News from the Archives

Biological rhythms are usually classified according to their period length or frequency. Those rhythms exhibiting periods less than 20 h are termed ultradian. A major difficulty encountered in contemplating the possible mechanisms giving rise to ultradian rhythms is that they exhibit a spectrum of frequencies. Even in one experimental system (*Mimosa pudica*), one encounters a range of period lengths ranging from seconds to minutes to hours (Roblin, 1977). Although these movements are all ultradian, it is unlikely that they are manifestations of the same fundamental rhythm.

Unlike circadian rhythms, ultradian rhythms, for reasons both practical and philosophical, have received little attention from plant biologists. Chief among the practical causes is the fact that ultradian rhythms are readily overlooked in experiments in which observations are made only intermittently (Due, 1989). Typically, the vagaries of data that occur during discontinuous measurements are either ignored or attributed to sampling error or poor technique rather than to biological rhythmicity. Secondly, the common practice of pooling and averaging data collected from different specimens will serve, given that no two specimens are likely to be completely in phase, to obfuscate rhythmicity.

It is important to recognize how philosophically ill-equipped modern plant physiology is to accommodate the study of ultradian rhythms. Ultradian rhythms are best studied in single specimens, using high-resolution, non-perturbing continuous recording techniques. Such a holistic approach to physiology runs counter to the prevalent reductionism that emphasizes the pooling and averaging of data collected from destructive measurements, usually upon as many specimens as practicable.

This month's column concerns an especially enigmatic subclass of spontaneous ultradian periodicities, here referred to as 0.1- to 10-Hz oscillations.

0.1- to 10-Hz Oscillations: A Physiologist's Nightmare

Most botanical researchers have ignored 0.1- to 10-Hz rhythms for two reasons. First, because the amplitudes of these rhythms are so small, it is easy to dismiss any single report as artifactual. The number of researchers, however, who have convinced themselves that 0.1- to 10-Hz rhythms are real is not small (this review is by no means exhaustive), and the possibility that all have been hoodwinked by subtle artifacts seems unlikely. A second reason why 0.1- to 10-Hz rhythms have engendered so little interest among plant physiologists is that they are fickle: They appear and disappear spontaneously. This fickleness has no doubt frustrated many researchers. Several reports are but breathless descriptions of some "newly discovered" 0.1- to 10-Hz phenomenon and of promises—ultimately unfulfilled—of more exciting data to come. Yet another reason for the neglect of 0.1- to 10-Hz rhythms is that even when they do occur, they often exhibit short-term variations in amplitude and frequency. Their fickleness and variability make them virtually impossible to explore pharmacologically. Indeed, such basic questions as whether 0.1- to 10-Hz oscillations are endogenous or exogenous, or affected by anoxia, metabolic inhibitors, or low temperature, remain unanswered.

The Discovery of 0.1- to 10-Hz Oscillations

Kashyap (1932), in an essentially anecdotal report, was the first to discover a 0.1- to 10-Hz rhythm in plants. During a botanical field trip to Sikkim on a still day in July 1930, he observed closely the leaves of *Molineria capitulata* (formerly *Curculigo recurvata*). He wrote that ". . . a leaf would begin to perform to and fro movements all of a sudden, go on for about a half-minute or so and then stop by itself. All of the other leaves of the plant would be absolutely still and no leaves of any other plants in the neighbourhood would show any movements. . . Sometimes it so happened that when one leaf had finished the movement another leaf of the same plant would take it up a little later. . . The rate of movement varied a good deal, between 40 to 120 complete oscillations per minute." Kashyap reported that some cultivated specimens in Gangtok also showed the movements, although more feebly and only in the morning. He was unable to observe the movements in specimens that he grew in Lahore. Nevertheless, he was able to capture the phenomenon on a cinematographic film, which he later presented at the Indian Science Congress.

0.1- to 10-Hz Leaf Movements Are Coupled to Bioelectric Rhythms

Semenenko (1972) used platinum plate electrodes and an electroencephalograph equipped with a frequency analyzer to record spontaneous electrical oscillations in several species of higher plants, including *Mimosa pudica*, *Phaseolus vulgaris*, *Primula veris*, and *Begonia lucerna*. These oscillations exhibited frequencies of 0.2 to 0.5 Hz and amplitudes of 100 to 250 μV. The frequency and amplitudes of the oscillations depended on the time of day, the pulsations being most pronounced at dawn and at dusk. Moreover, Semenenko (1972) asserts that frame-by-frame time lapse photography reveals that the plants exhibit rhythmic movements that resemble the electrical rhythms in form. Contemporaneously with Semenenko (1972), three additional research reports were published concerning the spontaneous occurrence of low-amplitude, 0.1- to 10-Hz bioelectric rhythms in plants (Karlsson, 1972; Pickard, 1972; Reinhold et al., 1972).

