OBSERVATIONS ON THE FLOWERING PHOTOPERIODICITY

by

G. L. FUNKE
(from the Botanical Institute of the Government University, Leyden)

(With Tab. I-IV).

CONTENTS

A The flowering photoperiodicity in different ranges of wave length.

1) Introduction.

From 1936 till 1940 in Ghent, Belgium, I investigated the flowering photoperiodicity of a large number of plant species in different ranges of wave length (19,a-b-c-d-e). The plants received full day light from 7 a.m. till 3 p.m.; for the rest of the day they were covered, partly by dark cases, partly by white (limed), red and blue glass; check plants remained in the open air. The different sorts of glass transmitted approximately an equal quantity of solar energy. The place of the experiment was such that during the hours when the plants were covered, the sun did not shine directly upon the glass. Temperature and humidity of the air under the glass cases, therefore, were only slightly different from those outside; yet flowering under the white glass was sometimes earlier than with the check plants, owing to a little more favorable conditions during the night.

"Dark" or *D* means plants which got full day light from 7 a.m. till 3 p.m.; "red" or *R*, "blue" or *B* and "white" or *W* means plants which were exposed to full day light from 7 a.m. till 3 p.m. and resp. red, blue and white light from sunrise till 7 a.m. and from 3 p.m. till sunset.

According to their reactions the plants could be divided into 4 groups:

Group I: $\boxed{W - R}$ $\boxed{B - D}$: "red" flowers at the same time as "white", "blue" at the same time as "dark"; the flowering of long day plants is favoured by a long white as well as by a long red day; "blue" and "dark" hasten the flowering of short day plants.

Group II: $\boxed{W - R - B}$ $\boxed{D}$: "red" and "blue" flower at the same time as "white"; the colour of the light is of no importance.

Group III: $\boxed{W}$ $\boxed{R - B - D}$: flowering of long day plants only in "white"; neither red nor blue rays have any furthering influence; vice versa for short day plants; only a small number of species belonging to this group were found up till now.

Between groups I, II and III all sorts of transitional cases occur.

Group IV: $\boxed{W - B}$ $\boxed{R - D}$: the opposite of group I: "blue" flowers at the same time as "white", "red" at the same time as "dark". This group seems to stand by itself; all species which in my experiments were found to belong to it are *Crucifers*; other members of this family, though, belong to groups II and III. (Since 1942 I can add *Cheiranthus Allionii* to group IV).

For the moment I am not able to give a satisfactory explanation of these opposite responses. The action of light exerted upon countless processes in plant life is so complicated and as yet so little understood in many respects, that a discussion on the present problem would be merely speculative; comp. No. 8.

During 1941 and 1942 I continued these researches in the garden of the Botanical Institute at Leyden. The red and blue glasses which I had at my disposal were of a rather dark colour; they transmitted less than half of the solar energy than did those which I used in Ghent[1]); especially on clouded days the light intensity in the different compartments was very low. Such conditions may cause errors for some species (see 47b), but those which I investigated appeared to be sufficiently sensitive to small quantities of light. (BORTHWICK and PARKER, 6c, observed in their experiments on Biloxi soy beans that any intensity above 0.5 f.c. of the supplementary light acts like natural day light.) Moreover, I repeated the experiments made with a number of species at Ghent under the glasses at Leyden and in both conditions they yielded identical results. One of them was *Lycopus europaeus*, a long day plant which is very typical for group I; the specimens used in 1941 proved to be quite consistent in these respects with those of 1938 (19c); the photograph made at Ghent (l.c., p. 411) could be that of the plants grown in the experiment at Leyden. Other species were *Anthemis tinctoria* and *Iberis amara*. Their responses to the different treatments have been described elsewhere (19c, f) and only a few supplementary remarks on them are needed here.

2) Supplemental observations on Anthemis tinctoria and Iberis amara.

Anthemis tinctoria is a long day plant and belongs very distinctly to group I. Short day treatment suppresses the longitudinal growth as well as the different stages of the reproductive organs (19d). A long day induction during April, however, followed by a short day treatment during the ensuing 3½ months is sufficient to determine a nearly normal growth of the whole plant (19f). Therefore I applied the opposite treatment in 1942, viz. eight hour days during April followed by natural day length. Specimens were subjected to resp. 10 (1-11/IV), 20 (1-21/IV), 30 (1/IV-1/V) and 40 1/IV-11/V) short days and then transplanted to the "white" compartment. These short day inductions had hardly any effect, all plants flowered in June simultaneously with the control specimens; only those which had

---

[1]) Transmission resp. ± 20 % and ± 40 % of the visible solar energy.

remained 40 days at 8 hours light were somewhat retarded, but not more than a few days. Therefore, an even considerable period of short day induction during April is of no importance, when it is followed by long days, whereas the opposite, a long day induction at the same time of the year counterbalances the retarding influence of a great number of ensuing short periods.

