

Diurnal Oscillatory Movements of Growing Leaves of Tobacco

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Abstract. The analysis of diurnal oscillatory movements of tobacco leaves was used in the diagnosis of viral infection of plants. The oscillatory helices circumscribed by a growing leaf of a healthy plant were regular, but some deviations, particularly in the transition points, were recorded.

In order to make clear the cause of these irregularities of trajectory, the course of elongation of leaf petiole and blade in relation to localization and shift of zones of elongation during ontogenesis was analysed. The present analysis is similar to that described by the author's earlier experiments with pea roots. Oscillatory curves circumscribed by petiole, projected on a horizontal plane, were compared with curves circumscribed by the blade tip. The analysis of the leaves of different ages enabled us to study this process in dependence on growth rate. It was confirmed that oscillations are a result of elongation; the extent of oscillations is quantitatively dependent on the growth rate. An analysis of the zones of growth showed that in petiole the active meristems are localized near to its base while in the leaf lamina they move gradually during the ontogenesis from the apical to the basal part of the leaf blade. Active meristems of young rapidly growing leaves are localized approximately in the middle of the blade while those of old leaves were found in close proximity to the base of the lamina. The growth rate of petiole can be expressed in hundreds of mm per hour ($4.8 \times 10^{-2} \text{ mm h}^{-1}$); half of this value was recorded for its apical part. The growth rate of leaf blade was found approximately ten times higher ($3.2 \times 10^{-1} \text{ mm h}^{-1}$).

The oscillatory movements of growing leaf consists of two integrate components: of oscillations originating in the base of the petiole and of oscillations of leaf blade the centrum of which is localized in the basal third of the blade.

The arrangement of the experiments did not enable us to determine to what extent the phototropic response of leaf blade participates in leaf movements. The movements of leaves of an intact plant are evidently affected by rhythmic stem oscillations. Stem is an integral part of a system which participates in the transfer of information in plants.

The changes in rhythm of the oscillatory movements of growing tobacco leaves were used for the diagnosis of viral infection (NOVÁK 1964, NOVÁK and SPURNÝ 1968). It was found that the leaves of healthy plants circumscribe during ontogenesis growth-helices the length of which is given by the time of elongation, its steepness being proportional to the growth rate. The frequency of oscillations displays an almost regular 12 h rhythm. Their amplitude is mainly determined by the age of the leaf. The oscillations of

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leaves infected by VTM are irregular with smaller amplitudes which reflect the growth inhibition of the plant. While the oscillatory movements are generally very regular, certain irregularities do exist, particularly in the transition points of growth helix. This suggests the possibility of the existence of side-oscillations of smaller amplitude (HEATHCOTE 1966). In all these studies, the growth movements were recorded by cinematography. It cannot be excluded that some irregularities of trajectory were due to phototropic changes in the shape of the leaf blade (BRAUNER 1959). It was necessary to determine in what way the oscillations depend on movements in the region of the base of the petiole (BÜNNING 1937, BAILLAUD 1958) and to what extent they are affected by other factors, as for instance, by the localization of the zone of maximum elongation and by its shift during growth as has already been demonstrated in roots (SPURNÝ 1965, 1966). The present study was undertaken in order to examine the side-mechanisms of the growth-oscillations of leaves and their relation to the growth rate of petiole and blade and to the localization of zones of growth during ontogenesis.

Material and Methods

Young tobacco plants, *Nicotiana tabacum* cv. Samsun, were used in this study. The cultivation, selection and classification of plants according to their development, illumination and cinematographic technique have been described elsewhere (NOVÁK and SPURNÝ 1968). In the present studies only a stem section with petiole (marked with 4 to 5 marks) and a part of the blade was photographed. Such records made it possible to register movements localized on the base of the petiole. In order to obtain the horizontal projection of oscillation without distortion, the plant was orientated in front of the film camera in such a way that a couple of petioles were in plane perpendicular to the lens axis. The dependence of the oscillation amplitudes on the distance from

TABLE 1

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the youngest leaf A of the experimental series No. 1

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | Total length of petiole (marks 1—4) | | Growth rate of the petiole segments in % of their original values | | |
|---------------|--|------|------|-------------------------------------|--------------------------|---|------|------|
| | 1—2 | 2—3 | 3—4 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 |
| 12 | 2.91 | 2.89 | 3.14 | 8.94 | 0 | — | — | — |
| 24 | 3.26 | 3.19 | 3.22 | 9.69 | 8.1 | 12.8 | 10.5 | 0.3 |
| 36 | 3.40 | 3.29 | 3.46 | 10.15 | 13.0 | 17.2 | 13.9 | 10.1 |
| 48 | 3.65 | 3.40 | 3.60 | 10.65 | 19.5 | 26.1 | 17.5 | 14.8 |
| 60 | 3.62 | 3.65 | 3.86 | 11.13 | 24.2 | 25.0 | 26.1 | 23.0 |
| 72 | 4.17 | 3.67 | 4.09 | 11.93 | 33.1 | 43.0 | 27.0 | 30.0 |
| 84 | 4.14 | 3.71 | 4.24 | 12.09 | 35.0 | 42.5 | 28.1 | 35.0 |
| 96 | 4.42 | 4.02 | 4.44 | 12.88 | 41.8 | 52.0 | 39.0 | 41.0 |
| 108 | 4.37 | 4.27 | 4.70 | 13.34 | 48.8 | 51.0 | 47.5 | 49.6 |
| 120 | 4.76 | 4.45 | 4.76 | 13.97 | 56.0 | 64.0 | 54.5 | 51.5 |
| 132 | 5.10 | 4.78 | 4.81 | 14.69 | 64.2 | 75.5 | 65.5 | 52.8 |
| 144 | 5.73 | 4.82 | 4.86 | 15.41 | 73.0 | 97.5 | 67.0 | 55.0 |
| 156 | 5.81 | 5.02 | 4.93 | 15.86 | 78.0 | 100.0 | 74.0 | 56.8 |
| 168 | 6.02 | 5.32 | 5.00 | 16.34 | 82.2 | 108.0 | 86.0 | 59.5 |
| 180 | 6.45 | 5.54 | 5.05 | 17.04 | 91.0 | 122.0 | 92.0 | 60.5 |

the base of the petiole have been evaluated from these records. The frequency of shooting was one frame per 30 min.

The elongation of leaves was also registered on cinematographic records. To prevent distortion of the length of measured parameters, the leaf blades of selected plants were orientated in a perpendicular position to the axis of the lens. The marking of concentric circles at 1 mm intervals was found useful for determining the frequency of shooting in these experiments. The calculation of the rate of elongation of the blade was based on measurements of the lamina intervals, from base to tip, determined by the principal lateral veins. The temperature, time, humidity and diminution marks were photographed together with the leaf (Fig. 1). Photographic records were interpreted using a special Zeiss microscope provided with an objective 3 and eyepiece 7×. By this technique the coordinates of points which illustrate the changes of positions of marks on petiole were determined. Coordinates of the extreme blade points along the middle ribs were found in the same way. From these data horizontal projections of oscillation curves were constructed and these were illustrated in the actual size on a millimetre network.

The course of oscillatory growth movements of 16 petioles from four experiments was recorded. The growth rate of the leaf blade was measured according to cinematographic records of four experimental plants.

