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The Role of Light in Leaf and Flower Bud Break of the Peach (*Prunus persica*)

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Abstract

The effect of light on peach leaf and flower bud break was examined. It was found that leafless dormant shoots were light-perceptive organs. Darkness, after light preconditioning during dormancy, reduced leaf bud opening; however, light was obligatory when the shoots were preconditioned in the dark. Relatively short exposures to light were sufficient to stimulate leaf bud break. Terminal buds were less inhibited by darkness than were laterals. Flower bud break was inhibited in light after dark preconditioning. The red region of the spectrum was found to be active; the phytochrome system seems to be involved in the light reactions, as the red light effect was reversible with subsequent far-red illumination. Supplementary light, producing long-day conditions, could partly compensate for insufficient chilling. A possible sequence of reactions in the plant is suggested.

Introduction

The fact that dormancy of woody plants is affected by light is well known. However, investigators such as Wareing (20) and Nitsch (12) mostly studied length of day as a factor for the induction of dormancy, and even classified the woody plants according to their response to short photoperiods (12), but little information is available regarding the importance of this factor in terminating dormancy.

Chilling has long been known as the natural rest-breaking factor as reviewed by Samish (16), and its effect on deciduous species is universal. On the other hand, the relative effect of light on bud burst in spring seems to vary among species and the amount of chilling received. Klebs (8) pointed out that dormant leafless *Fagus sylvatica* seedlings, grown in the green-

house, awakened when illuminated continuously, but remained dormant under natural light conditions. Kramer (9) showed that many leafless dormant plants, when placed in a greenhouse as early as January, awoke only in long-day conditions. Olmsted (13) showed that with partially chilled seedlings of *Acer saccharum*, bud burst was far better under conditions of long photoperiod than when the plants received a natural day length during spring and early summer.

Continuous illumination broke the dormancy of unchilled *Betula pubescens* (19, 7), *Larix decidua* (19), and *Cornus Florida* (4). Embryo-cultured peach seedlings were found to be light responsive. A long photoperiod could substitute for low temperature in insufficiently chilled seeds of peach and other species (10 and 4). Wareing (20), on the other hand, reported that certain species such as *Robinia pseudacacia*, *Acer pseudoplatanus*, *Betula pubescens* and *Populus* sp., when sufficiently chilled, will burst even in total darkness.

The beginning of cambial activity in spring, as well as its cessation in autumn, was found by Daubenmire (3) to be photoperiodically controlled in some woody forest species such as *Larix occidentalis*. Wareing (18, 19) showed that the photoperiodic behavior of dormant *Fagus sylvatica* was determined by a light perceiving site in the bud meristem.

In most of the described works young forest and fruit trees were used which had not as yet developed blossom buds. Therefore, they deal with only leaf buds, and no information was found concerning the response to illumination of dormant flower buds.

In the present work, we tried to elucidate the effect of illumination on the termination of dormancy by the leaf and flower buds of the peach.

Materials and Methods

The plant species used was *Prunus persica* L. The effect of light on peach bud burst was tested with excised shoots and young intact plants of the varieties Elberta and Redhaven. The variety Redhaven requires somewhat more chilling than does Elberta.

a. *Experiments with excised shoots.* — One-year-old dormant branches from adult trees having a uniform length of 50 cm and a basal diameter of 6–8 mm were collected. In the laboratory they were shortened to a length of 40 cm by removing the top, then placed upside down in running tap water for one hour. The branches were divided at random into groups of twelve and either packed in moist vermiculite and stored in the dark at 6°C, or tested without additional chilling. Then the shoots were placed for 20 or 21 days into a warm chamber of $25 \pm 1^\circ\text{C}$. Before transfer to the warm chamber, the basal cut of the branches was renewed and each group was placed in uniform 250-ml beakers with only the bases of the shoots submerged in water. Percentage of leaf and flower bud opening was recorded separately. The warm chambers were either dark or illuminated during various daily cycles or for continuous periods of time. Illumination was achieved by 20 W cool white fluorescent tubes, giving an incident radiation of $5650 \text{ erg cm}^{-2} \text{ s}^{-1}$ at the level of the shoots as measured by a Kipp & Zonen Solarimeter, type CM 2. When red light was used, the white fluorescent tubes were covered