This holds true for adult plants; seedlings appeared to deviate in their sensitiveness to photoperiod. In 1941 I collected seeds from plants which had been treated in various ways; they germinated and developed similarly when grown in similar conditions; when, however, they were sown in the different compartments, their growth deviated accordingly, viz. in C, W and R they developed into high growing plants which during the summer formed a great number of flowers; in B and D, on the other hand, they remained low and rosette-like and there was no trace of reproductive organs. This last fact is quite what we should expect, but the scanty vegetative development in B is rather surprising. For long day plants any long day, whether of the natural length, or 8 hours ordinary light supplemented by red or blue during morning and evening, allows sufficient formation of growth substances (11, 47, 48) or metaplasin (30e) for a normal vegetative development. I confirmed this in a large number of species during last summer, a.o. in seedlings of *Lysimachia ciliata*, *Scrophularia nodosa*, *Teucrium chamaedrys*, *Iberis amara*, several species of *Sedum*, etc.; in former years I observed the same phenomenon in e.g. *Centaurea montana*, *C. Cyanus*, *Escholtzia californica*, *Mimulus luteus*, *Trifolium pratense*. Adult plants behave similarly (e.g. *Matricaria inodora*, *M. chamomilla*, *Lycopus europaeus*, *Brunella vulgaris*, *Rudbeckia speciosa*), but in the case of *Anthemis* we see that 8 hours of day light supplemented by blue light are sufficient for adult specimens to allow a normal vegetative growth and that they are not for seedlings; a long red day is sufficient for both.

Short day plants, as a rule, develop equally well in short day as in any sort of long day, e.g. *Perilla*, *Hedera*, *Cosmos*; there are exceptions, however, e.g. several varieties of *Glycine* (see below) and of *Chrysanthemum indicum* (19a), which in this respect behave like long day plants; according to CAJLACHJAN and ZDANOVA (11) this should be the rule.

The seedlings of *Anthemis* deviate from adult plants in still another point. We saw that a month of long day induction in early spring overbalances the effect of 3½ ensuing months of short days. Seedlings which received long day treatment from the sowing time, March 18th, till June 4th, therefore during 2½ months, and which were then transported for not more than 6 weeks in the "dark" division, remained small and rosette-like; since July 20th they received again a long day illumination but nevertheless they did not elongate until the second half of August; yet at the end of the season they had hardly reached half of the height of the specimens in C, W and R and they showed no indication of flower buds. Therefore adult plants and seedlings behave similarly as far as the formation of reproductive organs is concerned, but their vegetative response to a long blue day is widely different. It would be worth while to investigate the content and the production of auxins in a long blue day in specimens of different age (comp. 43f).

Iberis amara is a long day plant and up till now the species most representative for group IV which I have ever found (19c); in 1938 at Ghent C, W and B flowered simultaneously in the end of June and the beginning of July; R flowered in the middle of August and D opened a small number of flower buds only during September. The retardation caused by the red glass, therefore, was about 45 days, that by the dark covering at least 75 to 90. The variety upon which I experimented in 1941 at Leyden was most probably not identical with that of Ghent; the flowers were purely white, whereas at Ghent they were a light violet. C, W and B flowered in the end of June, R in the middle of July and D in the beginning of August; the retardation, therefore, is much less than in the former experiment, viz. resp. about 20 and 30 days. If the colour of the red and blue glasses had indeed been too dark to give reliable results, we should have seen perhaps a retardation of flowering under the blue glass and certainly a stronger one than that which occurred under the red glass; as neither took place we may feel assured that the transmission of the solar energy, though slight, was sufficient. The results show that the variety of 1941 reacted principally in the same way as the one at Ghent, but that its flowering times are shifted closer together, owing perhaps to a stronger formation of florigen.

3) Glycine.

