

## Comparative Analysis of Growth and Movements of the Aboveground Parts in Some Deciduous Woody Species

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**Abstract.** Vertical projections of nutation movements in the epicotyls of sessile oak, Turkey oak, horse chestnut and hypocotyls of European beech were recorded by means of photography and time-lapse cinematography at the early stages of their ontogeny. Attention was paid to the kinetics of growth rate, diameter of the lower part of the elongating zone, and the form, amplitude and frequency of nutation turns. At the beginning of ontogeny the vertical projection of the movements of all woody species under study was represented by irregular curves, followed by elliptical trajectories, particularly when reaching the maximum growth rate. The highest average growth rate was recorded in horse chestnut, followed by oak, and the lowest values were exhibited by beech. As to the size of amplitudes opposite results were obtained. The frequency of turns proved to be a less sensitive parameter characterizing the movement. It is suggested that the geoccontrol system of horse chestnut is more effective than that of oak and, especially, of beech.

The growth and nutation oscillations of the aboveground parts were investigated and reported in model herbaceous plants (ČALÁBEK 1971 a, b, BRITZ and GALSTON 1983), in the case of woody species some conifers were involved (SPURNÝ 1975). Experiments were performed to study nutation oscillations associated with the growth of roots in pea and maize (SPURNÝ 1973, PILET 1983) and in oak (SPURNÝ *et al.* 1978). In the aboveground parts of seedlings of deciduous woody species no growth and oscillation movement analysis has been performed up to now.

The findings on nutation movements of plants, including deciduous woody species, their causes and mechanisms are of good use for elucidating growth regularities, as well as for explaining some processes associated with the transport of nutrients, metabolites and many other active substances.

The aim of the present paper is to analyse the kinetics of the growth of the aboveground parts of oak, chestnut and beech seedlings at the early stages of ontogeny and to characterize their movements expressed by the form, frequency and amplitude of turns.

### MATERIAL AND METHODS

The achenes of sessile oak (*Quercus sessilis* EHRH.), Turkey oak (*QUERCUS cerris* L.), European beech (*FAGUS silvatica* L.) and the nuts of horse chestnut (*Aesculus hippocastanum* L.) were stratified in a refrigerator in moist sand at 5 °C. Under these conditions the first phase of germination took place. The investigation of growth continued at the average temperature of 23 °C  $\pm$  2 °C, in the dark. Nutation movements of the aboveground parts of seedlings were recorded by means of a cinephone camera and a photographic apparatus Magnola. For their recording the method of light point was used intended for investigation of model seedlings (CALÁBEK 1966). The cinematographic recording was taken on ORWO NC 3, for the photographs plates ORWO MO 1 and paper FOMAPAN were used.

The trajectory and parameters of the movement were evaluated measuring photographic and cinematographic recordings. The exposure was 2,3 and/or 6 h. The evaluation involved the form, frequency ( $t\ h^{-1}$ ) and amplitude (mm) of nutation turns. The growth rate ( $mm\ h^{-1}$ ) and diameter of epicotyls and hypocotyls in the lower part of the maximum elongation zone (mm) were measured at regular intervals (3 to 12 h), directly on the plant subjects under investigation. The maximum elongation zone was marked with India ink. During ontogeny of seedlings nutation movements and growth were investigated, starting from the phase of epicotyl and/or hypocotyl erection to the vertical position. It occurred at the lengths of 40, 30, and 15 mm in oak, chestnut and beech, respectively.

### RESULTS AND DISCUSSION

The above-mentioned parameters of the growth and nutation movements were analysed in 53, 32, 20 and 25 seedlings of sessile oak, Turkey oak, horse chestnut and European beech, respectively. The evaluation lasted 12 days, during the long growth period. For the statistical evaluation of the parameters the standard deviations were calculated. With regard to the heterogeneity of the epicotyl growth in oak, the seedlings of sessile oak were divided into three groups, in accordance with the maximum length attained. In sessile oak the length attained 105  $\pm$  14 mm (Ist group, 28 per cent of seedlings), 140  $\pm$  19 mm (IIInd group, 58 per cent of seedlings), 179  $\pm$  20 mm (IIIrd group, 14 per cent of seedlings). In Turkey oak maximum length was 128  $\pm$  31 mm (Ist group, 42 per cent of seedlings), 162  $\pm$  27 mm (IIInd group, 58 per cent of seedlings). The growth of epicotyls continued very slowly and the movement was measurable with difficulty. The growth of beech hypocotyls was essentially well-balanced, the average length attained 61  $\pm$  9 mm on the average. For technical reasons the investigation of horse chestnut seedlings was interrupted at the length of 320 mm. Nevertheless, the seedlings continued growing. During the whole period under study (except the last slow phase) the average growth rate amounted to 0.45  $mm\ h^{-1}$  (Ist group), 0.71  $mm\ h^{-1}$  (IIInd group), 0.80  $mm\ h^{-1}$  (IIIrd group), 0.65  $mm\ h^{-1}$  (on the average in all groups) in sessile oak, 0.52  $mm\ h^{-1}$  (Ist group), 0.63  $mm\ h^{-1}$  (IIInd group), 0.58  $mm\ h^{-1}$  (on the average in both groups) in Turkey oak, 1.23  $mm\ h^{-1}$  in horse chestnut, 0.33  $mm\ h^{-1}$  in beech. To evaluate the growth and movement parameters during ontogeny, six growth intervals were determined, according to the course of changes in growth rate (Table 1, Fig. 2).