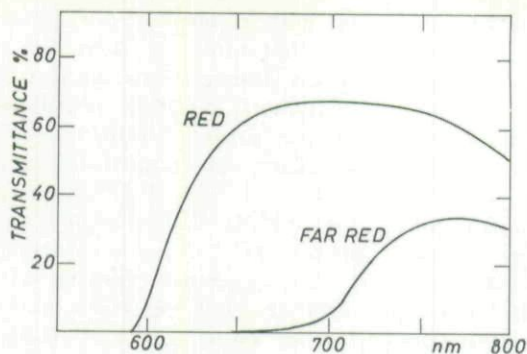


Figure 1. Percent of light transmittance of red and far-red filters at wavelengths between 550–800 nm.

with three layers of colored cellophane paper. Far-red light was achieved by using two adjacent lamps, each covered by three layers of blue and three layers of red cellophane. Transmittance of the cellophane filters between 550 and 800 nm is shown in Figure 1.

The red cellophane did not transmit any light below 590 nm and the far-red very little below 700 nm. The incident radiation emitted by the "red lamp" was $1350 \text{ erg cm}^{-2} \text{ s}^{-1}$ and by the double "far-red lamps" $980 \text{ erg cm}^{-2} \text{ s}^{-1}$.

b. *Experiments with whole plants.* — One- and two-year-old peach trees were grown in four-gallon tin containers. The plants were randomly divided into groups of six. Soil moisture was kept high during the experiment by frequent irrigation. When experiments were conducted under controlled conditions, the plants were kept in a cold dark room (6°C) for 71 days in order to supply their chilling requirement, then transferred to dark or illuminated warm chambers (23°C). Illumination was supplied by cool white fluorescent lamps supplying c. 480–700 lux at the level of the plants. The amount of bud breaking was recorded after 22 days in the warm room.

For outdoor experiments the plants were kept in natural outdoor temperature and light conditions at Bet Dagan (latitude 32°N , average mean temperature during Dec.–Feb., $12\text{--}13^{\circ}\text{C}$) during the winter until the beginning of March.

In the first experimental season, one-year-old plants were used and tested under three different light regimes: natural day, (day length during experimental period from $11\frac{1}{2}$ to $12\frac{1}{2}$ hours), continuous light, and total darkness.

The continuous light conditions were obtained by four 150 W tungsten bulbs, giving an intensity of c. 700 lux at the average height of the plants; the lamps were automatically switched on before darkness. For total darkness, the plants were placed under a shaded black cloth structure. The difference between the average mean air temperature in the open and under the cloth cover did not exceed 1°C although the daily temperature-amplitude was considerably larger in the former than in the latter.

During the second season, two-year-old plants were used. All the plants, irrespective of treatment, were shaded to prevent direct sunlight radiation. The continuous light was replaced by a 1-hour night break between 23.30 and 00.30 hours, using the same light source and intensity as the year before.

Statistical significance was expressed as standard error or LSD.

Results

a. *Effect of continuous illumination.* — Elberta peach shoots collected on Dec. 5, 1962 and chilled in the dark for 89 days, were tested for the effect of light on their bud opening. The percentage of leaf and flower bud burst after 21 days in a light or dark warm chamber is shown in Table 1.

A quite different response of leaf and flower buds became apparent. A marked inhibition of bud opening was found in the case of leaf buds by a dark forcing period, and with flower buds by light. The effect of red light on leaf and flower bud break in comparison to white light and darkness is shown in Figure 2.

Leaf bud opening in the red light was high and equalled that in the white light. In the dark, no leaf buds opened altogether. Flower bud opening did not show a significant response to either light. However, the highest percentage of flower buds opened in the dark.

b. *Effect of photoperiods.* — The photoperiodic nature of the light effect on leaf and flower bud burst was determined by means of various red light cycles in the warm chambers. Percent bud break on excised Elberta shoots, collected on Nov. 5, 1963 and chilled for 77 days, was recorded after exposure of 20 days to the different photoperiods (Figure 3).