On May 16th 1941 *Glycine hispida*, *G. hispida* var. *nigra* and *G. soja* were sown in a heated compartment and on May 28th they were between 6 and 8 cm high; the experiment began on that day with 6 specimens of each of the three varieties per division. After a few days differences were already visible in so far that the plants in D of all three varieties remained smaller than the others and that their leaves showed a yellowish green colour and were more or less crinkled, whereas those in C, W, R and B were bluish green and smooth. On June 27th the average height of the plants was as follows:

in C 23, W 22, R 25, B 29 and D 14 cm; and throughout the season the plants in D maintained this low growth. On July 7th the first flowers were seen in D and B, on July 14th there were ripening pods in these divisions whilst the first flowers appeared in R and soon afterwards also in C and W. The three varieties, therefore, are short day plants, although not very typical ones (comp. the variety *Biloxi*, 38 and 45a); they belong very distinctly to group I, which is illustrated by table 1.

TABLE 1. *Glycine*; number of ripening pods on July 15th 1941.

	control	"white"	"red"	"blue"	"dark"
G. hispida	0	0	1	8	7
G. hisp. var. nigra	0	1	2	7	9
G. soja	0	0	2	12	17

The advance of flowering in D and B as compared with R is not more than a week, with C and W a few days more, but as the pods ripened this difference became greater and especially C remained far behind. The dates of harvesting in the several divisions show this very clearly, especially for *G. hispida* and *G. nigra*; see table 2. The period between the average dates of harvesting in C on one side and W and R on the other is striking and presents another example of the far going influence of the temperature which must have been somewhat higher in the compartments W and R during the night when they were covered. There are many examples known where the temperature exerts an important action on the flowering and ripening processes, even more so than the photoperiod. PARKER and BORTHWICK (45b) observed in the *Biloxi* soy bean that the "initiation of flower primordia was influenced to a much greater extent by variation in temperature during the dark period than by variation during the photoperiod". This tallies well with my results; for the rest I refer to Nos. 1, 3, 12, 24, 29, 31, 34, 38, 46a, 46b, 51, 52, 57 and refrain from mentioning the effect of yarovization.

TABLE 2. *Clycine*; time of harvesting in 1941.

	control	"white"	"red"	"blue"	"dark"
G. hispida	6/X	17/IX	17/IX	4/IX	4/IX
G. hisp. var. nigra	6/X	17/IX	17/IX	27/VIII	27/VIII
G. soja	6/X	8/IX	8/IX	4/IX	27/VIII

Attention may be once more drawn to the fact that the short day determines a low growth in "dark" although *Glycine* is distinctly of the short day character, and that in "blue" the supplementary hours of blue light have a contrary effect on two processes: they act as white light as far as the vegetative growth is concerned, but as darkness on the formation of reproductive organs; these facts resemble those which we saw in *Anthemis*, *Lycopus* and others.

4) Hedera.

Well rooted cuttings of *Hedera amurensis hort. arborea* and of *H. colchica* Koch *arborea* were planted in April 1942, of the former 4 specimens, of the latter 2 in each compartment. In the end of June *amurensis* showed flower buds in D and a few days later in B; in R and D they appeared on July 15th and in C only on July 28th. *Colchica* presented the same order of appearance, but in all divisions about 3 weeks later. Both species, therefore, belong to group I and we see again that the higher temperature during the night under the glasses has some influence, though not so considerable as in the case of *Glycine*. The dates on which the first flowers opened presented an appropriate standard for the rate of development and therefore they are communicated in table 3. The different stages of flowering and ripening of the fruits proceeded in the same order. The covering was discontinued on August 5th but, as could be expected, this had no influence on the further development, because by that time the action of the photoperiodic induction could no more be altered. On October 26th all plants were put under white glass (not limed) to prevent them from freezing. In the middle of December the situation was as follows:

TABLE 3. Dates of opening of first flowers in *Hedera*; 1942.

	control	"white"	"red"	"blue"	"dark"
H. amur.; apical umbels	22/IX	14/IX	10/IX	18/VIII	18/VIII
lateral umbels	22/X	12/X	12/X	6/IX	6/IX
H. colch.; apical umbels	28/X	21/X	15/X	17/IX	10/IX
lateral umbels		16/XII	2/XII	28/X	25/X

amurensis C-W-R: most fruits have been shed; the remaining few still very small;
B-D: green and bluish ripening berries on the apical umbels; onset of fruiting on the lateral umbels;
colchica C: apical inflorescences just finished blossoming; lateral ones still closed;

W: apical inflorescences started fruiting; lateral ones still closed;
R: apical inflorescences started fruiting; flowers of the lateral umbels for the greater part opened;
B: green ripening berries on the apical umbels; the lateral ones have finished flowering;
D: green ripening berries on the apical umbels; most of those on the lateral ones have been shed.