Results

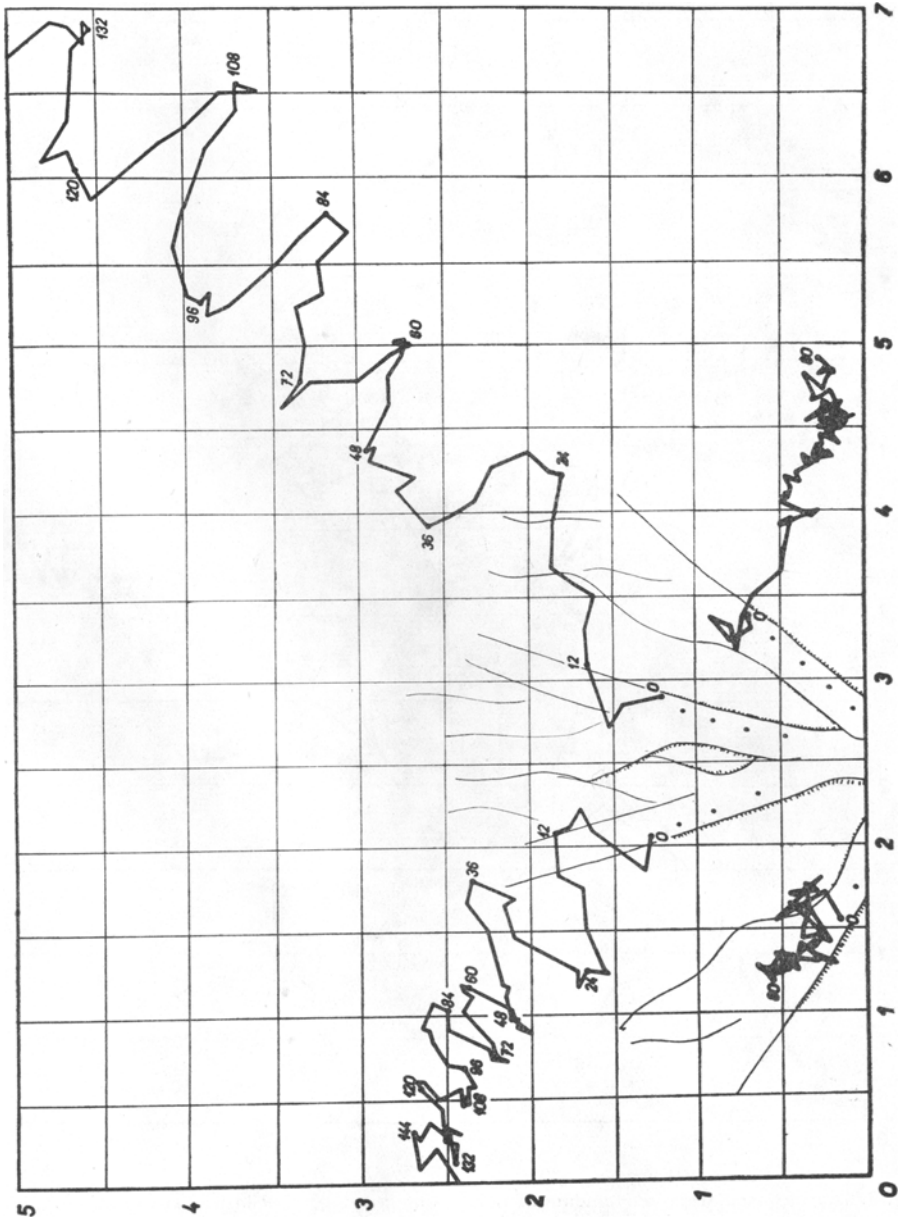
The horizontal projections of points marked on growing leaf petioles adjacent to leaf blade (Indian ink marks 4 or 5) registered at two hour intervals are presented in Figs. 2 to 5. The position of the corresponding leaves on the plant is described in the enclosed diagrams. These projections show the maxima of oscillation amplitude of growing petioles. The distribution of the zones of elongation on petioles (leaves of age-groups *A* and *B*) recorded in experiments Nos. 1, 3, 4 and 8 is apparent from Tab. 1 to 6. These data are summarized in Fig. 6 which shows the localization of zones of maximal elongation of petiole and blade during the development of

TABLE 2

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the young leaf *B* of the experimental series No. 1

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | Total length of petiole (marks 1—4) | | Growth rate of the petiole segments in % of their original values | | |
|---------------|--|------|------|-------------------------------------|--------------------------|---|------|------|
| | 1—2 | 2—3 | 3—4 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 |
| 12 | 3.96 | 3.10 | 3.35 | 10.61 | 0 | — | — | — |
| 24 | 4.30 | 3.46 | 3.54 | 11.30 | 6.8 | 8.5 | 11.2 | 5.6 |
| 36 | 4.61 | 3.30 | 3.60 | 11.51 | 8.6 | 16.5 | 7.0 | 6.0 |
| 48 | 4.71 | 3.65 | 3.70 | 12.06 | 11.9 | 19.0 | 17.5 | 10.5 |
| 60 | 4.83 | 3.88 | 3.77 | 12.48 | 18.1 | 21.5 | 25.0 | 12.8 |
| 72 | 5.02 | 3.95 | 4.15 | 13.12 | 23.8 | 26.5 | 27.0 | 24.1 |
| 84 | 5.37 | 3.90 | 4.20 | 13.47 | 27.0 | 35.0 | 25.9 | 25.4 |
| 96 | 5.39 | 4.09 | 4.27 | 13.75 | 28.9 | 36.0 | 32.0 | 27.1 |
| 108 | 5.42 | 4.13 | 4.25 | 13.80 | 29.9 | 37.0 | 33.3 | 27.0 |
| 120 | 5.51 | 4.07 | 4.34 | 13.92 | 31.0 | 39.0 | 31.0 | 29.5 |
| 132 | 5.70 | 4.07 | 4.36 | 14.13 | 33.0 | 44.0 | 31.0 | 30.1 |
| 144 | 5.90 | 4.15 | 4.31 | 14.36 | 34.8 | 48.8 | 33.9 | 28.5 |
| 156 | 6.02 | 4.17 | 4.36 | 14.55 | 36.8 | 52.0 | 34.4 | 30.1 |
| 168 | 6.10 | 4.26 | 4.40 | 14.76 | 38.5 | 54.0 | 37.0 | 31.0 |
| 180 | 6.13 | 4.26 | 4.42 | 14.81 | 39.4 | 54.3 | 37.0 | 32.1 |

Fig. 2. Diurnal oscillatory movements of petioles of growing tobacco leaves (*Nicotiana tabacum* cv. Samsun). Curves represent the horizontal projection of oscillations circumscribed by the extreme points of petioles given by the coordinates x and y and transcribed in the orthogonal millimetre net. Numbers on curves describe the period of growth [h]. Data from the Exp. 1.



