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Growth Studies in Woody Species V. Photoperiodism in Dormant Buds of Fagus sylvatica L.

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The seedlings of many woody species show well-marked photoperiodic responses in relation to dormancy. (For a review of this subject, see Wareing, 1948). In general, short days hasten the onset of dormancy (as indicated by cessation of shoot-growth and the formation of resting-buds) while long days have the reverse effect and delay or even entirely suppress the normal onset of dormancy. Not only may the onset of dormancy be prevented by exposure to very long photoperiods, but in certain species of Pinus premature expansion of the developing buds may be induced by exposing the plants to continuous illumination (Phillips, 1941; Wareing, 1951). The production of 'Lammas shoots' ('Johannistriebe') by seedlings of oak (Quercus spp) under long photoperiods appears to be an allied phenomenon (Leman, 1948). Since this premature expansion of the buds in Pinus occurs in seedlings in the leafy condition, it is possible that in such cases the photoperiodic stimulus originates primarily in the mature leaves and not directly in the bud itself. In this case, the position would be quite comparable with that in herbaceous species, where photoperiodic perception is well-known to be mediated through the mature leaves. Several instances have been reported, however, in which the breaking of dormancy was hastened by exposure of the buds to long day conditions even when the seedlings were in the *leafless* condition. Thus, Klebs (1914), in an exhaustive series of experiments, showed that leafless seedlings of beech break dormancy rapidly when exposed to continuous illumination from electric lamps. Kramer (1936) brought seedlings of various woody species into the greenhouse from out-of-doors in January, and

observed that the buds broke dormancy more rapidly under long days, although breaking ultimately occurred also under short days. Gulisashvili (1948) exposed leafless seedlings of various woody species to continuous illumination in a greenhouse, the treatment being commenced on 29th October for one batch of plants and on 9th January for the second batch. In both cases, breaking of dormancy occurred much more rapidly under continuous illumination than in the control plants, which were exposed to natural daylengths. Olmsted (1951) investigated the interaction between chilling and photoperiodic treatment in Acer saccharum, and found that breaking of dormancy in unchilled seedlings occurred more readily under a 20-hour photoperiod than under natural daylengths or short days. Van der Veen (1951), also, was able to obtain breaking of dormancy in unchilled seedling of Populus spp. by exposure to long photoperiods.

These various reports would seem to indicate that light may have a direct effect upon the buds of various woody species. The experiments cited above, however, cannot be held to have established beyond doubt that we are dealing here with a true photoperiodic effect. The more rapid bud-break observed under long photoperiods might simply indicate that the operative factor is the total duration of illumination over a number of cycles. This was, indeed, the opinion of Klebs, (loc. cit.). Moreover, temperature differences arising from the illumination conditions were apparently not eliminated in some of the experiments cited, and only in the case of the experiments by Olmsted and Van der Veen was any attempt made to distinguish between the responses of chilled and unchilled buds. The following experiments were, therefore, carried out with seedlings of beech (*Fagus sylvatica* L.) to determine (1) whether the effect of light upon bud-break is of a photoperiodic nature, and (2) if so, how far the associated phenomena are comparable with photoperiodic effects in herbaceous species.

Experimental

The experiments were carried out with 1-year beech seedlings. In the preliminary experiments the plants used had been grown in pots out-of-doors during the summer.

In order to avoid any effects due to exposure to cool temperatures, the plants were transferred to a warm greenhouse in early September and by the end of September all plants had ceased extension growth and had formed terminal resting buds. Since one of the first objects of the investigation was to determine whether or not bud-break is affected by the total duration of light received (i.e. the summation of the number of hours of light-exposure), on 3rd October the plants were defoliated by hand and transferred for storage to a dark cupboard in a sub-basement room, and were maintained at a practically constant temperature of 15° C.

Thus the plants received no light from shortly after the time the buds had fully developed until the commencement of the experiments. Not a single bud broke dormancy under the conditions of storage, although some of the plants remained viable in darkness for as long as 6 months.