It seems that shortening of the daily illumination not only hastens the flowering, but that it also favours the formation of fruits; this fact will perhaps appear to be of some practical value.

5) Sedum.

A large number of species were sown in the early spring of 1942; not all of them germinated satisfactorily and among those, which developed a sufficient number of specimens for the experiment, some did not produce flowers as is often the case in the first year with plants of this genus. Only those species will be described here which yielded explicit results.

VON DENFFER (13) showed that most species of *Sedum* present extreme types of long day plants; under short day treatment they only form tiny rosettes with very thick and dark green leaves and flowering never occurs. My plants have fully confirmed all this, but I can add that a long day induction during April, followed by short day treatment of more than 3 months stimulated the vegetative growth considerably; this recalls what we saw in *Anthemis*, but the long days in the early spring were never able to induce any reproductive stage. The response of the *Sedums* to a short day supplemented by faint red or blue light was rather remarkable.

S. Aïzoon. The experiment began on April 10th with 4 specimens in each division. Already after a few weeks it became clear that those in D stayed behind the others; they did not reach a diameter of more than a few mm and remained in this condition during the greater part of the season. The plants in C, W, R and B developed vigorously and showed no appreciable difference among each other. In the middle of July flower buds appeared in C, W, R and B; this indicates group II; soon afterwards these buds opened and the flowering lasted till the beginning of September and then most plants started flowering anew till the end of that month. The covering was discontinued on August 5th with the consequence that the specimens in D resumed their growth till the rosettes measured a few cm in diameter; they never developed beyond that. The figure 1, photographed on August 20th, gives an idea of the difference in size between the specimens in C, W, R, B on one side and in D on the other.

S. Telephium. The treatment of this species and of those which will be described further on was similar to that of *S. Aïzoon.* The contrast in size between D and C-W-R-B was as distinct as with *S. Aïzoon.*

In the end of July the specimens in C, W and B started blossoming; R and D remained vegetative; this points to group IV. In the beginning of August, however, the "red" plants formed also flower buds and since the middle of this month till the end of the season the four divisions C, W, R and B flowered abundantly, although on closer inspection it could be easily seen that R was always at a "younger" stage than the other three. None the less, anyone who had seen this species during August and September should not have hesitated to class it with group II. It therefore presents a very striking example of a transitional case between groups IV and II.

S. Selskianum. The experiment began on May 11th. Flowerbuds appeared in C and W about the middle of July and in B in the beginning of August. The plants in these three divisions blossomed since the middle of August; in R and D they were purely vegetative, but in R the supplementary light caused a development as vigorous as in C, W and B. This species, therefore, belongs to group IV. Towards the middle of September new flower buds appeared in most of the plants, also in the specimens in R, and these opened in the end of the month; this second flowering lasted till the middle of October. Whether this reproductive stage in R was determined by the discontinuation of the covering on August 5th or whether it would have taken place anyhow, can not be said for certain. The flowering of *S. Telephium* in R was certainly spontaneous, because here the buds appeared while the covering with the red glass had not yet ceased, but in the case of *S. Selskianum* we witness a further step in the direction of group IV in which this latter species should certainly be classed as far as its first blossoming stage is concerned; the restriction must be made, however, that it shows perhaps a feeble tendency towards group II which reveals itself during the second flowering stage.

S. spectabile. The first flower buds appeared towards the end of July in C, W and B. In the middle of August a few were also formed in R. The flowers opened only in the second half of September in C, W and B and on the 9th of October a small number of flowers started blossoming in R. D remained vegetative throughout the season. The retarded flowering in R combined with the poor development of the inflorescences make it probable that also *S. spectabile* belongs to group IV.

S. lividum. In the course of August part of the specimens in C and B flowered and so did some in W, but about a fortnight later; R and D remained sterile. We must wait for the full development in 1943 to decide whether we are entitled to class this species in group IV.

S. Kamtschaticum. During the last days of June flower buds appeared in C and W and a week later in R. Blossoming in these three divisions lasted from the end of July till the end of August. B developed vigorously and formed a great number of adventitious rosettes, but remained strictly sterile throughout the season. *S. Kamtschaticum*, therefore, must be classed in group I.