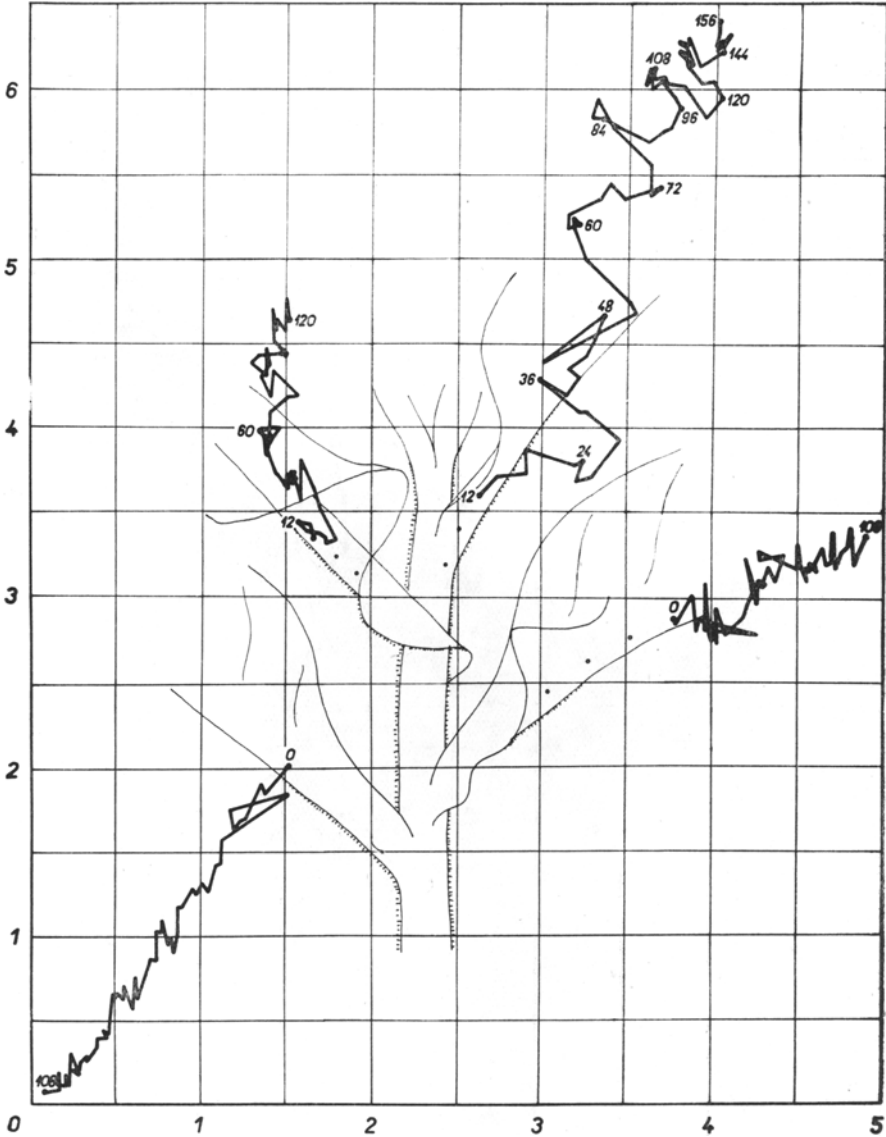


Fig. 3. Diurnal oscillatory movements of petioles of growing tobacco leaves (*Nicotiana tabacum* cv. Samsun). Curves represent the horizontal projection of oscillations circumscribed by the extreme points of petioles given by the coordinates x and y and transcribed in the orthogonal millimetre net. Numbers on curves describe the period of growth [h]. Data from Exp. 3.

TABLE 3

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the young leaf *B* of the experimental series No. 3

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | Total length of petiole (marks 1—4) | | Growth rate of the petiole segments in % of their original values | | |
|---------------|--|------|------|-------------------------------------|--------------------------|---|------|------|
| | 1—2 | 2—3 | 3—4 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 |
| 12 | 2.48 | 2.78 | 2.74 | 8.00 | 0 | — | — | — |
| 24 | 2.58 | 2.78 | 2.74 | 8.10 | 0.8 | 4.4 | 0.0 | 0.0 |
| 36 | 2.63 | 2.98 | 2.82 | 8.43 | 5.6 | 6.0 | 7.0 | 3.0 |
| 48 | 2.89 | 3.13 | 2.92 | 8.94 | 12.0 | 16.5 | 12.8 | 6.8 |
| 60 | 3.10 | 3.17 | 3.02 | 9.29 | 15.9 | 24.6 | 14.4 | 10.5 |
| 72 | 3.24 | 3.31 | 3.08 | 9.53 | 19.5 | 30.5 | 19.9 | 12.5 |
| 84 | 3.46 | 3.58 | 3.04 | 10.08 | 26.0 | 39.2 | 29.0 | 11.0 |
| 96 | 3.56 | 3.60 | 3.12 | 10.28 | 28.7 | 43.0 | 29.9 | 14.1 |
| 108 | 3.67 | 3.58 | 3.20 | 10.45 | 31.0 | 47.5 | 29.0 | 16.9 |
| 120 | 3.76 | 3.74 | 3.20 | 10.70 | 33.9 | 51.0 | 34.5 | 16.9 |
| 132 | 3.92 | 3.78 | 3.06 | 10.76 | 34.0 | 57.4 | 36.0 | 12.3 |
| 144 | 3.94 | 3.78 | 3.13 | 10.85 | 35.5 | 59.0 | 36.0 | 14.5 |
| 156 | 3.92 | 3.84 | 3.17 | 10.93 | 36.4 | 57.4 | 38.0 | 15.5 |
| 168 | 3.92 | 3.86 | 3.16 | 10.94 | 36.7 | 57.4 | 39.0 | 15.0 |

TABLE 4

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the leaf *C* of the experimental series No. 4

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | | Total length of petiole (marks 1—5) | | Growth rate of the petiole segments in % of their original values | | | |
|---------------|--|------|------|------|-------------------------------------|--------------------------|---|-----|------|------|
| | 1—2 | 2—3 | 3—4 | 4—5 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 | 4—5 |
| 0 | 2.33 | 2.09 | 1.86 | 2.29 | 8.57 | 0 | — | — | — | — |
| 12 | 2.33 | 2.09 | 1.90 | 2.31 | 8.63 | 0.7 | 0.0 | 0.0 | 2.5 | 1.0 |
| 24 | 2.33 | 2.09 | 1.99 | 2.31 | 8.72 | 1.8 | 0.0 | 0.0 | 7.0 | 1.0 |
| 36 | 2.41 | 2.06 | 2.06 | 2.42 | 8.95 | 4.4 | 3.5 | 0.0 | 10.8 | 6.0 |
| 48 | 2.48 | 2.17 | 2.00 | 2.43 | 9.08 | 5.8 | 6.5 | 4.1 | 7.8 | 6.7 |
| 60 | 2.60 | 2.27 | 2.08 | 2.50 | 9.45 | 10.4 | 11.8 | 8.5 | 12.0 | 9.3 |
| 72 | 2.68 | 2.25 | 2.08 | 2.55 | 9.56 | 11.8 | 15.0 | 8.0 | 12.0 | 11.3 |
| 84 | 2.76 | 2.29 | 2.10 | 2.55 | 9.70 | 13.6 | 18.5 | 9.5 | 13.0 | 11.3 |
| 96 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 108 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 120 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 132 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 144 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 156 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |
| 168 | 2.78 | 2.27 | 2.10 | 2.55 | 9.70 | 13.6 | 19.0 | 8.5 | 13.0 | 11.3 |

Fig. 4. Diurnal oscillatory movements of petioles of growing tobacco leaves (*Nicotiana tabacum* cv. Samsun). Curves represent the horizontal projection of oscillations circumscribed by the extreme points of petioles given by the coordinates x and y and transcribed in the orthogonal millimetre net. Numbers on curves describe the period of growth [h]. Data from Exp. 4.

