Investigations on the dormancy of *Fraxinus excelsior* L. buds

I. Sequence of growth period, correlated inhibition and rest of shoot apex in the annual cycle

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Abstract

The relation between the period of growth and the subsequent period of correlated inhibition and rest of the terminal bud on the main shoot of the 6-year-old *Fraxinus excelsior* trees was investigated. From July 21 to August 31, 1971, at ten-day intervals groups of 12 trees, each similar as regards the mean date of bud setting on the main shoot, were defoliated. The data of bud opening after defoliation was considered as index of the depth of dormancy. Statistical analysis demonstrated a rather strong correlation between the number of days after bud setting and the date of their opening after defoliation. The calculated regression curve reached its limit 65.4 days after bud setting, this empirically determining the duration of the period of correlated inhibition of buds of the given tree population. Rest of the terminal buds occurred, therefore, in particular trees at various times in dependence on the date of bud setting.

INTRODUCTION

The development of trees in the Temperate Zone occurs in annual cycles comprising periods of growth and dormancy correlated with the atmospheric changes (Doorenbos, 1953; Samish, 1954; Romberger, 1963; Kozłowski, 1971). The duration of the growth period influencing the height is a hereditary specific trait, but it varies in wide limits with the age of the tree and in dependence on the environmental conditions. In most trees the shoots elongate only during the part of the period when the weather conditions are favourable for growth. The end of growth and setting of buds are caused by correlative inhibition factors (Champagnat, 1965) and connected with internal changes in the

levels of nutrient or hormonal substances (Wareing and Phillips, 1970). For a certain time after setting, the buds are capable of growth, forming what is called proleptic shoots (Späth, 1912) in case of defoliation of the plant. This period of bud development is termed correlated inhibition, summer dormancy or predormancy. If, after defoliation, the buds do not start to break, they are considered to be in a state of rest, true dormancy or winter dormancy.

In investigations on young seedlings of a number of tree species it was found that rest occurs in many of them under conditions of short day (Wareing, 1956; Nitsch, 1957). In connection with this and under natural conditions the diminishing daylength in autumn is usually considered as the cause of bud rest (Wareing and Phillips, 1970). Some tree species, are, however, known (*Oleaceae*) which are relatively insensitive to changes in daylength, and yet their buds also pass through a period of rest. It was observed that in *Syringa vulgaris* the rest of axillary buds deepens gradually over the entire period of elongation growth of the shoot (Champagnat, 1951). In *Populus* $\times$ *berolinensis*, a representative of a genus known for its sensitivity to changes in daylength (Van der Veen, 1951; Witkowska-Żuk, 1970) it has been also found that in the terminal buds of shoots in various parts of the tree crown deep rest occurred gradually, along the line of bud setting from below towards the tree top. The rest was preceded by a period of correlated inhibition of similar duration for all buds (Witkowska-Żuk and Kapuściński, 1969).

The hypothesis that there exists a definite relation between correlated inhibition and rest has been discussed by numerous authors (Doorenbos, 1953; Libbert, 1961, 1964; Champagnat, 1965).

Investigations on the sequence of dormancy in *Fraxinus excelsior* reported in the present paper were undertaken in order to elucidate further the relation between correlated inhibition and rest in a species in which in preliminary studies it was found that it preserves its own rhythm of growth and dormancy, notwithstanding the photoperiodic conditions.

MATERIAL AND METHODS

The investigations were performed in the spring and summer of 1971 on six-year-old trees of *Fraxinus excelsior* spaced 50×90 cm on an experimental plot near the Agricultural Academy in Warsaw. The height of the trees was measured twice, before extension growth of the main shoot started in the spring and after it was completed in the autumn. The weather conditions in the course of the investigations are shown in Fig. 1.

From the beginning of April until autumn the state of the main shoots of the trees was observed at 3-day intervals and the following

Fig. 1. Weather conditions in Warsaw in 1971/72
 a — daylength, b — mean diurnal temperature, c — sum of diurnal precipitation.

dates were noted: a) of spring terminal bud-break (appearance of tips of leaves between the bud scales), b) of setting of the terminal bud (formation of greenish scales from the leaf base at the tip of the shoot) and c) of bud opening on the shoots after defoliation of the trees.

Finally the state of development of a given kind of buds in the group of defoliated trees was characterized by giving the number of shoots on which these buds have opened and the mean number of days after which they burst. For buds which did not open until autumn the date of their growth resuming was assumed as infinity (∞). In statistical analysis reciprocals of the number of days after which the buds opened were used. In order to avoid the inconvenient double characteristic of the state of bud development when comparing the data for several groups of trees, the theoretical number of days (T) was calculated, after which, on the average, break of all buds would occur on all shoots in the given group, according to the formula:

$$\frac{1}{T} = \frac{\frac{1}{t_1} + \frac{1}{t_2} + \dots + \frac{1}{t_n}}{N}$$

hence

$$T = \frac{N}{\frac{1}{t_1} + \frac{1}{t_2} + \dots + \frac{1}{t_n}}$$

where N — number of all shoots (or trees) in a group,

t — time of opening of a definite bud on each shoot expressed in days.