The experiments were carried out in a growth-cabinet consisting of two identical compartments, each of which contained ten 80-watt 'daylight' fluorescent tubes spaced 3 inches apart. The tubes were screened from the main growth section (containing the plants) by sheets of glass. A constant stream of cool air was drawn over the tubes by means of an extractor fan in the roof of the cabinet. In this way effective cooling was provided, and it was possible to maintain the growth sections at a constant temperature of 20° C in both light and darkness, by means of an electrical tubular heater, controlled thermostatically. The light intensity at plant level was approximately 10,000 lux as measured by a photocell.

Experiment 1.

On 22nd October, plants were transferred from the dark to the growth cabinet, and divided into 4 series, each containing 11 or 12 plants. The plants were exposed to daily photoperiods of 12, 16, 20 and 24 hours respectively. During the daily dark periods the plants were transferred to dark covers, and were maintained at a constant temperature of 20° C in both light and dark.

The dates were recorded on which the terminal bud of each plant broke dormancy. A bud was deemed to have broken dormancy when the tip of a new leaf became visible beyond the scales, although signs of swelling were observable for some days before this stage was reached. The time to break dormancy, using this criterion, will be a function of the rates of both internode extension and leaf-growth.

The data are given in Table 1. The buds of the plants kept under 20-hour and 24-hour photoperiods first began to break some 8—10 days after the commencement of the experiment, and all the plants of the 24-hour series had broken dormancy within 27 days. The plants of the 16-hour series began to break after 24 days of treatment, but only 5 out of 12 plants had broken dormancy when the experiment was terminated after 46 days of treatment. No buds of the plants of the 12-hours series expanded, although some of the buds showed an initial swelling, but they did not proceed beyond this stage.

There is thus no clear-cut 'critical' daylength for the breaking of dormancy, the response of the plants increasing progressively with increasing length of photoperiod. Nevertheless, there is no evidence that the total duration of light exposure over the whole period of treatment is the operative factor, for the total period of light exposure for the 12-hour series amounted to 552 hours at the end of the experiment and this was quite ineffective. On the other hand, the total period of light received by the 20-hour series at the date

Table 1. *Effect of length of photoperiod on breaking of beech buds.*

Daily light period (hours)	Total number of plants	No. of plants breaking dormancy after 46 days	Time for 50 % of plants to show breaking
12	11	0	—
16	12	5	46 days
20	11	9	14 days
24	11	11	14 days

on which 50 per cent of the plants showed breaking was 280 hours. It is evident that the total duration of light exposure over the whole period of treatment is not the factor determining bud-break in beech. This conclusion was fully confirmed by later experiments.

Experiment 2.

It is well-established that the flowering response in both 'short-day' and 'long-day' herbaceous species is markedly affected by the absolute lengths of the light and dark periods, and is profoundly modified if the dark period is interrupted by a period of illumination, even though the total daily periods of light and dark remain unchanged. A small-scale preliminary experiment was conducted to determine the effect on bud-break of interrupting the dark period. Three groups, each of six plants which had been maintained under warm, dark conditions since the onset of dormancy, were exposed to the following light regimes in the growth cabinet: —

Group A — Two 6-hour light periods, alternating with two 6-hour dark periods per day.

Group B — 12 hours light and 12 hours dark, the latter interrupted by 30 minutes of light at the full intensity (10,000 lux).

Group C — 12 hours light and 12 hours of uninterrupted darkness.

After 32 days of these treatments all the plants of Group A had broken dormancy, while those of Groups B and C remained fully dormant. This result provides striking evidence for the view that these effects in beech buds are of a photoperiodic nature, for the same total periods of light and darkness were received by both Group A and Group C, although the responses were entirely different. Interruption of the dark period by 30 minutes of light was not sufficient to bring about bud break (see Experiment 4 below, however).