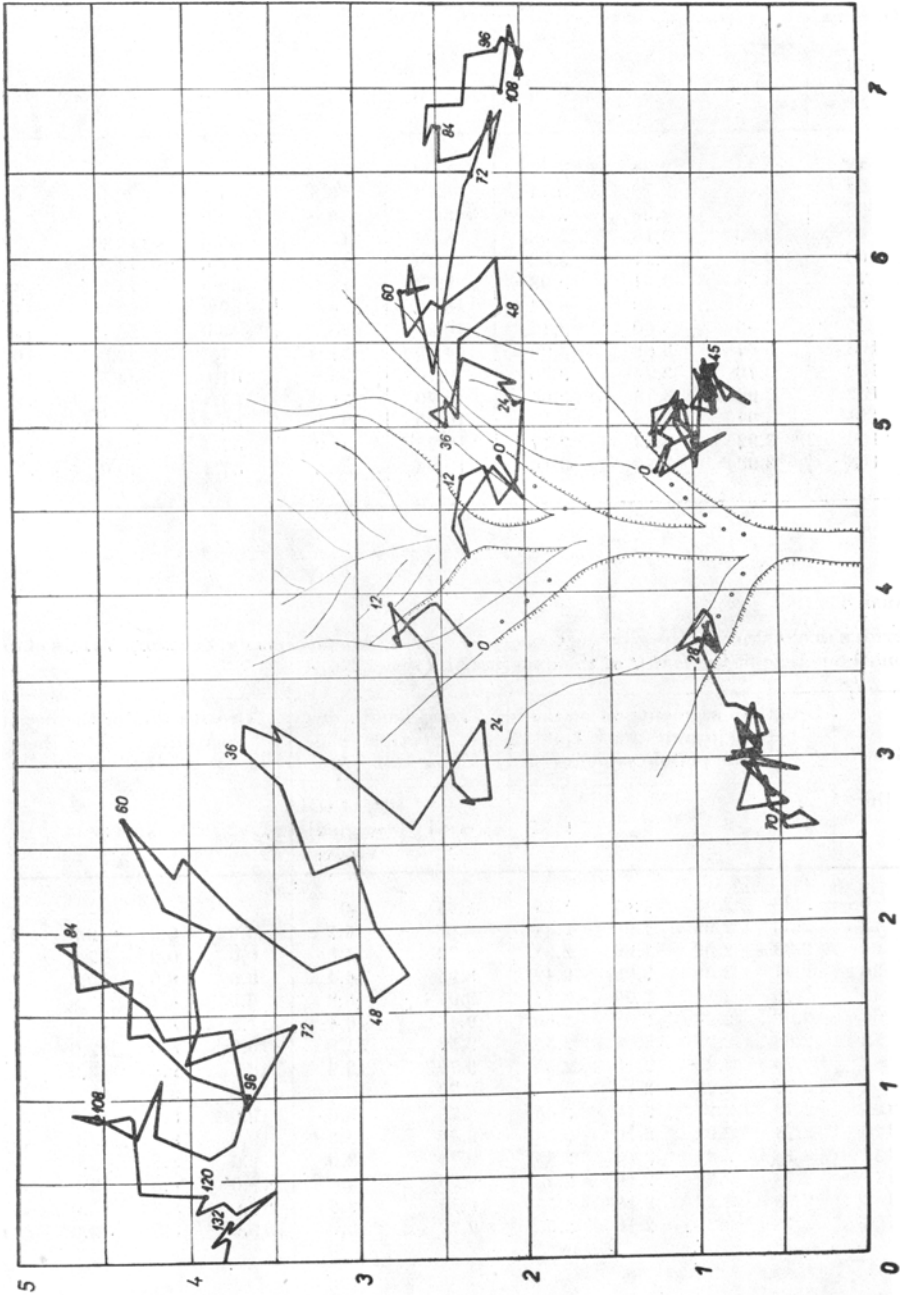


Fig. 5. Diurnal oscillatory movements of petioles of growing tobacco leaves (*Nicotiana tabacum* cv. Samsun). Curves represent the horizontal projection of oscillations circumscribed by the extreme points of petioles given by the coordinates x and y and transcribed in the orthogonal millimetre net. Numbers on curves describe the period of growth [h]. Data from Exp. 8.

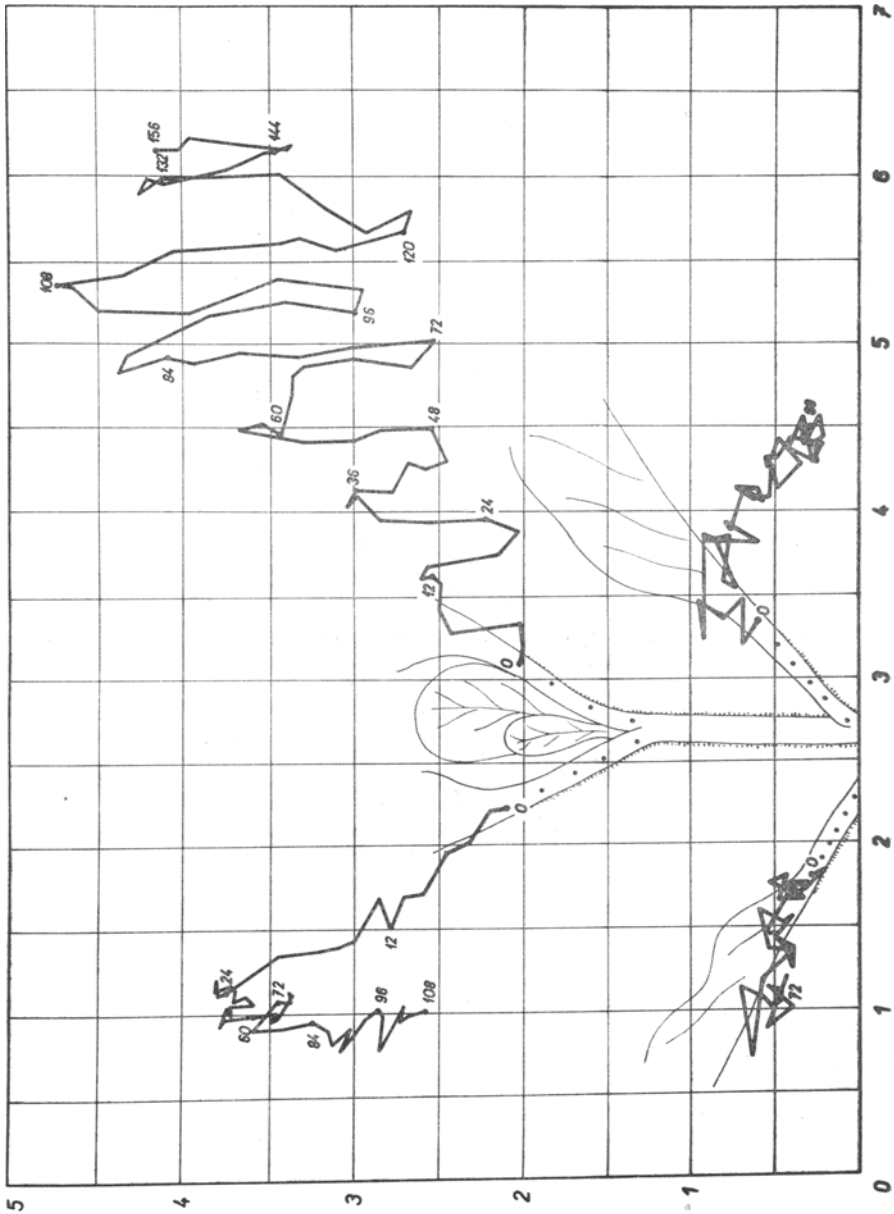


TABLE 5

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the young leaf *B* of the experimental series No. 4