TABLE 1

Growth analysis of *Quercus sessilis* EHRH. (group I [a], group II [b], group III [c]), *Quercus cerris* L. (group I [d], group II [e]), *Aesculus hippocastanum* L. [f], *Fagus sylvatica* L. [g] seedlings during ontogeny

Individual parameters	Length intervals of epicotyls or hypocotyls [mm]					
<b>a</b>	40-49	50-79	80-89	90-99	100-109	110-119
Mean time [h]	22.73	58.44	77.31	96.54	146.54	289.43
Growth rate [mm h <sup>-1</sup> ]	0.44±0.09	0.56±0.10	0.53±0.10	0.52±0.09	0.20±0.05	0.07±0.02
<b>b</b>	40-59	60-79	80-99	100-119	120-139	140-159
Mean time [h]	40.82	77.18	102.18	123.23	150.26	304.10
Growth rate [mm h <sup>-1</sup> ]	0.49±0.12	0.55±0.10	0.80±0.16	0.95±0.11	0.74±0.12	0.13±0.06
<b>c</b>	40-59	60-79	80-99	100-129	130-159	160-199
Mean time [h]	34.48	61.88	86.27	114.31	151.81	289.74
Growth rate [mm h <sup>-1</sup> ]	0.58±0.15	0.73±0.16	0.82±0.15	1.07±0.20	0.80±0.16	0.29±0.10
<b>d</b>	40-59	60-79	80-99	100-119	120-139	140-159
Mean time [h]	54.05	92.51	122.81	161.27	200.49	250.49
Growth rate [mm h <sup>-1</sup> ]	0.37±0.10	0.52±0.11	0.66±0.10	0.52±0.17	0.51±0.13	0.40±0.10
<b>e</b>	40-59	60-79	80-99	100-119	120-159	160-189
Mean time [h]	40.00	71.75	98.07	126.64	189.09	269.50
Growth rate [mm h <sup>-1</sup> ]	0.50±0.18	0.63±0.16	0.76±0.12	0.70±0.13	0.56±0.15	0.42±0.09
<b>f</b>	30-59	60-99	100-159	160-199	200-259	260-320
Mean time [h]	56.60	98.30	158.91	173.20	206.20	245.94
Growth rate [mm h <sup>-1</sup> ]	0.53±0.20	0.72±0.11	0.99±0.16	2.10±0.34	1.82±0.41	1.51±0.27
<b>g</b>	15-24	25-34	35-44	45-54	55-65	65-70
Mean time [h]	45.45	85.85	110.24	131.52	185.09	285.09
Growth rate [mm h <sup>-1</sup> ]	0.22±0.06	0.25±0.06	0.41±0.10	0.47±0.08	0.28±0.08	0.05±0.02

The values of mean time are added from the first interval. The values of growth rate are expressed for individual intervals.

Statistical evaluation of growth rate is analogous to Table 2.

The maximum amplitude values corresponded to the phases of the maximum growth rate (Table 2, Fig. 1).

At the beginning of growth the amplitude and frequency of movement were detectable only with difficulty, because the movement was considerably complicated, irregular and disturbed. The vertical axes of nutation turns in all the woody species under study and individual seedlings were shifted to the side, and/or the movement was not manifested by regular turns at all. This course may be provoked by the erection of the apex from the horizontal position between cotyledons, or by turning by 180° (Fig. 2). In the woody species a positively geotropic curvature of spruce apex and negative curvature of pine apex are well-known (HŘIB and LÁNÍČKOVÁ 1986). In some herbaceous plants, the positively geotropic curvature of the apex was experienced as related to growth substances (KÖHLER 1978, KRSEK and ŠEBÁNEK 1981, BRITZ and GALSTON 1982). During germination all the woody species under

investigation exhibited positively geotropic curvature of the apex. Nevertheless, seedlings with erected apex were selected visually for the study of growth movements. Other reasons for the shift of the movement to the side may be, for example, unequal thickening of the stem below the zone of elongation and/or curvature of different causes. A photoperiodical stimulus

