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Diurnal and Ultradiurnal Oscillations of Growing Organs Within the Framework of the Information System of the Plant

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Abstract. The analysis of growth and movements of seedling organs of kidney bean (*Phaseolus vulgaris* L.) provides a pattern of periodic phases of activity and relaxation. The existence of a central organ which would control the phase relationships, is not anticipated in the integrity of the plant. The cyclic activity of individual organs shows itself by growth associated with oscillation movements. One and the same organ may simultaneously accomplish oscillatory movements with a diurnal and ultradiurnal frequency. These rhythms originate during the organ development; the first pair of kidney bean leaves at first executes oscillation movements with a diurnal frequency and only after it is fully developed it exhibits a diurnal cycle with the photophil phase upwards and the scotophil downwards, the oscillations with an ultradiurnal cycle being maintained. The movements of the two leaves are synchronous, but there occur short sections with a desynchronous cycle. Simultaneously with these oscillations, in which the leaf petiole takes part, the adult leaf performs oscillatory movements perpendicular to the longitudinal leaf axis, the so-called side swings, controlled by periodical changes of the joint attaching the leaf blade. Their frequency is practically identical with that of the ultradiurnal cycle. Thus the periodic growth activity of the kidney bean results in growth oscillations passing in the diurnal cycle with a frequency of 0.043 rev.h^{-1}, their ascending and descending phases consisting of periodical ultradiurnal oscillations in cycles of 0.73—0.59 rev.h^{-1}. The epicotyl growth shows a similar pattern: into the basic diurnal nutation cycle with a frequency of 0.042 rev.h^{-1} ultradiurnal oscillation cycles are incorporated having a similar frequency to that revealed in leaves (0.69—0.64 rev.h^{-1}). The diurnal oscillatory cycles belong to a system established on the basis of periodicity of day and night and other geophysical cycles. The ultradiurnal rhythmic oscillations are presumed to be an expression of the geocontrol system of root and shoot growth direction and orientation of the organ in space. The shape of their trajectories in bean leaves is contradictory to this; they are not spatial helices, as the kybernetic model would presuppose, but have a vertical, upwards and downwards course in one plane. Since these oscillatory movements with an ultradiurnal cycle cease after petiole excision from the stem and after shoot apex amputation, one may presume that they are coupled with the low-frequency oscillatory system of the epicotyl.

Additional index words: Growth oscillations of the plant; synchronization of the growth activity, circumnutation of plant organs.

Oscillation rhythms of growing plants, investigated simultaneously in the leaves and stem, may have different frequencies and amplitudes (for critical survey of literature see Wassink 1972). The physiological basis of diurnal leaf oscillations is coupled with the regulatory kybernetic system in which the factors of epinasty and negative geotropism play a limiting part. From the biochemical point of view periodic variations in growth substance gradi-

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ents are concerned, occurring especially in petioles during photo- and scotophil phases (BÜNNING and STERN 1930, BÜNNING and MOSER 1973, BLUME 1975, SCOTT and GULLINE 1972). The frequencies and amplitudes of this system may be altered within wide limits by environmental factors, such as temperature (KETELLAPPER 1960, HOSHIZAKI and HAMNER 1969), induced periodicity of light and darkness and the light quality (GUREVICH 1967, HALABAN 1969, KRASTINA and LOSEVA 1972, KRASTINA and TSAREVA 1970), and by geophysical factors, such as cosmic irradiation, magnetic effects and barometric pressure.