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | | Total length of petiole (marks 1—5) | | Growth rate of the petiole segments in % of their original values | | | |
|---------------|--|------|------|------|-------------------------------------|--------------------------|---|------|------|------|
| | 1—2 | 2—3 | 3—4 | 4—5 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 | 4—5 |
| 12 | 2.36 | 2.88 | 3.01 | 3.24 | 11.49 | 0 | — | — | — | — |
| 24 | 2.48 | 2.88 | 3.03 | 3.43 | 11.82 | 3.0 | 5.1 | 0.0 | 0.4 | 6.0 |
| 36 | 2.60 | 3.08 | 3.04 | 3.41 | 12.13 | 5.4 | 10.4 | 7.0 | 0.5 | 5.7 |
| 48 | 2.83 | 3.12 | 3.10 | 3.59 | 12.64 | 11.2 | 20.0 | 8.3 | 3.4 | 10.8 |
| 60 | 2.96 | 3.20 | 3.16 | 3.59 | 12.91 | 12.5 | 25.1 | 10.8 | 5.0 | 10.8 |
| 72 | 3.14 | 3.49 | 3.26 | 3.78 | 13.67 | 19.0 | 33.0 | 20.7 | 8.4 | 16.9 |
| 84 | 3.32 | 3.51 | 3.24 | 3.76 | 13.83 | 20.9 | 41.0 | 21.9 | 7.9 | 16.4 |
| 96 | 3.37 | 3.60 | 3.30 | 3.96 | 14.23 | 24.3 | 42.9 | 25.0 | 9.5 | 22.3 |
| 108 | 3.41 | 3.62 | 3.32 | 4.00 | 14.35 | 25.0 | 44.8 | 25.6 | 10.3 | 23.2 |
| 120 | 3.43 | 3.71 | 3.35 | 4.04 | 14.53 | 26.4 | 45.2 | 29.0 | 11.4 | 24.8 |
| 132 | 3.51 | 3.71 | 3.34 | 4.04 | 14.60 | 27.0 | 48.7 | 29.0 | 11.0 | 24.8 |
| 144 | 3.51 | 3.73 | 3.34 | 4.04 | 14.62 | 27.5 | 48.7 | 29.5 | 11.0 | 24.8 |
| 156 | 3.51 | 3.76 | 3.34 | 4.05 | 14.66 | 27.7 | 48.7 | 30.7 | 11.0 | 25.0 |
| 168 | 3.51 | 3.76 | 3.40 | 4.13 | 14.80 | 28.2 | 48.7 | 30.7 | 13.0 | 27.2 |

TABLE 6

PETIOLE ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun). Values obtained from the petiole of the young leaf *B* of the experimental series No. 8

| Growth [h] | Length of segments on marked petiole in mm (mark 1 at the petiole joint) | | | | Total length of petiole (marks 1—5) | | Growth rate of the petiole segments in % of their original values | | | |
|---------------|--|------|------|------|-------------------------------------|--------------------------|---|------|------|------|
| | 1—2 | 2—3 | 3—4 | 4—5 | [mm] | % of the original values | 1—2 | 2—3 | 3—4 | 4—5 |
| 0 | 3.30 | 3.47 | 3.21 | 2.82 | 12.80 | 0 | — | — | — | — |
| 12 | 3.52 | 3.65 | 3.21 | 2.86 | 13.24 | 3.6 | 6.8 | 5.0 | 0.0 | 1.5 |
| 24 | 3.53 | 3.65 | 3.30 | 2.99 | 13.47 | 5.4 | 7.1 | 5.0 | 2.8 | 6.2 |
| 36 | 3.80 | 3.71 | 3.30 | 2.96 | 13.77 | 7.3 | 15.0 | 6.8 | 2.8 | 5.8 |
| 48 | 3.85 | 3.78 | 3.40 | 3.13 | 14.16 | 10.8 | 16.8 | 9.0 | 2.8 | 11.2 |
| 60 | 3.99 | 3.90 | 3.36 | 3.03 | 14.28 | 11.7 | 21.0 | 12.5 | 4.8 | 8.5 |
| 72 | 4.03 | 3.97 | 3.49 | 3.16 | 14.65 | 14.6 | 22.7 | 14.5 | 8.6 | 12.5 |
| 84 | 4.08 | 4.13 | 3.50 | 3.09 | 14.80 | 15.7 | 23.8 | 19.2 | 9.1 | 10.0 |
| 96 | 4.15 | 4.17 | 3.57 | 3.20 | 15.09 | 18.0 | 25.8 | 20.5 | 10.8 | 14.2 |
| 108 | 4.12 | 4.17 | 3.63 | 3.18 | 15.10 | 18.2 | 25.0 | 20.5 | 13.0 | 13.5 |
| 120 | 4.25 | 4.17 | 3.63 | 3.18 | 15.23 | 19.0 | 28.9 | 20.5 | 17.0 | 17.2 |
| 132 | 4.38 | 4.17 | 3.76 | 3.30 | 15.61 | 22.0 | 32.7 | 20.5 | 18.0 | 19.2 |
| 144 | 4.38 | 4.17 | 3.78 | 3.36 | 15.69 | 22.8 | 32.7 | 20.5 | 18.5 | 19.2 |
| 156 | 4.38 | 4.17 | 3.80 | 3.36 | 15.71 | 23.1 | 32.7 | 20.5 | 18.0 | 19.2 |
| 168 | 4.38 | 4.17 | 3.78 | 3.36 | 15.69 | 22.8 | 32.7 | 20.5 | 18.0 | 19.2 |
| 180 | 4.38 | 4.17 | 3.78 | 3.36 | 15.69 | 22.8 | 32.7 | 20.5 | 19.0 | 19.2 |

leaves. The results of the observation of old petioles (age-groups *C* and *D*) are not presented here because of their very limited growth.

Data describing the elongation of blade in the direction of longitudinal axis measured in lamina intervals are summarized in Tab. 7. Figure 7 shows the distribution of elongation and the shift of the zone of maximal elongation of blade during the development of the leaves. Details concerning the method of evaluation of cinematographic records and their graphical representation are discussed in the next chapter.