Following these small-scale preliminary experiments, several more extensive experiments were conducted. As the number of plants remaining from the original batch, which had been stored under warm, dark conditions, was not sufficient for more large scale experiments, plants were used which had

been grown in the open and had been left out-of-doors until early January. (These plants were kindly supplied by the British Forestry Commission and were derived from seed collected in Southern England). The seedlings were planted in pairs in pots on 12th January and were stored in darkness at 15° C. until required for use. All plants remained dormant under these conditions, even after 3—4 months. Although the plants had not been protected from chilling prior to the time at which they were potted, it was found that there was no objection to using these seedlings in the later experiments since there proved to be no appreciable difference between the photoperiodic responses of these plants and those used in Experiments 1 and 2, as shown by the following observations. Twenty pots of the plants brought from out-doors in January were immediately placed in a cold-room (maintained at 0—5° C) and stored there until 9th March. On the latter date, the plants were divided into three groups, which were transferred to the growth cabinet and exposed to (a) 18-hour day (b) 12-hour day and (c) continuous darkness. The only group which broke dormancy was that exposed to 18-hour daily photoperiods. Thus, there appears to be no appreciable effect of a period of low-temperature treatment on the subsequent photoperiodic responses of beech buds.

Experiment 3.

It is well known that two light-reactions are involved in the photoperiodic responses of herbaceous species viz. (1) a 'primary light reaction', in which the quantitative light requirements are relatively high, and (2) a 'secondary light reaction', which is effective at very low light intensities (of the order of 10 lux) when used to supplement a period of high intensity illumination (see for example, Lang, 1952). The primary light reaction of herbaceous species appears to be connected with photosynthesis and might, therefore, be expected not to occur in buds, but the presence of chloroplasts in the leaf primordia and in the basal tissue of the bud scales (see p. 700) indicates that the possibility of photosynthesis in such tissues is not excluded. Moreover Klebs (loc. cit.) observed that beech buds will not respond to continuous illumination in the complete absence of CO_2. The object of the present experiment was, therefore, to determine whether there is any evidence that two light-reactions are involved in bud-break, and if so, what are the quantitative requirements of such reactions.

The experiment was carried out with plants which had been brought from out-of-doors in January and planted in pots. One hundred and forty plants were selected and divided into 14 equal groups. Twelve of these groups were exposed to high intensity illumination (10,000 lux) for 3, 6, or 12 hours and then to low intensity illumination at one of the following intensities for periods of 15, 12 or 6

Table 2. *Effect of Light Intensity on breaking of dormancy.* Mean number of days to break dormancy (10 plants per treatment).

Light treatment		Intensity of supplementary illumination				
Full intensity (hours)	Supplementary illumination (hours)	250 lux	500 lux	1,000 lux	2,000 lux	10,000 lux
3	15	41.8 ± 1.4	40.5 ± 0.8	33.4 ± 0.5	—	33.0 ± 1.6
6	12	40.5 ± 0.6	38.5 ± 1.6	32.6 ± 1.7	32.8 ± 1.0	
12	6	40.0 ± 0.9	34.6 ± 1.1	33.1 ± 0.8	31.7 ± 1.2	

hours respectively, so as to make a total photoperiod of 18 hours in each case: viz. 250, 500, 1000 and 2000 lux. The two remaining series of plants were exposed to photoperiods of 18 and 12 hours respectively, given entirely at the high intensity. The lower light intensities were obtained by inserting sheets of white paper between the fluorescent tubes and the glass of the growth cabinet, the resulting spectral changes being only slight. In this way one side of the growth cabinet was divided into 4 sections, each at a different light intensity. The various combinations of high and low intensity exposures were obtained by transfer between the two sides of the growth cabinet.

The number of plants showing breaking of the terminal bud was determined for each group daily, and the results are summarised in Table 2.

Breaking of the buds was much slower than in the preliminary experiments, a fact which must probably be ascribed to a deeper state of dormancy in these plants which had previously been kept out of doors. It will be seen that the mean number of days of exposure necessary to break dormancy was practically the same for all treatments in which the intensity of supplementary illumination was 1000 or 2000 lux, i.e. with the latter intensities the duration of exposure to high intensity illumination did not affect the mean time to break dormancy. Moreover, the breaking of dormancy was no further hastened when 18 hours of full intensity illumination was used. On the other hand, with supplementary illumination at 500 and 250 lux there was a significant delay in bud-break.

The 12-hour photoperiod series behaved as previously, viz. there was a slight swelling of the buds, but after 50 days the buds of only three plants were sufficiently developed to be categorised as having broken dormancy.