Sedum appears to offer many possibilities as to the flowering photoperiodicity. At least 3 out of the 4 groups which I established have representatives in this genus:

group I: *S. Kamtschaticum*;
„ II: *S. Aïzoon*; *S. Telephium* with a tendency towards IV;
„ IV: *S. Selskianum*, with perhaps a slight tendency towards II;
S. spectabile en *S. lividum* probably also belong here.

Whether the reaction of group III occurs too in this genus is still doubtful; I have obtained indications in this direction, but I must await further conclusive results.

Up till now representatives of group IV were only found among the *Crucifers*. *Sedum* offers the first example of plants not belonging to this family which find their place here.

B The reaction of reversibility.

6) Perilla.

In 1939 I investigated the photoperiodic response of *Perilla ocymoides* var. *nankinensis* to the different treatments (19d). It presents an extreme example of a short day plant which flowers in nature not before the end of September. When seedlings are submitted to an 8 hours day their vegetative development is exactly as vigorous as in long days and the flowering is advanced not less than 3 months; it takes place in the course of June after about 40 days of short day induction. Eight hours day light supplemented by red light have the same influence as the ordinary length of daily illumination. Supplemental blue light advances the flowering, but not more than about one week. *Perilla* is therefore a representative of group II which shows a very slight tendency towards group I; (a similar case was shown by 7 varieties of *Chrysanthemum indicum*, 19a,b). Practically we may take it that any supplemental light above the 8 hours daily illumination causes a long day effect.

The experiments of 1941 and 1942 yielded results identical with those made at Ghent, notwithstanding the darker colour of the glasses. At Leyden I investigated how long the short day induction should last to obtain flowering in the middle of the summer. Plants were sown in the end of March; on the 1st of May, when the experiment began, they were a few cm high and had expanded their first two pairs of leaves; their age, therefore, was appropriate for the photoperiodic induction (6b, 9d, 43f). On May 28th 1942, after 28 short days, none of the young plants in D showed any onset of flowering yet. In *Perilla nankinensis* this can be observed very easily because the bright green young inflorescences make a strong contrast with the dark violet sterile parts of the plant. I never made a microscopical examination to detect the very first stages of flowering because this was superfluous for my purpose. On the day mentioned part of the plants in C, W, R and B were transported to D; some of these were brought back to their own division after 7 days (4/VI), others after 14 (11/VI) and after 21 days (18/VI). On June 29 th the whole material was transplanted in full day length, but at a shaded place, because strong light furthers the flowering (32c, 39, 55). The condition of the plants on this day was as follows: the specimens which had been under short day from 1/V to 29/VI were in full flowering since the middle of June; all the others were vegetative without any trace of inflorescences. In the course of July, however, the specimens which had received 14 and 21 short days started flowering, about 40 days after the beginning of the induction (comp. 43h); 7 short days had no influence at all; the critical induction period must therefore lie between 7 and 14 days (43e).

We see that 14 and 21 short days, followed by natural day length (or by long blue or long red days) have an influence similar to that of continuous short day treatment as far as the formation of flowers is concerned. The after effect of these induction periods, however, is fundamentally different. The plants which flower after 40 short days form seeds and then die; their life cycle is ended in the course of August. The others show the phenomenon which has been called by Russian scientists the reaction of reversibility (7, 9, 39, 55). This means that when the flowering stage comes to an end the stems of the inflorescences resume their growth so that new vegetative shoots are formed with large leaves. The axes elongate considerably during this process with the consequence that the remains of the flowers are shifted far from each other. This is clearly visible on the photo in figure 2 (comp. fig. 3 in 9c); in this specimen only the main axis was reverted; the lateral branches have the same capacity as can be seen in figure 3. This reversibility occurred in 100 % of my plants (comp. 55) and mostly in all branches, with the consequence that they gave the luxuriant impression which is clearly illustrated in figure 3. The phenomenon is easily explained: when the premature flowering, determined by artificial short days during the early part of the summer, is ended, the daily illumination is still sufficiently long to induce vegetative development. The florigen which has been synthesized during the 14 or 21 days of 8 hour induction has caused the formation of flowers and even of seeds (comp. 9d), but there was not enough of it to keep the plants in a condition of continuous sexual maturity and to prevent them from synthesizing auxins as well. The formation of the latter is apparently checked by an induction of 40 short days; (in one instance, though, I obtained a very fine reversal after an induction of 34 days). After a short induction period, therefore, external and internal conditions are favorable for a continuation of the growth and this is what actually takes place; I will come back to this point farther on.

In the second half of September, with the shortening of the days, all plants started flowering; that means that the specimens which had received the full daily illumination in C, W R and B blossomed for the first time; those which previously had been reversed did so for the second time. This reproductive stage lasted till the end of October and then all plants died.

