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Synchronization of Oscillatory Rhythms of Stems and Leaves

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Abstract. A previous report on the mechanism of diurnal oscillations is supplemented here by data concerning causes of irregularities in their oscillation trajectories. Cinematographic records showed that the final trajectory is significantly influenced by the circumnutation oscillations of the stem. Amplitudes of these oscillations which are small (*ca* 0.7 mm as compared with 5 × larger amplitudes of leaves when measured at the leaf tip) can be enlarged up to 10 times the value at the apical tip of the leaf. These nutations are responsible for side-deviations of space spirals of growing leaves in the direction of their shorter half axis. This explanation is based on the occurrence of side-deviations of leaf trajectories which correlate with the actual position of the nutation phase of the stem. Concurrent frequencies of the two oscillations (= diurnal rhythm) indicate that nyctinastic oscillations of the leaves are controlled by the same mechanism as is the circumnutation of the stem.

The existence of biological rhythms in higher plants was proved by BÜNNING (1957) and BAILLAUD (1958, 1967). Subcellular and biochemical aspects of measurement of time in biological systems was studied by SCHWEIGER (1971) and HASTINGS (1970). In spite of a certain simplification the biological rhythms can be methodically interpreted in terms of sinusoid function parameters, *i.e.* frequency (period of revolution), amplitude and phase. Synchronization may be defined by these parameters: two oscillations are synchronous when they have the same frequency and are in phase, *i.e.* when their phase difference is zero (MILLET 1972). Most attention has been paid to the rhythm oscillations of growing plant organs. These oscillations are induced during endo- and exogenously controlled growth as has been described for hypocotyl (HEATHCOTE 1972, SPURNÝ 1974, JOHNSSON and HEATHCOTE 1973), primary root (SPURNÝ 1966) and leaf (BÜNNING and BLUME 1963, BÜNNING and MOSER 1972).

Much less understood is the synchronization of oscillation rhythms of two or more simultaneously growing organs of the same plant. It has been shown that leaves of young tobacco plants execute diurnal oscillation movements synchronously: the photophil movement upwards of all leaves

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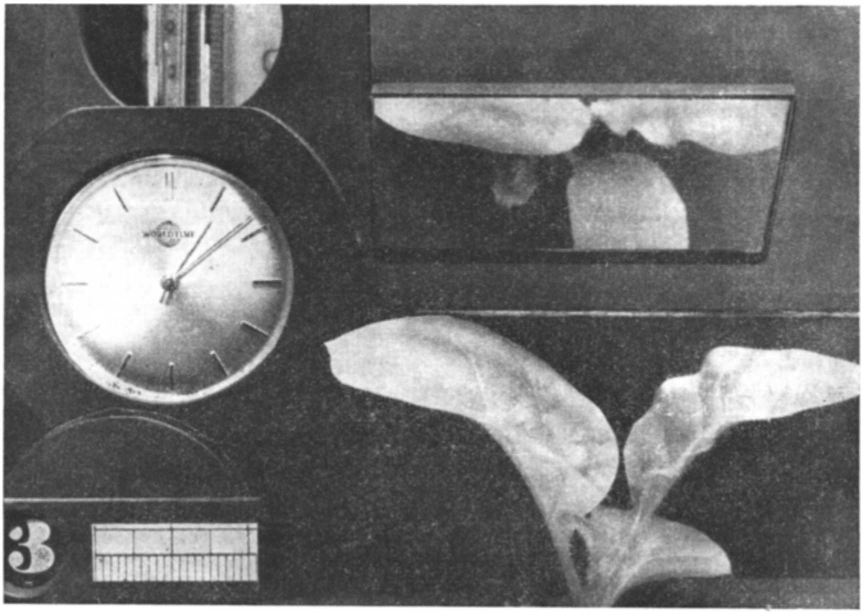


Fig. 1. A picture taken by the apparatus for simultaneous registration of horizontal (bottom) and vertical projection of nutation oscillations of the stem and periodical oscillations of tobacco leaves (*Nicotiana tabacum* L. cv. 'Samsun'). Time, temperature, size mark and designation of the experimental set are taken together with the object.

during the day is synchronous in phase as well as their scotophil movement downwards at night. This report is an attempt to explain the irregularities of oscillation trajectories of leaves on the basis of synchronous circumnutation oscillations of the growing stem.