A diurnal cycle of one hour light was sufficient to cause a major increase in leaf bud break. Further increase in the duration of the daily illumina-

Table 1. *The effect of constant light or darkness on bud break of excised Elberta peach shoots after 89 chilling days at 6°C. Results in % recorded after 21 days in the warm chambers at 25°C.*

Material	Bud bursting %		LSD P = 0.01
	dark	light	
Leaf buds	4.1	45.7	11.2
Flower buds ..	33.4	9.7	15.0

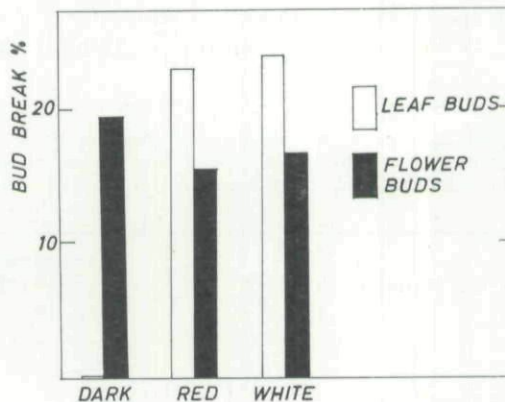


Figure 2. *The effect of red light, white light, and darkness on leaf and flower bud burst of excised Elberta shoots. Shoots collected March 7, 1963; chilled 21 days at 6°C in the dark; recordings made after 21 days in the warm (23°C) chamber.*

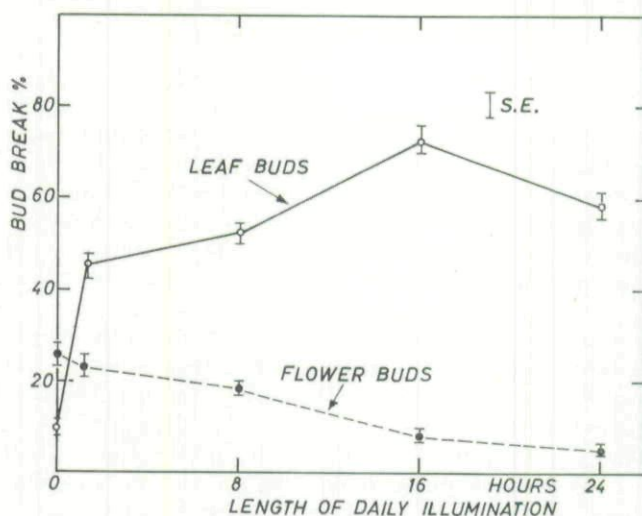


Figure 3. The effect of various daily photoperiods (red light) on leaf and flower bud burst of the Elberta peach. Excised shoots collected Nov. 5, 1963; held at 6°C in darkness for 77 days; forcing for 20 days at 23°C under 0, 1 1/4, 8, 16, or 24 hours light daily.

tion resulted in increased leaf bud break up to a maximum under long-day conditions. However, continuous light would seem less effective in promoting leaf bud break. Flower bud opening was negatively correlated to the length of the daily light cycle. The continuous dark treatment caused the largest amount of flower bud opening, corresponding to results of earlier experiments.

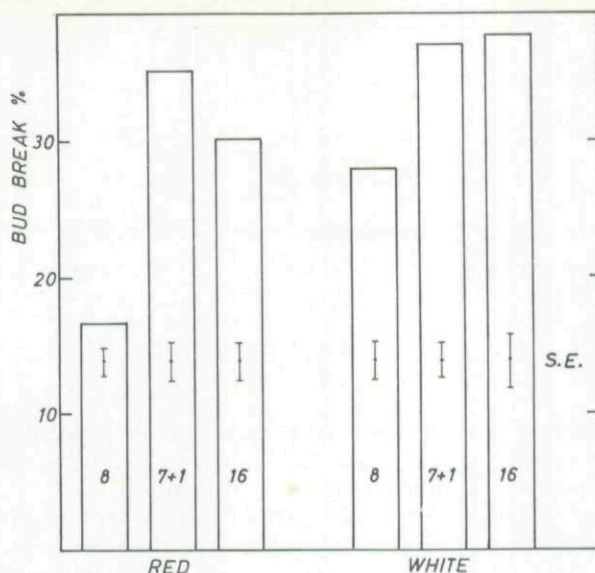
In view of the steep rise of the leaf bud curve after a relatively short period of illumination, we studied the effect of rather small amounts of light, when given during a continuous period or by cyclic illumination. Elberta shoots collected on Dec. 12, 1963 and chilled for 61 days were transferred to warm chambers. There they were exposed either to continuous red illumination for 32 and 80 hours followed by darkness, or to a 75-minute daily light cycle; an additional lot was subjected to complete darkness. Leaf and flower bud opening was recorded after a total of 20 days in the warm chambers, as shown in Table 2.

With leaf buds, continuous 32-hour illumination caused only a moderate

Table 2. The effect of various short periods of continuous and cyclic illumination on Elberta peach leaf and flower bud break. Shoots cut on Dec. 12, 1963; chilling for 67 days in the dark; bud break in % recorded after 20 days in the warm room at 23°C. Bud break in %.