In a series of plant organs rhythms shorter than diurnal were found out; BAILLAUD (1965) described ultradiurnal rhythms in leaf joints at circumnutated stems of twining plants. On studying the process of control and maintenance of the plagiotropic leaf position, BÜNNING *et al.* (1964) found oscillatory cycles of 2—3 h. HEATHCOTE (1966) referred to hypocotyl micronutations in *Phaseolus multiflorus* with a frequency of 2—5 rev.h^{-1}. In addition to diurnal rhythms in growing leaves of *Phaseolus angularis*, ultradiurnal ones with a frequency of 2.5 h were also described (ALFORD and TIBBITS 1970). The growing hypocotyl of pine seedlings exhibited an oscillatory rhythm of about 3.5 h (SPURNÝ 1975). The ultradiurnal cycles are considered to be strictly autonomous and any coordination between them and diurnal cycles is negated (BAILLAUD 1965). These phenomena have become of great importance in the study of information system in the plant, especially in the induction of synchronization of organ oscillations by artificially entrained photoperiodical cycles (GUREVICH 1967, ENRIGHT 1965, GUREVICH and IOFFE 1970, KÜBLER 1969).

The present paper deals with the ultradiurnal oscillatory rhythms in the organs of kidney bean seedlings and their phase relationship to cycles with a diurnal frequency.

Material and Methods

For the experiments kidney bean seedlings (*Phaseolus vulgaris* L., cv. Bílá perlička) were employed. Five-day old seedlings were transferred into the soil and the pots were fixed in a cultivation chamber in the position to ensure the level of the first leaf pair to be perpendicular to the optical axis of the camera. Throughout the whole experiment the plants were illuminated by fluorescent tubes (1200 lx) from a distance of 40 cm. Growth and oscillatory movements were registered by a time lapse cinematographic method using a device for a simultaneous shooting of the horizontal and vertical projections of plants (SPURNÝ 1975). The frequency of shooting, chosen with respect to the growth of the plants, equaled 1 frame per 15 min. Only one plant was always shot, the records obtained were reduced as least as possible (1 : 12 or 1 : 15), so that the coordinates of the points determining the spatial trajectory of organs could be read as accurately as possible. The evaluation was carried out microscopically at a 14-fold magnification. The cinematographic records obtained altogether from 6 experimental plants gave 12 trajectories of the nutating epicotyl, 24 trajectories of the petiole at the site of leaf blade setting, and 24 trajectories of the leaf blade (according to the blade tip) in the vertical and horizontal projections. For the quantitative evaluation of trajectories the oscillatory curves were transcribed into a transformed orthogonal millimeter network, where one of the coordinates of trajectory points was plotted against the time in h. Of the coordinates that which determined maxima of nutation amplitudes in the respective projection was selected. Oscillatory curves in the form of sinusoids were thus obtained from which both fundamental parameters, frequencies and amplitudes, were calculated (SPURNÝ 1976a).

Results and Discussion

The quantitative analysis of cinematographic records as obtained from the projection of the infinite loop of film records has revealed that the individual organs — leaves, petioles with blades and epicotyl — accomplish rhythmic oscillatory movements, with diurnal (petioles with leaf blades and epicotyl) and simultaneously with ultradiurnal frequencies (Fig. 1A—D). Since the oscillation rhythms proceeded in dependence on the ontogenesis of the plant, the quantitative analysis was performed, *i.e.* calculation of oscillation parameters, separately in the young and adult plants (Table 1). The results obtained show that the plant forms a multilevel oscillatory system controlled by the individual growth of the individual organs. The phases of this system are formed by the following processes:

TABLE 1

The oscillatory parameters of growing organs of kidney bean (*Phaseolus vulgaris* L.) seedlings as evaluated from oscillatory sinusoids according to cinematographic records of the plants No. 1—6

	Degree of development of the plant and its organs			
	I. Experimental plants 1, 5 Growth duration 35.3 and 117.1 h		II. Experimental plants 2, 3, 4, and 6 Growth duration 16.1, 50.7, 48.5 and 96.1 h	
Ultradiurnal cycle	Amplitude [mm]	Frequency [rev . h^{-1}]	Amplitude [mm]	Frequency [rev . h^{-1}]
Petiole	5.11* ± 0.22 s = ± 0.31	0.43 ± 0.02 s = ± 0.09	2.64 ± 0.16 s = ± 0.81	0.63 ± 0.03 s = ± 0.24
Leaf blade tip	5.06 ± 0.29 s = ± 4.75	0.73 ± 0.02 s = ± 0.39	3.19 ± 0.19 s = ± 1.72	0.59 ± 0.02 s = ± 0.13
Blade-side swings	—	—	*3.8 up 2.0 down	*0.48
Epicotyl apex	1.73 ± 0.17 s = ± 1.56	0.69 ± 0.03 s = ± 0.31	1.64 ± 0.08 s = ± 0.43	0.64 ± 0.02 s = ± 0.07
Diurnal cycle				
Petiole	—	—	—	—
Leaf blade tip	15.8 ± 2.10 s = ± 9.16	0.043 ± 0.002 s = ± 0.007	12.17 ± 1.30 s = ± 4.30	0.042 ± 0.001 s = ± 0.003
Epicotyl apex	—	—	*2.5	*0.042