0.1- to 10-Hz Oscillations Are Unlikely to Be Related to Action Potentials (APs)

The most popular hypothesis to account for 0.1- to 10-Hz bioelectric oscillations in higher plants attributes them to trains of APs elicited by a single cell or a small cluster of cells within the vicinity of the electrode (Pickard, 1972; Glebiçki et al., 1986). A major problem with this hypothesis is that it does not take into account the relatively long refractory periods (typically on the order of 10 min) that immediately follow plant APs. Although repetitive trains of APs can be elicited in higher plants (e.g. Ping and Lou, 1990), their frequencies are, under physiological conditions, generally about two orders of magnitude lower than the 0.1- to 10-Hz oscillations. A second problem is that 0.1- to 10-Hz oscillations, unlike typical plant APs, do not propagate (Pickard, 1972).

Are 0.1- to 10-Hz Oscillations Related to Geomagnetic Pulsations?

Fraser-Smith (1978) found that the spontaneously arising geomagnetic variations of smallest amplitude (0.05–0.1 nT) and shortest period (0.2–5 Hz), the Pc1 class of geomagnetic pulsations, could be readily detected in an oak tree using two nails as electrodes. In fact, the resolution of the tree was not too much worse than that of a nearby loop antenna (a 20,000-turn steel-cored solenoid). Such geomagnetic pulsations gave rise to approximately 100 μV amplitude electric potential oscillations in the tree. The virtually identical occurrence and spectral characteristics of the geomagnetic pulsations measured by the tree electrodes and by the conventional geophysical recording equipment indicated that the tree potentials were largely induced by time variations of the geomagnetic field. To investigate this possibility further, Fraser-Smith circumnavigated the tree with a portable search coil powered by a 1-Hz signal generator. He found that a 1-Hz oscillation of the potential difference between the tree electrodes was produced only when the search coil was oriented with its moment vector in the north-south direction. When the two electrodes were moved to the north face of the tree, a response could be observed only when the search coil was oriented in the east-west direction.

Pc1 pulsations change during the 11-year solar cycle (Saito, 1969). During descending years in the solar, such as 1930 and 1971–1972, Pc1 pulsations are rare on geomagnetically quiet and moderately disturbed days. However, during the main phase of the magnetic storms that occur during these years, Pc1 pulsations of a special kind, the so-called "pearls with diminishing periods" are noted (Saito, 1969). At mid and low latitudes, the diurnal variations of Pc1 pulsations show maxima during the early morning hours and the evening (Saito, 1969). A typical characteristic of Pc1 pulsations is a tendency for them to recur on consecutive days, approximately at the same hours, or to disappear for days and even weeks. Semenenko's electroencephalograph recordings of plants are virtually identical to pearls with diminishing periods in terms of their amplitudes, periods, fickleness, pearl necklace-like appearance, and favored time of occurrence. In light of Fraser-Smith's (1978) findings, it appears that plants do act as antennae for these weak geomagnetic variations. The mechanism and the reasons why they do remain mysterious, but this property of plants may go a long way in explaining the anomalous 0.1- to 10-Hz rhythms recorded in plants

LITERATURE CITED

Due G (1989) Frequency as a property of physiological signals in plants. Plant Cell Environ **12:** 145–149

Fraser-Smith AC (1978) ULF tree potentials and geomagnetic pulsations. Nature **271:** 641–642

Glebiçki K, Hejnowicz Z, Pijanowski A (1986) Localized spontaneous fluctuations of electrical potentials in shoots of different plants. Acta Soc Bot Pol **55:** 67–76

Karlsson L (1972) Nonrandom bioelectrical signals in plant tissue. Physiol Plant **49:** 982–986

Kashyap SR (1932) Autonomous movements in the leaves of *Curculigo recurvata*. Curr Sci **1:** 7–8

Pickard BG (1972) Spontaneous electrical activity in shoots of *Ipomoea*, *Pisum* and *Xanthium*. Planta **102:** 91–114

Ping Z, Lou CH (1990) Rhythmic excitation in *Rorippa nasturium-aquaticum*. CR Acad Sci Paris **310:** 545–549

Reinhold L, Sachs T, Vislovska L (1972) The role of auxin in thigmotropism. *In* DJ Carr, ed, Plant Growth Substances 1970. Springer-Verlag, New York, pp 731–737

Roblin G (1977) Les rhythmes endogenés des mouvements foliaires chez *Mimosa pudica* L. J Interdiscip Cycle Res **8:** 89–109

Saito T (1969) Geomagnetic pulsations. Space Sci Rev **10:** 319–412

Semenenko AD (1972) Electrophytogram of pulsation rhythm. Dokl Bot Sci **206:** 124–126

Peter V. Minorsky
Department of Biology
Vassar College
Poughkeepsie, NY 12604