TABLE 7

DISTRIBUTION OF THE RATE OF LAMINA ELONGATION of the growing tobacco leaf (*Nicotiana tabacum* cv. Samsun)

Average length of lamina intervals obtained by evaluating of film-records of the six young leaves of *A* and *B* type.

| Growth [h] | Midrib intervals delimited by the principal lateral veins. Interval 1 is at the lamina base. <i>a</i> – length in mm, <i>b</i> – in % of the original value | | | | | | | | | | | |
|---------------|---|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | |
| | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> |
| 0 | 2.07 | — | 3.94 | — | 6.84 | — | 9.82 | — | 12.89 | — | 19.79 | — |
| 24 | 1.98 | 22.3 | 4.54 | 34.9 | 8.35 | 22.2 | 12.42 | 38.4 | 16.43 | 46.6 | 25.22 | 28.8 |
| 48 | 2.68 | 53.1 | 6.02 | 77.0 | 11.32 | 74.1 | 16.73 | 87.9 | 21.41 | 77.0 | 31.24 | 54.6 |
| 72 | 3.22 | 102.6 | 7.93 | 150.0 | 14.32 | 116.4 | 21.16 | 141.0 | 26.45 | 114.0 | 34.06 | 57.6 |
| 84 | 3.47 | 165.6 | 9.04 | 237.6 | 17.20 | 195.5 | 26.15 | 241.0 | 31.75 | 180.8 | 40.21 | 103.0 |

Discussion

The diurnal oscillatory movements of the petioles of growing leaves of tobacco in their horizontal projection were found similar to those described by NOVÁK (1964) and NOVÁK and ŠPURNÝ (1968). An approximately 12-h period of oscillations was distinct for young leaves from age-groups *A* and *B* (Figs. 2 to 5). The maximal vertical amplitudes of oscillations of the youngest leaves during their maximal elongation were about 2 mm. The oscillations

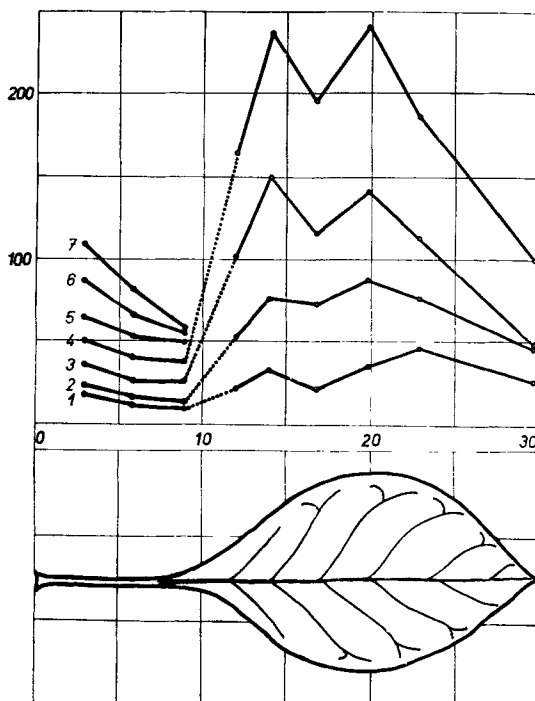


Fig. 6. Distribution of the rate of petiole and lamina elongation of tobacco leaf (*Nicotiana tabacum* cv. Samsun). Abscissa: length of the organ in mm, ordinate: elongation in % of the original length.

of old leaves (age-groups *C* and *D*) were irregular with the maximum amplitudes of several tenths of a millimetre. The range of amplitudes of oscillations and their regularity decreases during leaf development. Oscillations disappear when the elongation terminates. The rate of elongation of petioles is dependent on the development of the leaves. Calculated on the basis of the original length, the elongation of petioles of very young leaves (*A*) was 91%, of young leaves (*B*) 31.7% and of old leaves (*C*) less than 20%. The

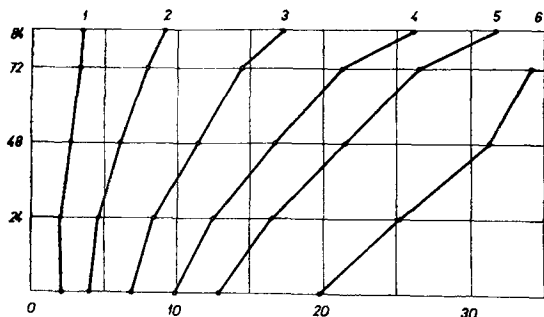


Fig. 7. The shift of zones of maximal elongation of tobacco leaf blade (*Nicotiana tabacum* cv. Samsun) during ontogenesis.

Length of segments 1-6 delimited by the principal lateral veins of leaf blade.

Abscissa: length of lamina segments [mm], ordinate: growth [h].

The zone of maximal elongation of both young and old petioles is located in the region between 2 and 4 mm from the base of the petioles (Tab. 1 to 6). With the increasing distance from the base, the elongation of petioles decreases up to one half of the recorded maximum rate. A close relation between the oscillatory movements and growth is apparent from these data. In the petiole, where the epicentrum of movements lies, the oscillations are small, several tenths of a millimetre, but at a distance of 30 mm corresponding to the length

of young leaf (*B*), the tip of blade may circumscribe a helix with a maximum amplitude of 5 mm in a horizontal projection.

The results describing the localization of the zone of maximal elongation of young leaves near to tip are in agreement with earlier findings (AVERY 1933, FRIMMEL 1954). Figure 6 shows that the minimum elongation of blade at the beginning of the experiment was situated in this region (see curve for the first day). During the further development of leaves, the zones of

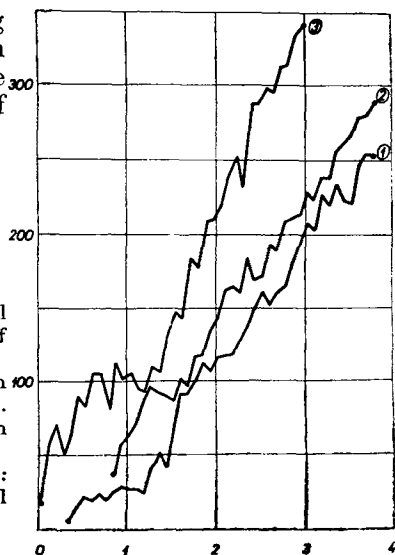


Fig. 8. The course of elongation of the lamina interval delimited by the 2nd and 3rd principal lateral vein of tobacco leaf. (*Nicotiana tabacum* cv. Samsun).

Periodical changes of length caused by optical distortion are negligible because of small oscillations in this zone. Illustrated according to original records of leaves from age-group *A* (1-3).

Abscissa: growth period of lamina in days, ordinate: changes in length of intervals expressed in % of original values.

growth are shifted nearer to the middle part of the blade and to the petiole (see the curve for the second day). The distance between the principal lateral veins in these regions increased 2.5 fold. Due to the very high rate of elongation, oscillating leaves moved periodically to and from the plane of the lens. These changes of distance of the object cause distortion of its size on photographic records (SPURNÝ and NOVÁK 1962). This variation shows a regular twelve hour cycle and was eliminated by the classification only of those records which were taken in periods corresponding to the multiples of a 12 h interval. The elimination of this effect involving a time-absorbing calculation of corrections (SPURNÝ 1964) was not justified. The growth curve recorded in the region close to the petiole does not show a periodical variation because of small oscillations (Fig. 7).