* Not evaluated statistically because of a small n.

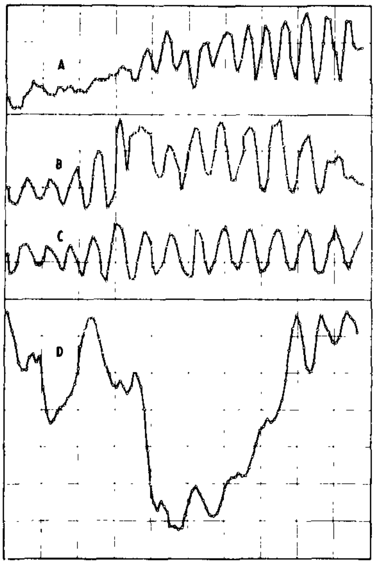
a) In the initial phases of leaf development the elongation is associated with irregular movements passing after 12 h into oscillatory ultradiurnal cycles with a frequency of 0.73—0.59 rev.h^{-1} (Fig. 1A). This movement is affected especially by the oscillatory system of the petiole (Fig. 1C), similarly as in tobacco leaves (SPURNÝ 1972, 1976b). The diurnal cycle does not manifest itself in the petiole.

b) In the course of its elongation epicotyl at first undergoes the phase of oscillatory movements with an ultradiurnal cycle of low amplitudes. The phase of the most rapid elongation, accompanied with oscillatory movements with a frequency of 0.69 rev.h^{-1} and maximum amplitudes of 1.73 mm passes into a retarded growth accompanied with a suppression of oscillation amplitudes. Simultaneously a diurnal cycle occurs with a frequency of 0.42 rev.h^{-1} and amplitudes of 2.5 mm. Both oscillatory systems are realized in spatial simultaneously circumscribed helices circular in section (Fig. 2A, B), similar to the lunar orbit: the ultradiurnal cycle corresponds to the revolution of the Moon around the Earth and the diurnal one to its revolution around the Sun. The shape and course of these trajectories correspond to the model of the geocontrol system of the spatial organ orientation (HEATHCOTE 1966).

c) The circumnutation system of epicotyl carries along the leaves with itself, so that the trajectories registered always depict a movement consisting of the oscillation of leaves proper and of epicotyl circumnutation (Fig. 2E). The extent of the trajectory deformation of leaf oscillations is dependent on the magnitude of epicotyl oscillation parameters in the individual growth phases. The coordination of the two rhythms can be supported by the fact that the ultradiurnal leaf oscillations with a frequency of 0.73 rev.h^{-1} correspond to the circumnutation frequencies of epicotyl, but only in early phases of the organ growth — 0.69 rev.h^{-1}. Similar relations were found by ALFORD and TIBBITS (1970) in *Phaseolus angularis*. From this an identical control system of the two mechanisms may be inferred. This is also evidenced by the cessation of ultradiurnal oscillations following leaf excision.

d) The start of the diurnal leaf cycle with a frequency of 0.043 rev.h^{-1} and amplitudes of 15.8 mm is associated with a periodic activity of the joint which attaches the blade to the petiole. The amplitudes of ultradiurnal oscillations of 5.06 and 3.19 mm are distinctly affected by the movement of the joint. The coordination of the two rhythms is manifest from the fact that the amplitudes of ultradiurnal oscillations are affected by the phases of the diurnal cycle: during the photophil phase the amplitudes are lower, during scotophil they are higher (Fig. 2C, D).