Material	Constant darkness	Continuous light hours		75-min daily light cycle 20 hours	LSD P = 0.05
		32	80		
Leaf buds	1.1	7.8	24.7	30.5	10.8
Flower buds	31.9	29.2	18.9	38.0	11.4

Figure 4. The effect of a short photoperiod with a midnight light break, as compared with short and long photoperiods, on leaf bud burst of the Redhaven peach. Shoots collected March 2, 1964; forcing at 23°C for 4 days under 8, 16 or 7+1 (midnight) hours of white and red light daily, followed by darkness for an additional 16 days.



increase in leaf bud burst while the cyclic light totaling only 20 hours had a very marked effect on their breaking in spite of the shorter total light exposure. Even with 80 hours of continuous illumination — a total light duration, four times as long as in the cyclic system — the percent of leaf bud break did not reach the high values under the cyclic light. Similarly, it was shown above (Figure 3), that with long illumination periods, cyclic illumination was more effective than continuous, when both treatments were applied for the same period of time. While here this cyclic form of illumination increased the effectiveness of light on leaf bud burst, it did not cause a similarly strong differential effect on flower buds. Relatively short periods of illumination (20 and 32 hours), applied as cyclic or constant light, respectively, did not cause any inhibition of flower bud opening. Furthermore, the one hour cycle caused even a slight (N.S.) enhancement. The more prolonged light treatment of 80 hours, however, caused a definite inhibition of flower bud break. It seems also that the long dark period following a relatively short illumination did not antagonize the light effect.

In order to verify the photoperiodic nature of the strong cyclic effect of light on leaf bud opening, we examined the night break effect. Redhaven shoots collected on March 2, 1964 were tested, without additional cooling, for leaf bud break under short and long day conditions and compared with the bud behavior after a short-day treatment with a night interruption. The shoots were subjected to only four light cycles in the warm chambers, followed by 16 days of darkness. Results with both white and red light are shown in Figure 4.

Although the *F* of this experiment was not significant because of the high variability, the effects of both white and red light strongly indicated a photoperiodic reaction. When one hour of the short (8 hours) photo-

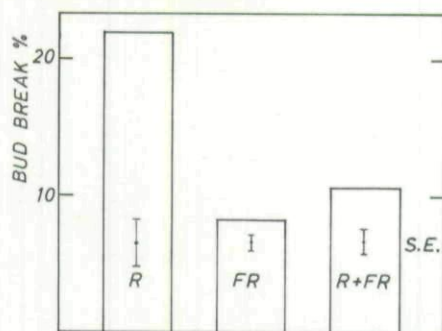


Figure 5. The effect of illumination with red and far-red light on leaf bud burst of the Redhaven peach. Shoots collected March 2, 1964; forcing at 23°C; illumination in four daily cycles of one hour red, far-red or red followed by far-red, and subsequent darkness for an additional 16 days.

period was applied as a night break, long-day conditions were simulated. A total of only four light cycles was sufficient to show the advantage of long-day conditions for leaf bud break.

c. *The mechanism of the light effect.* — Since a photoperiodic response was thus established, the leaf buds were tested for activity of the phytochrome pigment system. Excised Redhaven shoots were treated by four 1-hour cycles of red (R), far-red (FR) or red followed by far-red illumination. The percentage of leaf bud break after 16 additional days in the dark is shown in Figure 5.

Although the percentage of leaf bud break in this experiment was small, possibly due to the short total duration of illumination, the inhibiting effect of far-red light became obvious. The far-red illumination, following the red, completely reversed the bud-breaking effect of the red light.

In order to verify the results obtained with excised shoots, one-year-old intact plants were tested. Potted Redhaven and Elberta plants were chilled for 71 days in the dark and transferred to illuminated or dark warm chambers. After 22 days, the percentage of open terminal and lateral leaf buds were recorded (Table 3).

Darkness inhibited lateral leaf bud break on the intact plants, similarly as with the excised branches. Inhibition of terminal buds by darkness was considerably smaller than that of the laterals. The still relatively high degree of opening of lateral buds (Elberta) which was obtained in the dark might be due to the approximately two-hour exposure of these plants to diffused

Table 3. The effect of continuous light or darkness on the bud opening of chilled one-year-old potted Elberta and Redhaven peach plants. Chilled Dec. 27, 1963–Mar. 8, 1964; subsequently transferred to warm chambers \pm light; bud break in % recorded after 22 days.