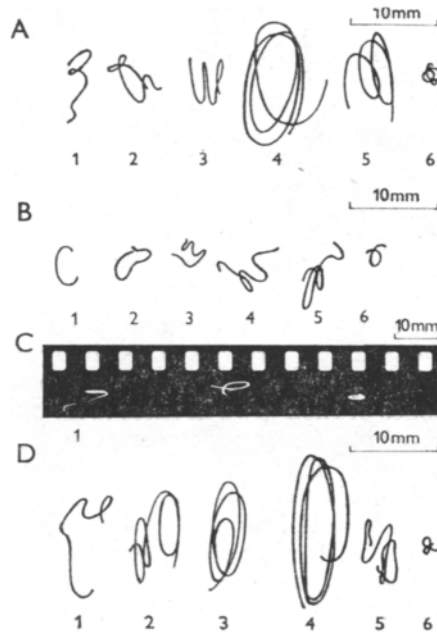


Fig. 1. Vertical trajectories of epicotyl nutation movements (A) *Quercus sessilis* EHRH. (the seedling No. 25, group III), (B) *Quercus cerris* L. (the seedling No. 3, group II), (C) *Aesculus hippocastanum* L. (the seedling No. 5), and of hypocotyl nutation movements (D) *Fagus sylvatica* L. (the seedling No. 25) during ontogeny. The recordings A,B,D represent the interval length 6 h, the recording C represents only 3 h. Initial length of aboveground parts in the recordings 1, 2, 3, 4, 5, 6 amounted to 49, 62, 99, 125, 142, 175 mm (A), 42, 60, 86, 105, 125, 141 mm (B), 165 mm (C), 24, 34, 43, 50, 55, 67 mm (D), respectively.

was not probable, because the movement was recorded in the dark and under the same conditions as in the later period, when the turns of nutation movement were regular. The sideway movement may also be associated with an oriented transport of nutrients and growth substances from the cotyledons to the aboveground part. Furthermore, when evaluating the parameters of growth and movement it can be considered that the growth and movement were investigated in etiolated plants with supported elongation growth and thus growth and movement parameters were probably slightly changed in comparison with the seedlings grown in the light.

During later phases of ontogeny, the seedlings of the woody species under study exhibited changed amplitudes, in accordance with the increase of growth rate in such a way that they increased successively up to the phase of the maximum growth and the vertical movement projections acquired

TABLE 2

Nutation movement parameters of *Quercus sessilis* EHRH. (group I [a], group II [b], group III [c]), *Quercus cerris* L. (group I [d], group II [e]), *Aescullus hippocastanum* L. [f], *Fagus sylvatica* L. [g] seedlings at the stage of the maximum growth rate

Seedlings	Amplitude [mm]	Frequency [t h <sup>-1</sup> ]
a	6.5 ± 1.3	0.50 ± 0.05
b	10.3 ± 1.7	0.50 ± 0.05
c	12.5 ± 2.5	0.47 ± 0.10
d	5.0 ± 2.0	0.44 ± 0.07
e	5.2 ± 1.8	0.46 ± 0.04
f	6.0 ± 2.5	0.54 ± 0.04
g	16.0 ± 4.0	0.58 ± 0.05

Each value represents the mean ± standard deviation;  $n=15$ [a],  $n=31$ [b],  $n=7$ [c],  $n=13$ [d],  $n=58$ [e],  $n=20$ [f],  $n=25$ [g].

a normal elliptic form. Later, the amplitude decreased rapidly along with the retardation and cessation of growth. The changes of amplitude during ontogeny exhibited an analogous character in all the seedlings under study, with regard to the changes of their growth rates (Fig. 1). As to the irregularity of movements at the beginning of ontogeny, the frequency of turns was exactly determined up to the phase with the maximum amplitude (Table 2). Nevertheless, the recording of vertical projections indicates that the frequency of turns was lower at the initial stages of ontogeny and increased when attaining a regular movement, though the maximum amplitude had not yet been reached. The direction of the turns in all woody species under study was predominantly clockwise, but changes in the direction of rotation were also recorded in some cases. While the seedlings of sessile oak differed in the growth rate (both the average rate during ontogeny and the maximum rate) and in the total length (see groups I, II, III), more significant differences were recorded in the amplitudes but not in the frequency of turns. In the frequency of turns, there was no considerable response even to growth differences between the woody species. Nevertheless, some differences in the frequency of turns were reported by other authors (SPURNÝ 1975), and/or this dependence has not been manifested (CALÁBEK 1962, SPURNÝ 1968).