e) In fully developed first leaves both oscillatory movements were registered distinctly after 1-day growth: the diurnal with a frequency of 0.042 rev.h^{-1} and amplitudes of 12.17 mm, and ultradiurnal cycles with a frequency of 0.59 rev.h^{-1}. Thus on the average 4—6 oscillations of the ultradiurnal cycle fall to the 12-h phase (movement of leaves upwards), and the same number to the scotophil phase (Fig. 2D). Their amplitude fluctuates on the average about 3.19 mm. The photophil and scotophil phases in both leaves are in principle synchronous; however, sections were still registered where desynchronization occurred (plants of the experimental series 4 and 6). Excised leaves do not exhibit ultradiurnal oscillations (GUREVICH 1967, BÜNNING and MOSER 1973), which supports the view that the mechanism



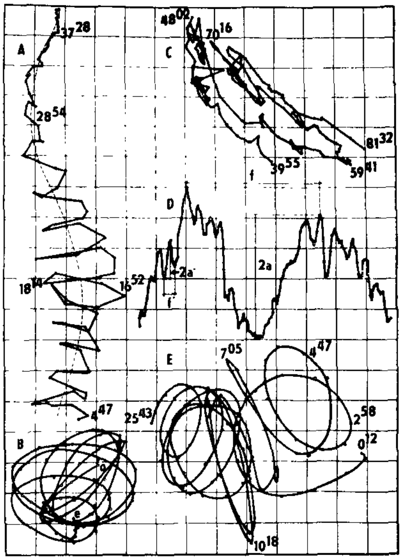


Fig. 1. The development of oscillatory rhythms of growing kidney bean (*Phaseolus vulgaris* L.) leaves during ontogenesis.
A — oscillatory sinusoid of the leaf blade tip with an ultradiurnal frequency in the earliest growth phase (plant No. 3); B — oscillatory sinusoid of the leaf blade tip with an ultradiurnal frequency at a later phase with an indication of diurnal cycle; C — oscillatory sinusoid of the leaf petiole with ultradiurnal cycles; D — oscillatory sinusoid of the leaf blade tip with a diurnal cycle, with the photo- and scotophil phases formed by ultradiurnal oscillations (plant No. 6).
Abscissa: growth in h (2.5 h net), ordinate: oscillation amplitudes in mm (5 mm net).

Fig. 2. A — horizontal, and B — vertical projection of oscillatory trajectories of growing kidney bean (*Phaseolus vulgaris* L.) hypocotyl apex in a millimeter orthogonal net à 6 mm. The ultradiurnal cycle trajectory — full line, diurnal cycle — dashed line. 0 = beginning of the shooting at 10^{45}h, e = end after 28^{45} h, plant No. 5; C — horizontal projection of a leaf blade tip trajectory with a diurnal cycle. Photophil phase — full circles, scotophil — open circles. The values express the leaf growth in h. Periodical accumulation of points indicate the occurrence of oscillations with an ultradiurnal frequency. Plant No. 6; D — trajectory (C) plotted into a transformed net in the form of an oscillatory sinusoid.
Abscissa: growth in h (net à 5 h), ordinate: amplitudes in mm (net à 5 mm); f, f′ = frequencies of diurnal and ultradiurnal cycles; a, a′ = amplitudes.
E — vertical projection of the trajectory of oscillation movements of the leaf blade tip with an ultradiurnal frequency in an orthogonal 5 millimeter network. The values express growth in h, plant No. 5.

of motion is not autonomously limited only to the leaf, but is connected with periodic epicotyl oscillations of low frequencies.