Variety	Lateral buds			Terminal buds		
	dark	light	LSD P = 0.05	dark	light	LSD P = 0.05
Elberta	20.0	91.3	14.7	74.0	99.3	18.2
Redhaven	4.8	85.3	13.0	47.3	98.3	20.3

Table 4. *The effect of different light conditions on the opening of lateral leaf buds of Elberta peach plants under outdoor conditions. Treatments started on Mar. 2, 1964 and Mar. 7, 1965; recordings made Apr. 6, 1964 and Apr. 19, 1965.*

Year	Lateral leaf bud break %			LSD P = 0.05
	Continuous darkness	Natural daylight	Nightly light supplement	
1964	0.8	14.0	34.8	11.8
1965	6.8	12.0	24.3	8.7

light at the time of transfer from the cold to the warm rooms. With the intact plants, cyclic illumination of 16 hours daily had about the same effect on bud break as did the continuous 24-hour treatment.

After having established the effect of light on leaf bud break under controlled conditions, its occurrence was examined with naturally wintered plants under outdoor conditions. Potted Elberta plants, standing in the open, were supplemented, shortly before expected bud break, with additional artificial light during the night, or covered for complete darkness. Plants left under natural conditions were used as controls. The experiment was conducted in two successive seasons, on one- and two-year-old plants, respectively (plants were severely cut back after the first spring). The percent of lateral leaf bud break in both years is shown in Table 4.

In spite of the different conditions in the two years, and therefore the different level of the figures, it was established quite clearly that darkness reduced and additional light enhanced lateral leaf bud opening in both of them. It should be noted, however, that the chilling requirements for breaking of dormancy of the leaf buds was not fulfilled in either of the two years, as the percentage of lateral leaf bud burst in the control was rather low.

Discussion

We have shown in this paper that a light stimulus is perceived by leafless dormant peach shoots. This was shown by Wareing (19) for certain dormant forest trees, and recently by May and Antcliff (11) also for the grape vine. Evidence supporting such a characteristic in the apple was obtained in our laboratory (unpublished data). However, this sensitivity to light of the dormant leafless shoots is not currently recognized as a general feature, and its significance in tree development is not as yet widely appreciated.

Bud opening in spring on deciduous trees was thought to be governed in nature exclusively by the chilling requirement and spring growth temperatures as reviewed by Samish (16). In this paper evidence is presented that in order to permit leaf buds of the peach to break, a light stimulus is required in addition to chilling. On the other hand, flower bud burst showed no requirement for light under our experimental conditions, and was even inhibited by it. These observations could be explained by the hypothesis that rest is overcome by cold, and bud opening is governed by light.

The two processes are not entirely independent, as light could partly compensate for insufficient chilling while a complete fulfilment of the chilling requirement would be likely to increase the number of buds affected by light. A dark preconditioning of the shoots or plants markedly increased the sensitivity to light, *i.e.*, promotion of leaf bud opening and inhibition of flower bud opening. However, a dark period after the illumination did not cancel the light effect on bud opening. Furthermore, the light was more effective when given in a daily cycle than as continuous illumination. In all our experiments, leaf buds opened best under long-day conditions, which is in agreement with Lammerts' findings (10) concerning peach embryo growth. Still it does not seem that the light effect could be explained only on a photoperiodic basis. The high sensitivity of the buds to short illumination periods indicates that a photomorphogenetic process with a rather low light saturation level governs the peach leaf bud break. In this respect, the light effect in the bud resembles that found in seeds requiring prolonged illumination for germination as indicated by Evenari (5) and Borthwick and Hendricks (2). Furthermore, the red light was found to be active, and its effect on buds, as in seeds, was reversible by a subsequent far-red illumination, indicating a phytochrome pigment system.

It is suggested, therefore, that the leaf bud opening of peach is governed by a combination of two types of processes: a light reaction, producing the photochemical impulse for bud opening, and a dark reaction, regenerating a precursor for the light reaction. Light transfers the phytochrome pigment to the far-red form, and the dark restores the inactive red form of the pigment. It would seem that the phytochrome pigment must be kept for a long period in the active far-red form in order to cause leaf bud burst; this is similar to the views expressed by Borthwick and Hendricks (2) concerning the prolonged illumination required by seeds and spores for germination. This situation is achieved by prevention of any long dark period during the active stage.