It seems clear from these results that under the conditions of the experiment the light requirements for breaking were fully met by an intensity of 1000 lux and that there is no evidence that two distinct light reactions are involved. These results agree with those of Klebs, who found that beech buds broke dormancy at approximately the same rate under continuous illumination at various intensities from 700—6000 lux. With 400 lux, however, the buds broke only with difficulty and at 250 lux there was no breaking.

Experiment 4.

The following experiment was carried out to obtain confirmation of the results of Experiment 2, in which it was found that short light periods are effective in promoting bud break, provided the accompanying dark periods also are short.

Eighty four plants were selected and divided into seven equal groups. The experiment consisted essentially of two sections. In the first section, four groups of plants were exposed to either (a) 18-hour photoperiods and 6-hour dark periods, or (b) 6-hour photoperiods alternating with 6-hour dark periods. Each treatment was run at two different light intensities viz. 1000 and 2000 lux. The results are summarised in Table 3.

A number of points of interest emerge from the results. Firstly, it is seen that an 18-hour photoperiod given entirely at an intensity of 1000 lux is quite effective in bringing about breaking of the buds. Indeed, breaking occurred significantly faster at 1000 lux than at 2000 lux. The new shoots produced under 1000 lux intensity were more etiolated than at 2000 lux i.e. they had longer internodes and had smaller leaves than was the case with the plants at 2000 lux. It seems possible that the more rapid breaking observed at 1000 lux was due to the rapid extension of the internodes at this intensity.

Secondly, it is seen that breaking occurred almost as quickly under a regime of (6 hours light+6 hours dark) as under (18 hours of light+6 hours dark). The object of giving a (6+6) regime at two different intensities was to ascertain whether the 'saturation' intensity was increased by this treatment. The results give no evidence that this is the case, however.

In the second section of the experiment, which ran concurrently with the first, there were three groups of plants. It was found in Experiment 2, that interruption of a 12 hour dark period by 30 minutes of light was not effective in promoting bud break. In the present experiment, two groups were exposed to 11 hours at the full light intensity, together with 1 hours' illumination during the middle of the 13-hour dark period. This 'light break' was given at two different light intensities viz. 2000 lux and 10,000 lux respectively. The third group constituted a 'control' series, exposed to 12 hours of light and 12 hours of uninterrupted darkness. These latter plants behaved as previously viz. after 30 days the majority were still dormant, but three plants had advanced sufficiently to be classed as having broken dormancy, although even then these buds remained at a very early stage of development. On the other hand, breaking in the plants which received a 'light break' during the dark period was very markedly hastened by this treatment and 1 hour at 1000 lux produced even more rapid breaking of the buds than at 2000 lux. (Table 3).

Table 3. *Effect of various photoperiodic treatments on breaking of dormancy.* (12 plants per treatment).

Photoperiod	Dark period	Mean time to break dormancy (days)
18 hours (1,000 lux)	6 hours	10.5 ± 0.9
18 hours (2,000 lux)	6 hours	14.3 ± 1.1
6 hours (1,000 lux)	6 hours	14.2 ± 0.9
6 hours (2,000 lux)	6 hours	14.3 ± 1.1
11 hours (full intensity)	12 hours, interrupted by 1 hour of light at 1,000 lux	19.1 ± 0.6
11 hours (full intensity)	12 hours, interrupted by 1 hour of light at 2,000 lux	23.0 ± 1.5
12 hours (full intensity)	12 hours	—

Thus, although the preliminary experiment (Experiment 2) indicated that a 30 minutes light-break was ineffective, a light-break of 1 hour is effective, even at the comparatively low intensity of 1,000 lux.

The results of both sections of this experiment provide convincing evidence that we are dealing here with photoperiodic effects.

Experiment 5.

In herbaceous species there is generally no flowering (in either 'long day' or 'short day' species) when the plants are subjected alternately to inductive and non-inductive cycles. (Long, 1939; Naylor, 1941). That is to say, under such conditions there is very little, if any, summation of the effects of favourable photoperiodic cycles. In order to test whether this is true also for bud-break, a series of plants was exposed alternately to 18-hour and 12-hour photoperiods. The 'control' was the 12-hour series of the preceding experiment, which ran concurrently with the present experiment. It was found that under such conditions the buds broke dormancy rapidly (the mean time to bud break being 18.3 days), so that it is clear that there is here a definite summation of the effects of 'long days', although alternating with 'short days'.