f) The oscillatory system of side swings of the leaf blade along its main rib has a similar cycle as the ultradiurnal oscillations in the vertical projection — 0.48 rev.h^{-1}. The oscillations are located unambiguously in the joint where the blade is attached to the petiole. Both these oscillatory systems have a common organ of motion. The cause of periodical changes in this organ has not been fully elucidated (for the survey of previous literature see Bünning *et al.* 1964); with regard to the stomatal cycle in leaves it is likely that rather the changes induced by turgor pressure are concerned than those brought about by an uneven growth of the upper and lower petiole edges. It is a question whether, or not, this is a control system determined to a plagiotropic orientation of the leaf, similarly as is the case in the root and epicotyl in the geotropic orientation of the organ. The difference consists in that the trajectory of leaf oscillatory movements does not correspond to the fundamental requirement of a kybernetic model: the time delay between the perception of the error and its correction should result in a spatial helix in roots (SPURNÝ 1973) and epicotyl (SPURNÝ 1975). In the case of trajectories of both low-frequency oscillatory systems occurring in leaves, or leaf blades, polarized trajectories are concerned, *i.e.* strictly vertical in one case, and a swinging movement in a perpendicular plane in the other (the finding of circular trajectories of the petiole at the site of joint in the vertical projection must be evaluated with respect to the fact that these are complex trajectories whose circular component is to be attributed to circumnutations of the epicotyl by which the leaves are carried — to compare B and E in Fig. 2).

Since the kidney bean leaves are a model subject in the investigation of diurnal rhythms in the plant (BÜNNING and MOSER 1973, GUREVICH 1967), it is questionable whether the results obtained from the study of "joint" leaves are of general validity; it appears necessary to extend the research to rhythmic oscillations in plants with "jointless" leaves.

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BOOK REVIEW

EAMES, A. J., MACDANIELS, L. H.: **An Introduction to Plant Anatomy.** Second Edition. — McGraw-Hill Book Company New York-London 1947. 427 S.

Diese zweite Auflage der Einführung in die Pflanzenanatomie wurde 1977 in Photooffset-Reprintform erneut herausgegeben. Es wurden keinerlei Veränderungen oder Ergänzungen vorgenommen. Das Lehrbuch ist in sechs Abschnitte und die in gesamt vierzehn Kapitel gegliedert. Nach einem kurzen einleitenden Kapitel über die allgemeine Struktur des Pflanzenkörpers folgen drei Kapitel über Zytologie (Aufbau von Pflanzenzellen) und Histologie (Meristeme, Dauergewebe, Gewebekomplexe wie z. B. Xylem, Phloëm und Gewebesysteme). Des weiteren werden die Primär- und Sekundärstruktur des kompletten Pflanzenkörpers und einzeln die Struktur der Hauptkomponenten der Pflanze: der Wurzel, des Sprosses, des Blattes und der Blüte, Frucht und Samen behandelt. Im letzten Abschnitt, der ökologischen Anatomie, wird der Leser mit den strukturellen Besonderheiten der Meso-, Hydro-, Xero- und Epiphyten, der Schattenblätter, der parasitischen, saprophytischen und fleischfressenden Pflanzen bekannt gemacht. Das Buch schliesst mit einem Pflanzen- und Sachregister, ist reich illustriert (186 Zeichnungen und Photographien) und am Ende jedes Kapitels steht ein Literaturverzeichnis mit ausgewählten Zitationen zum Weiterstudium.

Das Buch ist als Lehrbuch für Hochschulen gedacht, d. h. Verfasser waren bemüht Übersichten zusammenzustellen und die elementaren Kenntnisse herauszugreifen, ohne dabei in allzufeine Details einzugehen. Es soll dem Studenten die Grundlagen der Pflanzenanatomie beibringen. Diese Aufgabe ist den Verfassern zweifellos gelungen. Da das Buch vor 30 Jahren erschienen ist und den damaligen Stand der pflanzenanatomischen Kenntnisse widerspiegelt, sollte der Leser seine Kenntnisse in manchen Abschnitten wie z. B. Struktur der Chloroplasten, Mitochondrien, Peroxisomen, Blattanatomie bei C_3- und C_4-Pflanzen usw. durch das Studium rezenter Lehrbücher der Pflanzenanatomie ergänzen.

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