Much more apparent differences were observed in the maximum amplitude in the woody species under study, which was the smallest in fast-growing horse chestnut and the largest in the hypocotyl of beech. The results obtained can be evaluated from the point of view of effectiveness of the geocontrol systems of the seedlings under investigation. While the average (as well as the maximum) growth rate of chestnut was nearly 4times higher than in beech, the maximum amplitude of beech was 3times the maximum amplitude of chestnut. The amplitude of sessile oak was higher than that of Turkey oak but their average growth does not differ greatly (the average of all groups was 0.65 and 0.58 mm h<sup>-1</sup> in sessile oak and Turkey oak, respectively). The above-mentioned results indicate that the geocontrol system of chestnut balances the growth deviations from the vertical axis most effectively. A higher effectiveness was manifested in sessile oak than in Turkey oak and the lowest one was exhibited by beech.

Furthermore, one of the causes of different parameters may consist in different diameter and thus the area of the section of the aboveground organs in the zone responsible for movement and/or its length. With regard to the finding that the centre of movement is localized predominantly in the lower part of the elongation zone (SPURNÝ 1975), the average diameter of epicotyls attained the following values during ontogeny: in sessile oak (in the phases according to the group II) 1.92, 1.71, 1.59, 1.59, 1.53, 1.57 mm, in Turkey oak (in the phases according to the group II) 2.2, 2.2, 1.9, 1.8, 1.7, 1.7 mm, in horse chestnut 3.4, 3.2, 2.7, 2.6, 2.7, 2.7 mm. The differences between the species and during ontogeny indicate that a lower diameter of the organ may probably participate in the increase of the movement amplitude. This finding is in accord with the opinion that movement is caused by unequal growth on the opposite sides of the growing organ (CALÁBEK 1962). Inversely, the size of amplitude may be affected by a shortened representation of elongation zone in the total length of the aboveground part during ontogeny. At the initial stages of ontogeny of sessile oak the average length of the elongation zone amounted to about 50 %, at later stages to about 20 %. In chestnut 54 and 19 %, were exhibited, respectively.

The above-mentioned relations suggest that the dependence of the growth parameters and characteristics of movement of growing organs is rather complicated. Furthermore, nutation movements, the parameters of which are controlled by the growth rate, are not merely an accompanying manifestation of growth but they are a phenomenon which is considered to be independent to a great extent. They must be understood as a part of rhythmical processes in plant life, their essence being derived from rhythmical physiological manifestations. The resulting rhythm of the movement is a sum of a number of individual rhythms. It also concerns the rhythmical transcription of nuclear genome and thus cell division, likewise rhythmical manifestations of membranes (VAN DEN DRIESCHE 1980), especially in close association with phytohormones (MERTENS and WELLER 1983).

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*Fig. 2 at the end of the issue.*

#### BOOK REVIEW

HOLMAN, J., PELIKÁN, J., DIXON, A. F. G., WEISMAN, L. (ed.): POPULATION STRUCTURE, GENETICS AND TAXONOMY OF APHIDS AND THYSANOPTERA. (Proc. Internat. Symp. Smolenice, Czechoslovakia, Sept. 9—14, 1985. — VEDA, Bratislava/SPB Academic Publishing, The Hague 1987. XIV + 542 pp., 96 figs., Kčs 54,—.

The book is a collection of symposium papers, with all advantages and necessary weak points of such a type of publications. It brings a good overview of current topics in aphid and Thysanoptera research, presented or summarized by leading authorities. Comprehensiveness is sacrificed to being up-to-date.

The first major part (411 pages) contains 39 papers concerning aphids. Most of the papers deal with morphological and functional diversity of the aphid species, a fascinating aspect of the life of these insects. These works appear in the first three sections and are devoted to reproductive strategies and evolution, enzyme polymorphisms and genetics, and growth and morph differentiation. As aphid polymorphism is largely an adaptation to a host plant change, the papers may be of interest also to plant science specialists. Papers of the sections 5 and 6 discuss aphid identification, taxonomy and faunistics. Only two papers of section 4 (Ecology and population dynamics) directly concern the aphid-plant relationships.

The minor second part of the book contains 18 papers dealing with diverse aspects of Thysanopteran biology: taxonomy, determination, ecology, distribution and problems of sampling. Plant scientists will find much interesting information about the pests of agricultural crops in particular. Reading the book may be stimulative to those working in borderline field between plant science and entomology.

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