RESULTS

The data concerning tree height and the date of spring terminal bud-break and bud setting after the end of growth indicated wide differences of the traits examined between the individual trees in this even-aged population (Table 1). The differences in tree height reached 115 cm. Bud break on the particular trees occurred within 25 days beginning on 8 April, and their setting lasted from 2 June for a period of 35 days.

In order to establish whether there is a relation between the height of the tree and the period of its growth, the correlation coefficient (r) and linear regression (x^* and y^*) were calculated. A moderately strong correlation was found ($r = 0.670$) between the height of the tree measured in spring and the increment in the length of the main shoot. The higher the tree the greater was this increment (Fig. 2). On the other hand, only a rather weak, although significant ($r = 0.496$), correlation was noted between the height increment of the main shoot and the date

Table 1

Height and course of growth of main shoot of 6-year-old *Fraxinus excelsior* trees in 1971; data for 60 trees

Traits	Mean	Range observed
Height of trees before beginning of growth, cm	145±45	61—276
Yearly height increment of trees, cm	62±18	10—110
Height of trees after end of growth, cm	207±59	71—386
Date of terminal bud break	April 19±6	April 8—May 3
Date of terminal bud setting	June 18±10	June 2—July 7
No. of days of growth of main shoot	60±10	35—90

of terminal bud setting on it. On trees with a smaller growth increment the terminal bud was set earlier than on those with a larger increment (Fig. 3).

No correlation could be revealed between the height (or height increment) of the tree and the date of opening of its bud in spring ($r = 0.192$ and $r = 0.213$) as well as between the date of opening of the terminal bud in spring and the date of bud setting ($r = 0.279$).

Since a group of even-aged trees exhibiting various growth rhythms was available in which the differences in the time of bud setting reached 30 days, the whole material was divided into five groups of

Fig. 2. Height of tree before beginning of growth and yearly height increment of main shoot of 6-year-old *Fraxinus excelsior* trees in 1971

Coefficient of correlation and linear regression; $r = 0.6705^{**}$, $y^* = 23.2 + 0.268x$, where x and y = height of tree and yearly height increment, respectively.

Fig. 3. Yearly height increment of main shoot and date of terminal bud setting on it in 6-year-old *Fraxinus excelsior* trees in 1971

Coefficient of correlation and linear regression; $r = 0.496^{**}$, $y^* = 3.83 + 0.223x$, $x^* = 43 + 1.097y$, where x and y = yearly height increment and date of terminal bud setting, respectively.

12 trees each so that the mean date of terminal bud setting would be similar for all groups (June 18), and that in each group there would be trees with various dates of bud setting (from 2 June to 7 July). Every 10 days beginning with 21 July and ending with 31 August, one group was defoliated and opening of terminal and axillary buds was observed on main and lateral shoots. The results shown in Table 2 indicate, that

Table 2

Breaking of terminal bud on shoots of 6-year-old *Fraxinus excelsior* trees defoliated at various times after bud setting in 1971; at each date 12 trees were defoliated

Kind of shoot	Traits	Date of defoliation					
			July 21	July 31	August 10	August 20	August 30
Main shoot	No. of days between terminal bud setting and defoliation	Mean Range	33.9 14—49	43.0 24—59	53.8 44—64	60.5 44—79	74.6 63—89
	No. of opened buds		11*	9	2	0	0
	Opening after days	Mean Range	16.9 12—29	16.1 13—24	14.0 14	— —	— —
	Theoretical time of break of all buds, days		17.0	19.4	84.0	—	—
Lateral shoots	No. of opened buds		56*(11)**	25(6)	6(2)	0	0
	Opening after days	Mean Range	21.1 12—34	15.0 13—24	16.5 14—20	— —	— —

*) Opening of few axillary buds on shoots observed

**) In parentheses no. of trees (from among 12) on which buds opened.

Fig. 4. Period of time from terminal bud setting on the main shoot to tree defoliation and date of its opening after defoliation in 6-year-old *Fraxinus excelsior* trees in 1971

Coefficient of correlation and linear regression; a — defoliation on 21 July: $r = 0.682^{**}$, $y^* = \frac{1}{1126 - 15.8x}$; b — defoliation on 31 July: $r = 0.891^{**}$, $y^* = \frac{1}{1473.6 - 22.8x}$; c — defoliation on 21 July, and 31 July, and 10 August (jointly): $r = 0.735^{**}$, $y^* = \frac{1}{1171.7 - 17.9x}$; where x and y = number of days elapsed from terminal bud setting to tree defoliation and from defoliation to opening of terminal bud, respectively.