The zone of maximal elongation, which is localized in young leaves near to the blade tip, proceeds gradually in maturing leaves to the middle region of the blade and to the petiole. The growth rates of petioles were found generally lower than those of blades. They can be expressed in hundreds of millimetres ($4.8 \times 10^{-2} \text{ mm h}^{-1}$) for petiole; half of these values were recorded in their apical regions close to the blade. One degree higher growth rates were found for leaf lamina ($3.2 \times 10^{-1} \text{ mm h}^{-1}$). The maxima of oscillatory amplitudes circumscribed by the terminal points of petioles of young leaves (A) varied between 1 and 2 mm. The projection of these values to the blades suggest the theoretical oscillation of the tips of leaves of about 5 mm. However, in our previous experiments the oscillation maxima of leaf tips of similar age were found to be 15 mm (NOVÁK 1964). This difference indicates that another oscillatory momentum participates in the registered total amplitudes of oscillations. The already-mentioned dependence of oscillations on the growth can be used to localize the source of these secondary oscillations. According to the results presented above, the zones of maximal elongation of leaves are localized in the middle region of the blades where the maxima of oscillatory amplitudes also occur and this may be identified as the secondary centrum of oscillatory movements. The final amplitude circumscribed by the tip of the blades is a sum of both partial amplitudes. This oscillatory system is described in Fig. 9 where a young leaf (A), about 30 mm long is presented in the phase of maximal blade elongation. Active meristems are located around point B_0 . The vertical oscillation of the leaf is caused first of all by the elongation of the base of the petiole (point 0). The maxima of these amplitudes reach the extreme points A_m and B_m . The experimental values of these amplitudes measured at the apical end of the petiole varied between 1 and 2 mm. Such amplitudes in the absence of any other oscillatory momentum would cause movements of the blade tips between the two extreme points C — a distance that corresponds to the maximum amplitude of 5 mm. The actual maxima, however, were found about three times higher. 15 mm. It is assumed that the highest rates of elongation recorded in the region around point B_0 induce secondary oscillations which increase the amplitude of the blade tip up to the values found experimentally.

This explanation is supported by a visual analysis of the cinematographic records repeatedly projected as an infinite loop. Using this kind of projection the significant oscillatory movements in the region around point B_0 were revealed.

The oscillations of tobacco leaves can be defined as growth movements which consist of two integral parts: of oscillations originating at the base of the petiole and of oscillations of growing leaf blade localized in the meristematic zone in the middle part of the blade and gradually moving toward its base. It has not been possible to determine to what extent phototropic movements of blade participate in this complicated system. However, the registration of oscillations of blades by the cinematographic method may, in contrast to petioles, be influenced by many other factors.

In an integral plant system some other factors, such as oscillatory movements ("circumnutation") of stem (GUREVICH and IOFFE 1968), must be taken into account. It seems probable that coordinated and synchronized oscillatory mechanisms of separate organs are a part of a system which participates in the transfer of information in plants (GUREVICH and IOFFE 1970). Attention has already been paid to the endogenous metabolic factors which

may induce oscillatory movements (BÜNNING and BLUME 1963, BÜNNING and MOSER 1968, BLUME 1961, KARVÉ and JAGAJINNI 1966, MILLET 1970) and an attempt made to explain the autonomous periodicity of oscillations by variation in the production of auxin and by its uneven distribution in the lower and upper part of petiole (YIN 1941). Another possibility, *i.e.* that oscillations originate during orientated tropical growth when the deviations from the plagiotrophic direction are corrected by a feedback mechanism, cannot be ignored. The schema of such a self-regulating system has already been proposed for the geotropical growth of roots of pea seedling (SPURNÝ 1968 a, b). The fact that there is no elongation without oscillation and *vice versa* is in agreement with this proposal.

Figures at the end of the issue.

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M. SPURNÝ, Ústav experimentální botaniky ČSAV, oddělení pro studium životních dějů filmem, Brno: Denní oscilační pohyby rostoucích listů tabáku (*Nicotiana tabacum* ev. *Samsun*). Biol. Plant. 14 : 14—27, 1972.

V předložené práci jsou sledovány faktory ovlivňující pravidelnost trajektorie oscilačních pohybů rostoucích listů tabáku (*Nicotiana tabacum* ev. *Samsun*) registrovaných sběrnou filmovou metodou (obr. [2—3]). Detailně byly sledovány oscilační pohyby rostoucích řapíků listů a zvláště jejich čepelí (tab. 1—6, obr. [2—5]). Velikost amplitud oscilačních pohybů v horizontálním průmětu byla porovnána s polohami zón nejrychlejšího dloužení a s hodnotou růstových rychlostí v řapíku a čepeli během ontogeneze listů (tab. 7—11, obr. [6—8]). Zóny nejrychlejšího dloužení řapíku se nacházejí v těsné blízkosti kloubu řapíku (2—4 mm), směrem k čepeli dloužení poklesá až na polovinu maximálních hodnot. V rostoucí čepeli se posunuje zóna maximálního dloužení od špičky k bázi. V době největšího růstu jsou meristémy lokalizovány ve středu čepelce a v dalším vývoji se posunují k její bázi (obr. 6).

V řapíku kolísá růstová rychlost řádově v setinách milimetrů za hodinu ($4,8 \times 10^{-2}$ mm h⁻¹), v čepeli jsou zjištěné rychlosti dloužení v průměru o jeden řád větší ($3,2 \times 10^{-1}$ mm h⁻¹).

Výsledky potvrzují základní tezi o spojitosti oscilací s dlouhivým růstem: čím mohutnější dlouhivý růst orgánu, tím lze očekávat větší amplitudy oscilací. Naopak, s ustávajícím růstem odeznívají i oscilační pohyby.

Byly porovnávány obě metody registrace oscilačních pohybů listů tabáku opisované jednak špičkou listové čepelce, jednak krajními body vyznačenými na řapíku [obr. 9]. Ukazuje se, že druhý způsob registrace (dle oscilací řapíku) odstraňuje nepravidelnosti trajektorie dané druzhivými pohyby čepelce a eventuálně fototropickými pohyby listu. V rámci celé rostliny k tomu ještě přistupují cirkumnutace osy (GUREVIČ a IOFFE 1968, 1970).

Je diskutována možnost interpretovat oscilační pohyby rostoucích listů v rámci systému plagiotropicky řízeného dlouhivého růstu, kde odchylky značí zpětně vazebné opravy směru, obdobně jak to navrhl autor pro geotropicky řízený růst klíčného kořene hrachu (SPURNÝ 1968 a, b).

