators exhibits periodic, quasiperiodic, chaotic and higher chaotic attractors generically [11]. Low-frequency modulation of such a system (as might be imposed by circadian variation) could account for the observed switching between qualitative types of attractors.

The underlying biochemical mechanism of the autonomous leaflet movements and oscillations are not yet understood in detail. A turgor change brought about by ion fluxes as a result of hyperpolarizing proton pumps in the plasmalemma leads to swelling of the cells, until, at a critical value, depolarization is induced. This leads to an efflux of K^+ ions and water loss [12]. As a consequence the cells shrink. The trigger of depolarization and the cause of the well coordinated swelling and shrinking of the motor cells in a pulvinus are not yet known. There are indications of an important role of Ca^{2+} ions [13] and of the IP_3 cycle [14] in these events. It is well known that the IP_3 cycle controls Ca^{2+}-release [15, 16, 17, 18]. In two models (IP_3-Ca^{2+}-crosscoupling and calcium-induced-calcium release, respectively) nonlinear oscillations have been used for simulation [17, 19, 20]. It would be interesting to see how these or other models relate to the *Desmodium* oscillation. Whether they can explain the individual complex dynamics of ultradian leaflet rhythms described here remains to be checked.

Acknowledgement

We want to thank J. Schuster for improvement of the recording and analysis programs and Klaus Wegmann for discussion. G. B. is supported by the Deutsche Forschungsgemeinschaft.

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