Material and Methods

Young tobacco plants (*Nicotiana tabacum* cv. 'Samsun') were used. Classification of plants according to their development and method of their cultivation in a moist chamber have been described elsewhere (SPURNÝ 1972). Using a system of mirrors the cinematographic method of growth registration was modified in such a way as to allow simultaneous taking of vertical and horizontal projection of growth trajectories of the stem and leaves (SPURNÝ 1975). In experiments designated X 1—3 the plants were taken from above only. Trajectories of nutation of their stem tip and nyctinastic movement of their leaves were recorded only in vertical projection. In the case of experiments marked Y 1—6, both these movements were recorded simultaneously in the vertical and horizontal plane using a device shown in Fig. 1. In all these experiments plants were continuously illuminated with fluorescent tubes (1200 lx). The frequency of shooting, 1 frame per 15 min, was chosen according to the growth rate of the plants. Altogether cinemato-

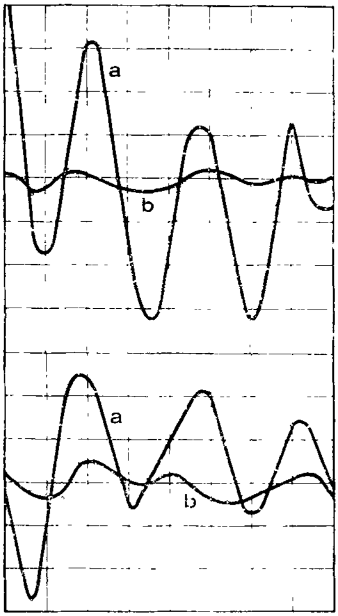


Fig. 2. Oscillation sinusoids of nyctinastic movements of leaves (a) and circumnutation oscillations of the stem (b) of young tobacco plants (*Nicotiana tabacum* L. cv. 'Samsun'). Film records of experimental sets X1 (top) and X 3 are transcribed into the orthogonal network. Abscissa: time (10 h network); ordinate: size of oscillation amplitudes (1.6 mm network).

graphic records of 9 experimental plants were obtained. Nine of these records were taken in vertical and six in horizontal projection.

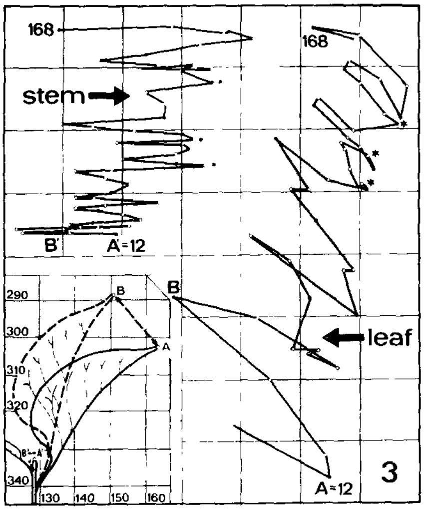
Results and Discussion

Tobacco plants execute oscillation movements consisting of day and night phase even when they are cultivated under continuous light. Trajectories of

Table 1

Parameters of the nyctinastic leaves movement and nutational stem oscillation of the young tobacco seedlings (*Nicotiana tabacum* cv. 'Samsun'). Data of original film recordings of the experimental series X 1—3 and Y 1—6

Oscillation parameters $\bar{x} \pm s_{\bar{x}}$ $\pm s$	Stem	Young leaves	Well developed leaves (growth in hours) 0—120	120—240	240—360
Oscillation Amplitudes [mm]	0.72 ± 0.01 0.05	0.91 ± 0.09 0.46	3.04 ± 0.26 2.15	3.91 ± 0.29 1.75	3.36 ± 0.45 1.78
Oscillation Frequency [h per turn]	**22.81 ± 0.54 3.35**	**24.30 ± 0.83 3.80**	**23.47 ± 0.53 4.30**	**25.31 ± 0.51 2.98**	**24.91 ± 0.60 2.33**
Oscillation Frequency [turn h^{-1}]	**0.046 ± 0.001 0.011**	**0.042 ± 0.002 0.008**	**0.044 ± 0.001 0.011**	**0.040 ± 0.001 0.004**	**0.040 ± 0.001 0.004**



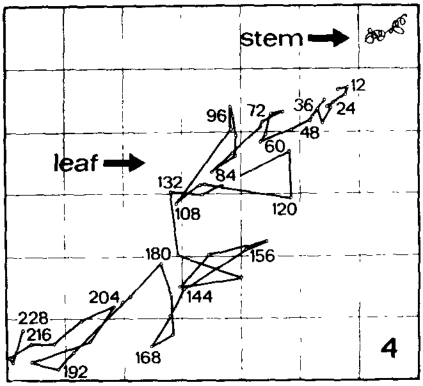


Fig. 3. Synchronization of diurnal oscillations of growing leaves (right) and circumnutations of the stem (left) of young tobacco plants (*Nicotiana tabacum* L. cv. 'Samsun'). Horizontal projection of trajectories of experimental set Y 5 is transcribed from the film record into 5 mm orthogonal network. In the case of the stem, intervals of the net are 5 × enlarged and represent 1 mm each. Marginal points of trajectories of nyctinastic oscillations of the leaf blade tip (A—B) correspond to the positions of nutation spiral of the stem (A'—B') at certain intervals of time (marked with asterisks). Mutual position of the two oscillating organs is shown in the scheme below. Micrometric net of the microscope represents 10 mm intervals.