M. SPURNÝ
DIURNAL OSCILLATORY MOVEMENTS OF LEAVES

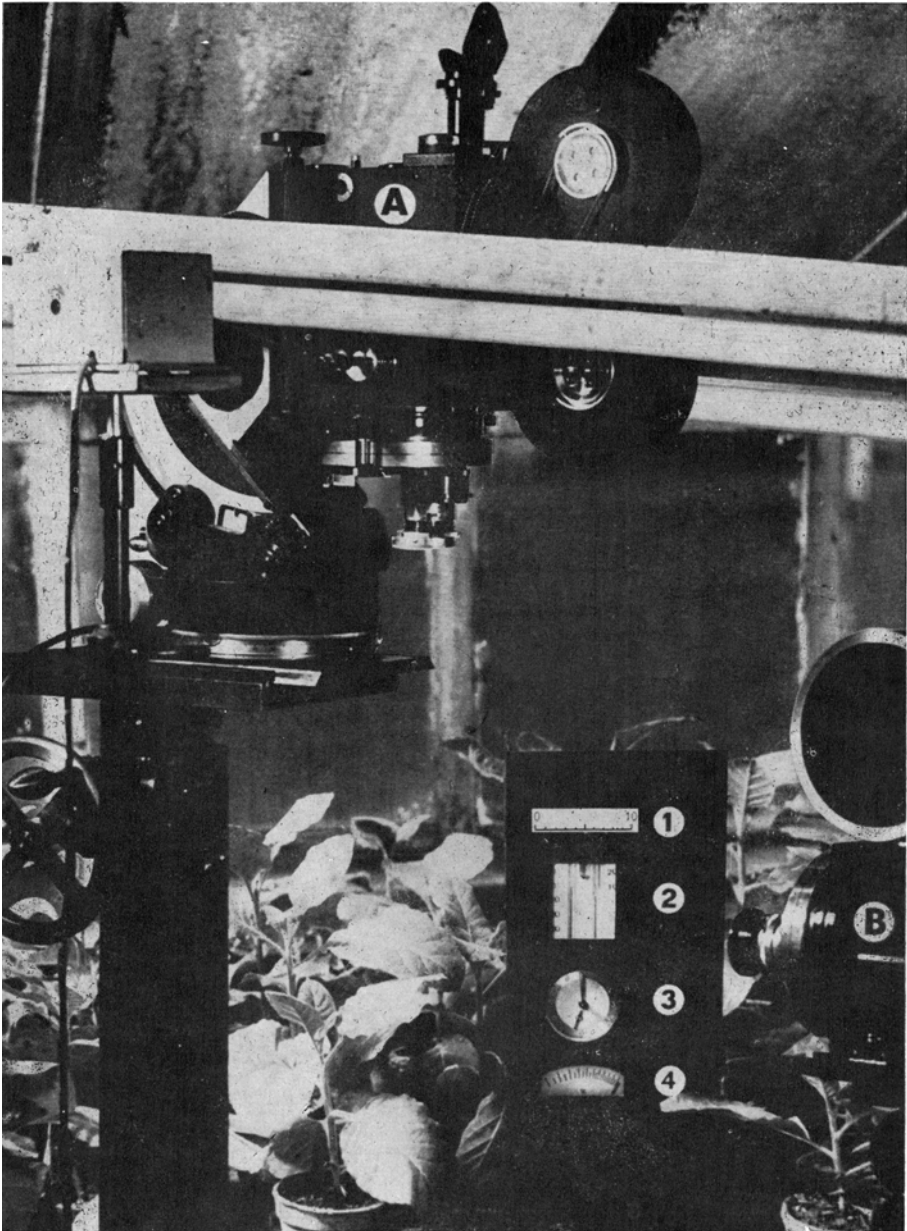


Fig. 1. Cinematographic apparatus for registration of oscillatory movements of tobacco leaves. *A*, *B* = moving film picture camera Cinephone 35 mm, recording the vertical and horizontal projections of oscillations. Diminution marks (1), temperature (2), time (3) and humidity (4) are registered simultaneously with the object.

M. SPURNÝ
 DIURNAL OSCILLATORY MOVEMENTS OF LEAVES

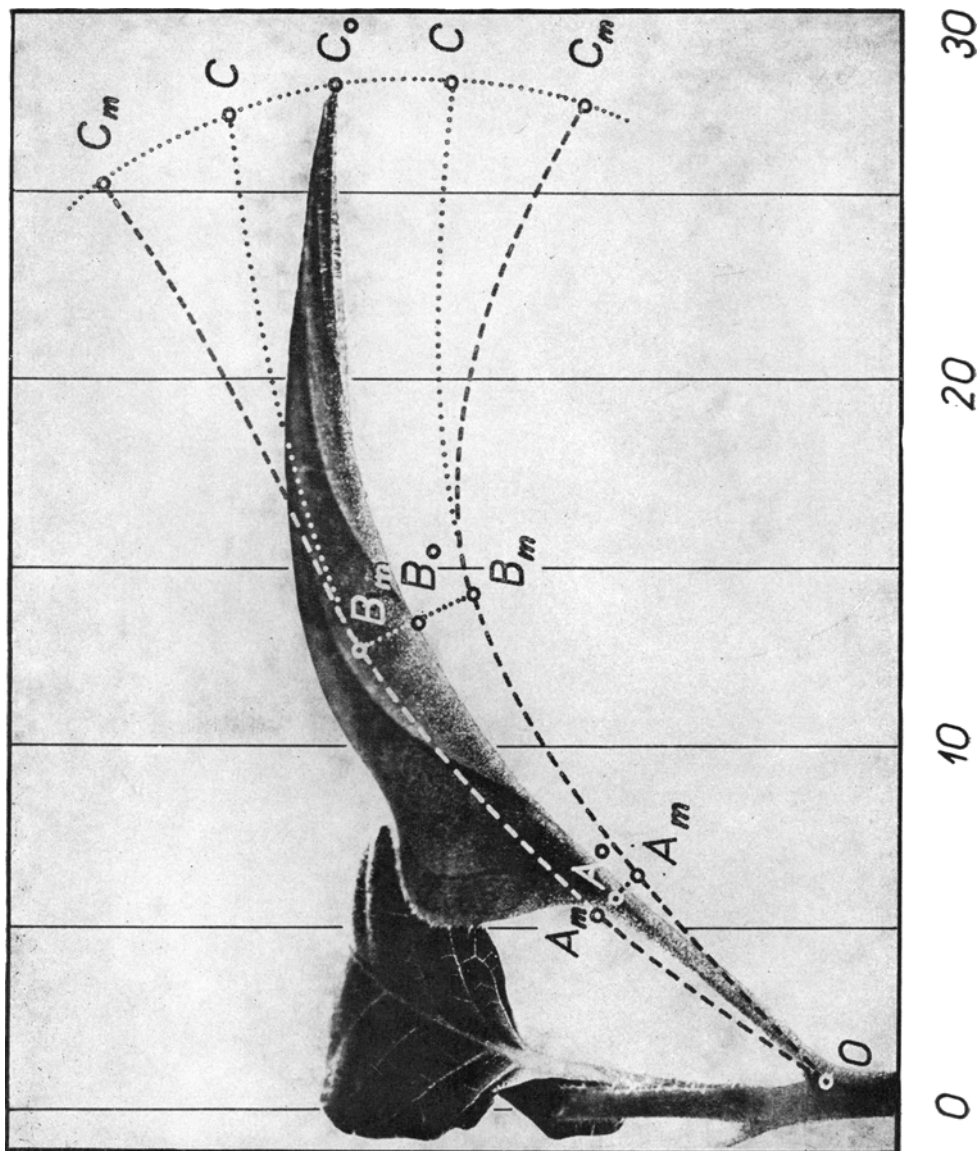


Fig. 9. Vertical oscillation of growing tobacco leaf (*Nicotiana tabacum* cv. Samsun) in horizontal projection.

O = base of petiole, OA_0 = length of petiole, B_0 = location of the zone of extensive elongation and centrum of the secondary lamina oscillations, C_0 = tip of lamina, C = erroneous extrapolation of oscillation maximum (see text for explanation), A_m , B_m , C_m = oscillation maxima of separate parts of leaf. Abscissa: length of leaf [mm], ordinate: oscillation amplitudes [mm].