Experiment 6.

It was shown by Klebs (loc. cit.) that in order to effect the breaking of dormancy, the buds themselves must be directly exposed to the light. This was done by covering the buds with tin-foil and exposing the remainder of the twig to continuous illumination. Under these conditions no bud-break occurred. Similar experiments by the present author have confirmed these results. This establishes that photoperiodic perception arises in the buds themselves. Dissection of the buds shows that the scales are brown and

scarious where exposed, but that where they overlap each other at the base they consist of fresh, almost transparent, living tissue. It seemed possible therefore, that photoperiodic perception is mediated through this living tissue of the bud-scales and that there is no direct effect upon the primordial tissues. This possibility was therefore investigated. The bud-scales can be pulled off by means of forceps, leaving the intact leaf-primordia exposed and undamaged (Figure 1). The buds of 20 seedlings were prepared in this manner and each bud was then covered with a transparent gelatine capsule plugged at the base with cotton-wool, in order to reduce the water loss resulting from removal of the bud scales. Ten of the treated plants were then exposed to continuous illumination at 3000 lux, while the remaining 10 treated plants were exposed to daily photoperiods of 10 hours. An equal number of plants with intact buds were also exposed to these two photoperiodic treatments. After 6 weeks, the plants under continuous illumination had broken dormancy in both the 'intact' and 'descaled' series, but the plants of neither series had broken dormancy under 10-hour photoperiods. Thus continuous illumination promotes the growth of the buds, even in the absence of the bud-scales, and hence there must be a direct effect of light on the primordial tissue itself.

Since the light must penetrate the scales to reach the leaf and internode primordia, an attempt was made to estimate the fraction of the incident light penetrating the scales. In order to determine their transmission characteristics, bud scales were removed, placed between slides and cover-glasses and mounted in a photographic enlarger. The mean light intensity at bench level was then measured with a photocell, with and without a bud scale in position. In this way an estimate of the percentage of light transmitted by the upper and lower portions of the bud scales was obtained, and indicated that approximately 7 per cent of the light was transmitted by the brown portion and 35 per cent by the transparent basal portion. (These figures take no account of spectral changes resulting from transmission through the bud scales.) Examination of the buds showed that any given leaf-primordium is usually overlapped by one thickness of dead (brown) scale tissue, and two or three layers of the transparent basal portions of scales. On this basis approximately 0.7 per cent of the incident light would actually penetrate the bud scales to the leaf primordia. Now it was found in Experiment 3 that with 18-hour photoperiods an intensity of 1000 lux was fully effective in bringing about breaking of dormancy in intact buds, and this would correspond to an intensity within the bud of 7 lux. Further evidence that light intensities of this order are effective in stimulating bud-break in beech was obtained as follows. The scales were removed from the terminal buds of 36 plants, which were then divided into three equal series. Two series of plants were exposed

Figure 1. *Terminal bud of beech from which scales have been removed and showing rudimentary leaves.* (×2)

to continuous illumination from 60-watt tungsten-filament lamps which were situated on two opposite sides of the plant, and at distances which produced an intensity of 20 lux in the case of one series of plants and of 100 lux in the case of the other. The third group was maintained in continuous darkness. Both series of plants exposed to continuous illumination had clearly broken dormancy within 18 days, development being slightly more rapid at the higher intensity. At this time all the plants in darkness were still dormant. Thus, intensities as low as 20 lux are effective in stimulating growth when the bud-scales are removed.

After the experiment had been terminated, the 'dark' series of plants was inadvertently left to continue in darkness, and several weeks later it was found that the descaled buds of several of the plants had grown and had formed long etiolated shoots. As the growth of intact buds had never been observed to occur in complete darkness, it is possible that the operation of removing the bud scales had stimulated growth by a 'wound reaction'. The matter requires further investigation.