bud break occurred after a period of 12—34 days following defoliation, when this was done in July and the first half of August, but on a gradually diminishing number of trees and lateral shoots. Calculation of the coefficient of correlation between the time elapsed after terminal bud setting and tree defoliation and the time of opening of the same bud after defoliation demonstrated a moderately strong correlation ($r = 0.682$) for trees defoliated on 21 July and a rather strong correlation ($r = 0.891$) on 31 July. The course of the regression curves was similar

(Fig. 4a, b). On this basis the data of three successively defoliated tree groups in which bud break was observed were pooled, and an empirically graduated curve (Fig. 4c) was plotted. The results ($r = 0.735$) indicate that between the time elapsed from bud setting (i.e. the bud's age) and the possibility of its breaking there is a rather strong correlation. The regression curve reached its limit after 65.4 days, that is so many days after bud setting not one bud was capable of resuming growth.

DISCUSSION

Similarly as in others papers (Wareing and Phillips, 1970), bud break after defoliation was adopted as criterion of correlated inhibition; the lack of bud opening after this treatment was considered as a symptom of rest. The data of bud break was thus an index of the depth of dormancy.

From the experimental data obtained after defoliation repeated at equal time intervals for trees of similar groups, but differing within the group in the time of terminal bud setting on the main shoot, it is seen that rest occurred not earlier than after 49 days and not later than after 59 days of correlated inhibition. The empirical curve representing the relation between the age of the buds and their ability of growth reaches its limit after 65 days, this determining the duration of the period of correlated inhibition of the buds in the given population of *Fraxinus excelsior*. Since bud setting occurred on the average on 18 June, theoretically the buds would be on the average in a state of rest on 22 August. This was confirmed by the results of defoliation on 20 August after which not one bud opened. Even earlier, after defoliation on 10 August, on most trees no bud break was noted (83%), although daylength was about 15 h and air temperature was favourable to growth still for at least 34 days, that is the longest observed period after defoliation in which buds could grow.

The results here presented indicate that bud rest occurred at various times in the particular trees of this even-aged population of *Fraxinus excelsior*, and the beginning of rest depended on the date of bud setting preceding it, that is on the length of the period of correlated inhibition. It may, therefore, be supposed that the progress of rest in the buds of *Fraxinus excelsior* was not dependent on external conditions but associated with internal changes occurring in the plants during correlated inhibition.

The results discussed above and those earlier obtained in investigations on bud dormancy on shoots in various parts of the tree crown of *Populus × berolinensis* (Witkowska-Żuk and Kapuściński, 1969) indicate that in both these tree species, so different as regards

sensitivity to day-length, a relation exists between the duration length of correlated inhibition of the buds and the coming of their rest.

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Badanie nad spoczynkiem pączków Fraxinus excelsior L.

I. Następstwo okresu wzrostu, spoczynku względnego i spoczynku głębokiego wierzchołka pędu w cyklu rocznym

Streszczenie

Do doświadczeń przeprowadzonych w 1971 roku użyto 6-letnich drzewek jesiona wyniosłego. Wysokość roślin, termin wiosennego rozwoju pączka wierzchołkowego na pędzie głównym oraz założenia go, po zakończeniu wzrostu, były różne u poszczególnych drzewek. Badania statystyczne wykazały występowanie słabej, chociaż istotnej korelacji między terminem założenia pączka wierzchołkowego a wielkością przyrostu wysokości pędu głównego.

Od 21 lipca do 31 sierpnia co 10 dni defoliowano grupę dwunastu drzewek. Średnie terminy założenia pączka wierzchołkowego na pędzie głównym drzew w poszczególnych grupach były podobne, ale różnice między drzewami w obrębie każdej grupy sięgały do 30 dni. Szybkość rozwoju pączków po defoliacji była wskaźnikiem głębokości ich spoczynku. Podjęcie rozwoju pączka po defoliacji wskazywało na fazę spoczynku względnego, brak rozwoju pączka był kryterium spoczynku głębokiego. Badania statystyczne wykazały istnienie dość silnej korelacji między szybkością rozwoju pączka po defoliacji, a czasem jaki minął od założenia pączka. Wyliczona krzywa regresji osiągnęła granicę po 65,4 dniach, co empirycznie wyznacza długość okresu spoczynku względnego pączków badanej populacji drzew. Spoczynek głęboki pączka wierzchołkowego następował u poszczególnych drzew w różnym czasie, zależnym od terminu uprzedniego założenia pączka na drzewie.