Fig. 4. Trajectories of nutation oscillations of stem (right at the top) and diurnal oscillations of a growing tobacco leaf (*Nicotiana tabacum* L. cv. 'Samsun') in vertical projection. Film record of a plant from the experimental set Y 5 is transcribed into 5 mm orthogonal network. Points on trajectories represent periods of growth in hours.

oscillation of tobacco leaves can be registered either on intact plants or on abscissed ones (Gurevich and Ioffe 1968, 1970). As was shown in the previous report (Spurný 1972), the final trajectory of the leaf blade tip is affected by the movement of the petiole base, growth of the petiole and by changes in the blade shape caused by growth and phototropic torsions. Trajectories obtained from registration of petiole movements were more regular than those circumscribed by the tip of the leaf blade. According to present results these movements are supplemented by nutation oscillations of the plant stem. This movement significantly affects growth oscillations of leaves registered according to positions of the petiole or the blade tip. Mean values of parameters of circumnutation oscillations of the stem and leaves calculated from all cinematographic records are summarized in Table 1. Because the differences in the size of amplitudes of leaves are dependent on the leaf age, the leaves were divided into two age-groups: young leaves A and older leaves B (Spurný 1972). Leaves of each group were further classified into three classes according to their development, which is characterized by the period of their growth in hours. The frequency of all leaves studied (including the youngest ones) is very close to 24 h (0.042 rev. h^{-1}), which consists of 12 h movement upwards and downwards, respectively. The frequency of nutation oscillations of the stem is about the same (value 22.8 h rev.$^{-1}$ is insignificantly higher than that found for young leaves). This important finding is demonstrated in Fig. 2. The effect of circumnutation of the stem on the trajectory of a leaf which has the same frequency of oscillations can be understood from Fig. 4. This shows trajectories of the nutating stem (right above) and nyctinastic movements of growing leaves in vertical projection. While the maxima of branches of nutation spirals of leaves reach 5 mm, the amplitudes of nutation revolutions of the stem are expressed in tenths of mm and the nutation space of the whole stem did not exceed 5 mm during the whole experiment. As is shown in Fig. 3, the side-deviations of growth spirals of the leaf (here in horizontal projection) do correspond to the actual position of the nutating stem. Analysis of cinematographic records indicates that even this small movement of the nutating stem (mean size of amplitudes 0.7 mm) is transmitted on the leaf and at the tip of a 25—30 mm long leaf may be enlarged up to 10 times. It is evident that the resultant trajectory of the leaf is a movement composed of leaf's own motion influenced by factors reported elsewhere (SPURNÝ 1972) and of oscillation movements of the stem transmitted and enlarged on the leaf. Irregularities in trajectories of the leaf caused by oscillations of the stem become evident on growth spirals as side-deviations (NOVÁK 1964) as is apparent on vertical projection of the trajectory of the blade tip in Fig. 2. A total picture of the oscillation system of growing tobacco plants can be described in the following way. When the stem makes one nutation revolution per day with amplitude 0.7 mm and simultaneously elongates in the apical part in the zone of rapid growth, then the resultant trajectory is a more or less circular space spiral. Leaves which execute synchronous nyctinastic diurnal oscillations with amplitudes 5 mm are carried up by the nutating stem. Movement of the stem is transmitted to the leaves. The resultant trajectory is a space growth spiral of elliptical shape in transversal section. The longer half axis is given by amplitudes of nyctinastic oscillation of the leaf in the upward and downward direction and the shorter half axis is determined by amplitudes of circumnutation oscillation of the stem transmitted and enlarged on the leaf.

Synchronization of nutation rhythms of the growing stem and leaf is given by coincident frequency of their oscillations (Fig. 2). Because the nyctinastic oscillation of all the leaves of one plant were not simultaneously examined in the present experiment it is not possible to determine whether the time synphase is also accompanied by a space synphase. With respect to this limitation the question of whether a regular relationship exists between the actual position of the leaf and photo- scotophil phase of the oscillating leaf cannot be answered at present. The coincident period of the two oscillations has been supposed by ALFORD and TIBBITTS (1970) to indicate the existence of a common mechanism which controls both, the nyctinastic oscillations of leaves and circumnutations. This problem can be studied in experiments in which nutations of the stem are disturbed by decapitation of the stem at various oscillation phases of the leaf. Such experiments are in progress in our laboratory.

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