Discussion

It is clear from the experiments described above that the stimulation of growth in beech-buds by light is of the nature of a photoperiodic phenomenon. It is of interest, therefore, to consider how far photoperiodism in dormant buds in comparable with the well-known phenomena in herbaceous species. There is good evidence that the basic light and dark reactions involved in the photoperiodic responses of *leafy* seedlings of woody species are of the same nature as those occurring in herbaceous species (Wareing 1951). Hence it might be anticipated that the processes involved in the responses of dormant buds would also show certain features common to all

plants showing photoperiodic phenomena. It has been shown that in beech buds there is evidence for only a single light reaction, which reaches 'saturation' at quite low light intensities (of the order of a few lux within the bud itself). There is no evidence for any reaction involving high light intensities as is the case with herbaceous species. This observation agrees with the view that the 'high' light reaction is connected in some way with photosynthesis, (Hamner, 1947; Lang, 1952) and hence would be expected to occur only in plants with mature green leaves. The low light intensities involved in these effects with beech buds suggest that possibly the reaction corresponds to the 'secondary' light reaction of herbaceous species. It is well-known that the effect of darkness in both 'short-day' and 'long-day' plants can be nullified by quite low light-intensities, of the order of 10 lux or less. Moreover, the action spectrum for this secondary light reaction appears to be the same as that involved in leaf-growth and stem-growth in etiolated peas and barley (Parker et al., 1949; Borthwick et al., 1951). This latter observation is of special interest for the present discussion, since in beech buds it is primarily leaf- and internode-growth which are affected. In the case of etiolated seedlings, however, extension of the internodes is *inhibited* by those spectral regions most active in photoperiodism, whereas the present experiments indicate a stimulation of both leaf-growth and internode extension by light. This anomaly can possibly be resolved by the observations of Thomson (1950, 1951) who found that growth of internodes in Avena seedlings during the phase of cell division is actually *promoted* by light, and it is only in the later stages of development that internode growth is inhibited, apparently due to the earlier cessation of both cell division and cell-extension under the influence of light. Moreover, a high proportion of long-day species develop extended internodes under long photoperiods but have a rosette-habit (i. e. unextended internodes) under short photoperiods. Internode extension is promoted by interrupting the dark period by a light-break, however, and the action spectrum for this photo reaction in the long-day species Wintex barley (Hordeum vulgare) is apparently the same as that for flower-initiation (Borthwick et al. 1948) and for internode-inhibition in etiolated barley. The effects of various spectral regions on leaf and internode development have been studied by Wassink and his co-workers (Wassink et al. 1951, 1952; Stolwijk, 1952.), who find that whether stimulation or inhibition occurs at any given spectral region depends partly on the intensity of the radiation used.

The locus of perception for photoperiodic stimulation of internode growth is not known for herbaceous species, but in Pinus silvestris the effect of low intensity radiation appears to be 'perceived' directly in the extending internodes and is not mediated through the mature leaves (Wareing, 1950). There

is thus much evidence that light may have a direct promoting effect on meristematic tissues, and hence the photoreaction involved in the growth of beech buds may be one which is of general occurrence in the normal internode- and leaf-development of all higher plants.

The postulation of a growth-promoting light-reaction does not, of itself, fully account for the *photoperiodic* nature of the effects in beech buds, for it has been shown that the operative factor is not simply the total number of hours of light-exposure, but that a certain total duration of illumination given as long photoperiods is much more effective in breaking dormancy than the same duration given as short-days. Moreover, a total daily light exposure of 12 hours in two periods each of 6 hours' duration is effective, whereas a single period of 12 hours' illumination per day is not. This latter observation suggests that the absolute length of the *dark period* is important (rather than the length of the photoperiod), as is the case also in certain herbaceous species. (Hamner, 1950; Lang, 1952). Nevertheless, there appears to be no clearly defined 'critical' dark period in beech buds (Experiment 1), as there is for the flowering response in both short-day long-day species. It is generally held that in the latter there is an active 'dark reaction', the effect of which may be completely nullified if the dark period is interrupted by a short period of illumination. A similar type of 'light-break' effect was observed in beech buds (Experiment 4), but sufficient evidence is not yet available to determine how far the phenomena are comparable in the two cases. In the case of the flowering response in short-day plants, the effectiveness of the dark period depends upon a prior period of illumination at relatively high light intensity (primary light reaction') but this requirement may alternatively be met by artificially supplying the leaves with sugar (Bonner, cited by Lang, 1952). The absence of any corresponding high-intensity light requirement in beech buds may be due to the presence of adequate reserve materials in the twigs. If there is a positive dark reaction in beech buds, its effect must be inhibitory of growth and the response of the bud would then depend upon an interaction between the growth-promoting effects of light and the inhibitory effects of darkness, such as has been postulated for seedlings of Pinus silvestris (Wareing, 1951).