Such a system might explain the high efficiency of diurnal cyclic illumination versus that of continuous light, the better effect of long photoperiods compared to short ones, the advantage of a midnight light break, and the strong effect of relatively short illuminations (4 days) not annulled by subsequent darkness.

Terminal buds were markedly less inhibited by darkness than were the lateral leaf buds, which corresponds to their lower chilling requirement. This quantitative difference might be associated with the different level of growth-regulating substances in those buds, as was long noted by Thimann and Skoog (17). Auxins were found by Blommaert (1), flavonoid compounds (naringenin) by Hendershott and Walker (6), and gibberellin by Philips (15) to take part in the dormancy breaking and bud opening metabolism. The ability of naringenin to induce a light requirement in seeds, and the counteracting activity of gibberellin have been shown by Philips (14). The different levels of these substances in the lateral and terminal buds could account for the differential response to light. Such substances may play a primary role in the dark and light reactions as part of the phytochrome pigment system, whose existence in the peach leaf buds is indicated.

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References

1. Blommaert, K. L. J.: Winter temperatures in relation to dormancy and the auxin and growth inhibitor content of peach buds. — *S. Afr. J. Agric. Sci.* 2: 507–513. 1959.
2. Borthwick, H. A. & Hendricks, S. B.: Effect of radiation on growth and development. — *Encyc. Plant Physiol.* 16: 299–330. 1961.
3. Daubenmire, R. F.: Relation of temperature and daylength to the inception of the growth in spring. — *Bot. Gaz.* 110: 464–475. 1949.
4. Downs, J. & Borthwick, H. A.: Effect of photoperiod on growth of trees. — *Ibid.* 117: 310–326. 1956.
5. Evenari, M.: Seed germination. — *Radiation Biology* (A. Hollaender ed.) 3: 519–549. McGraw Hill, New York. 1956.
6. Hendershott, C. H. & Walker, D. R.: Seasonal fluctuations in quantity of growth substances in resting peach flower buds. — *Proc. Am. Soc. Hort. Sci.* 74: 121–129. 1959.
7. Kawase, M.: Dormancy in *Betula* as a quantitative state. — *Plant Physiol.* 36: 643–649. 1961.
8. Klebs, G.: Über das Treiben der einheimischen Bäume, speziell der Buche. — *Abhandl. Heidelberger Akad. Wiss.* 3: 1. 1914. (as cited by P. F. Wareing in *Physiol. Plant.* 6: 692–706. 1953.)
9. Kramer, P. J.: Effect of variation in length of day on growth and dormancy of trees. — *Plant Physiol.* 11: 127–138. 1936.
10. Lammerts, W. E.: Effect of photoperiod and temperature on growth of embryo-cultured peach seedlings. — *Am. J. Bot.* 30: 707–711. 1943.
11. May, P. & Anteliff, A. J.: Fruit bud initiation. — *J. Aust. Inst. Agric. Sci.* 30: 106–112. 1964.
12. Nitsch, J. P.: Photoperiodism in woody plants. — *Proc. Am. Soc. Hort. Sci.* 70: 526–544. 1957.
13. Olmsted, C. E.: Experiments on photoperiodism, dormancy, leaf age and abscission in sugar maple. — *Bot. Gaz.* 112: 365–393. 1951.
14. Phillips, I. D. J.: Induction of a light requirement for germination of lettuce seeds by naringenin and its removal by gibberellic acid. — *Nature* 192: 240–241. 1961.
15. — Some interactions of gibberellic acid with naringenin (5, 7, 4' trihydroxyflavanone) in the control of dormancy and growth. — *J. Exp. Bot.* 13: 213–226. 1962.
16. Samish, R. M.: Dormancy in woody plants. — *Ann. Rev. Plant Physiol.* 5: 183–203. 1954.
17. Thimann, K. V. & Skoog, F.: Studies on growth hormone of plants. III. The inhibiting action of the growth substance on bud development. — *Proc. U.S. Natl. Acad. Sci.* 19: 714–716. 1933.
18. Wareing, P. F.: Growth studies in woody species. Photoperiodism in dormant buds of *Fagus sylvatica* L. — *Physiol. Plant.* 6: 692–706. 1953.
19. — Growth studies in woody species. VI. The locus of photoperiodic perception in relation to dormancy. — *Ibid.* 7: 261–277. 1954.
20. — Photoperiodism in woody plants. — *Ann. Rev. Plant Physiol.* 7: 191–211. 1956.

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