This conclusion is quite compatible with the hypothesis put forward by Borthwick, Hendricks and Parker (1952) for the light-sensitive reactions in lettuce seed, and it may well prove that the basis of dormancy in beech-buds is directly comparable to that in light-sensitive seeds.

It is of interest to consider how far the time of bud-break in beech is controlled by daylength under natural conditions. It is well-known that with many woody species it is necessary to chill the buds for a certain period before normal breaking will ocur. Once this low-temperature requirement

has been met, however, the buds will expand when transferred to higher temperatures regardless of the daylength conditions, and even in complete darkness. This is true, for example, of Pinus silvestris (Wareing, 1950), Acer pseudoplatanus, Quercus robur, Robinia pseudacacia etc. (author, unpublished). The behaviour of beech is markedly different, however, since even after a prolonged period of chilling the buds still require exposure to relatively long photoperiods before they will expand (p. 696). This agrees with the observations of Klebs (loc. cit.) that even when beech twigs were collected from out-of-doors as late as 25th March, the buds did not break dormancy if transferred to a warm, dark cupboard. Klebs also observed that beech seedlings kept in a warm greenhouse remained dormant throughout the winter, but expanded in March, and the present author has confirmed this result. These observations suggest that under warm conditions the breaking of dormancy of beech will not occur until the natural daylength exceeds about 12 hours. Under natural conditions in Great Britain, however, bud-break in beech occurs somewhat later than in the greenhouse, which suggests that temperature conditions may be the controlling factor in this region. In regions with higher spring temperatures (the geographical distribution of beech includes, for example, Spain and the Crimea), daylength may, however, possibly become the controlling factor for the time of bud-break. The occurrence of a photoperiodic mechanism controlling the time of bud-break in a species which has no chilling requirement suggests that photoperiodism may be of special importance for the breaking of dormancy in woody species in tropical and sub-tropical regions.

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Summary

1. It is shown that the stimulation of bud-break in beech (*Fagus sylvatica* L.) by light is a photoperiodic phenomenon. The buds of leafless seedlings of beech readily break dormancy under long days, but remain dormant under daylengths of 12 hours or less.

2. With intact buds, the light-requirement is fully 'saturated' at an intensity of approximately 1000 lux, and there is no evidence for more than one light-controlled reaction.

3. The response of the buds appears to be governed by the length of the daily dark period, rather than by the length of the photoperiod. The buds break dormancy with cycles which include short light periods, provided that the associated dark periods also are short. Interruption of a long dark

period by a 'light-break' of one hour nullifies the effect of the dark period and results in bud-break.

4. Bud-break occurs when favourable and unfavourable cycles are given alternately.

5. When the bud-scales are removed by hand, so that the meristematic tissue is left intact, growth of the leaves and internodes is promoted by exposure to continuous illumination indicating a direct effect of light on the meristematic tissue.

6. Determinations of the light-transmissive properties of the bud-scales indicate that approximately 0.7 per cent of the incident light penetrates to the meristematic tissue. Hence with incident light of 1000 lux intensity, the effective intensity within the bud is of the order of 7 lux. Stimulation of growth of 'de-scaled' buds occurs with light intensities as low as 20 lux.

7. It is shown that beech buds appear to have no 'chilling' requirement, and that the time of bud-break under natural conditions may in some regions be controlled by seasonal changes in daylength.

8. It is postulated that the photo-reaction involved in these effects corresponds to the 'secondary light reaction' observed in the photoperiodic control of flowering in herbaceous species. This same reaction may be of general occurrence in normal leaf- and internode-development.

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