Therefore it is possible to obtain two reproductive stages during the same season in *Perilla nankinensis*, alternating with vegetative ones, by the simple method of giving 14 short days in the beginning of the summer; all other sorts of interference, grafting, stripping off the inflorescences, decapitating, etc. are unnecessary.

In 1941 I obtained similar phenomena by grafting branches of short day specimens on long day stocks and vice versa (wedge in split grafts). The combinations remained in long day conditions. Also in these experiments it appeared to be quite unessential whether the long day was the natural one or that in "blue" or "red". Most of the short day scions or stocks showed the reversal as has been described above and also a second flowering stage in the autumn. Short day scions acted upon the long day stocks and caused them to flower earlier than normally and the same is true for the action of short day stocks on long day scions; the florigen, therefore, can be transported upward and downward; this is only a confirmation of what has been found by others (9b, c, e, f; 10; 28; 43g; etc.).

CAJLACHJAN cut the flowering branches of the short day partner in order to induce the reproductive stage in the other one with greater certainty; he also cut the leaves from the long day scions grafted on the blossoming stock (10). It appears that this is not strictly necessary, although those leaves certainly exert a retarding influence on the formation of flowers.

I observed another fact which is worth while mentioning. Not all short day partners showed the reversal, but their contact with the long day ones in this case made itself felt all the same, in so far that it lasted a very much longer time, between 1 and 2 months, before they ended their flowering and died; their life cycle, therefore, was considerably lengthened and in my opinion this can only be explained by the assumption that they got auxins from the long day partners which enabled them to continue their existence beyond the normal period. CAJLACHJAN and ZDANOVA (11c) come to the conclusion that "the growth hormones play no decisive part in plants passing from the vegetative growth to reproductive development". This is not necessarily in contradiction with my views. The movement of auxins in grafts, therefore, can also be achieved in both directions. If my interpretation of these facts is correct, it confirms what I said above; there seems to be a balance between the production of auxins and of florigen; the former keeps the plant in a vegetative condition; a great amount of the latter induces flowering and a rapid closing of the life cycle; with a smaller quantity of it and provided the circumstances, viz. the length of the day, are appropriate, the synthesis of auxins is resumed and we observe the phenomenon of reversal. CAJLACHJAN in describing this reaction (9b) says a.o. the following: "In plants having a high capacity of regenerating new growing points, as, for example, hemp and perilla, these new formed growing points receive an insufficient quantity of the flower hormone, since a large part of it has already gone into the earlier formed shoots. Consequently, the shoot, on beginning to flower, passes again to vegetative growth — that is, the phenomenon of reversibility of reaction occurs." He seems to take it for granted that an amount of florigen, insuffient for flowering, implies automatically the possibility of further vegetative growth. We see that in my experiments the amount was quite sufficient for the formation of flowers and even of seed and yet vegetative reversal remained possible.

BORMANN (5) supposes that florigen should be destroyed in order that reversal may occur (l.c., pag. 727: „Entsprechend wäre für die Umstimmung zur vegetativen Phase vielleicht eine Zerstörung dieser Wirkstoffe anzunehmen."). This idea does not deviate far from mine; there is indeed nothing which opposes itself against a new formation of florigen towards the second flowering stage; (compare also the very interesting suggestions of STEIN, 50).

Perilla ocymoides differs considerably from its variety *nankinensis* in many points and also its responses to photoperiodic induction, though principally the same, deviate from that of *nankinensis* in more than one respect. It is a short day plant, but less distinctly so because in natural surroundings it flowers in the end of August, at least a month earlier than *nankinensis*. Long red and blue days have the same effect as natural day length.

When seedlings are kept under continuous 8 hour treatment during May, flowering sets in after about 40 days and is finished in the end of June; the plants die in August or in the end of July. (From VAKULINS description I must conclude that his material deviated from mine; the same holds true for that of BOUSLOVA and LUBIMENKO; that of MOSHKOV, 43f, agrees with my experience).

A number of specimens were subjected to 7, 14 and 21 short days, resp. from 9 till 16/VI, from 9 till 23/VI and from 9 till 30/VI; their development is summarized as follows:

TABLE 4. Development of *Perilla ocymoides*.

	in the end of July	in the beginning of September
specimens which got 7 short days	onset of flowering; beginning of reversal	reversal and second flowering
idem 14 sh. days	flowering, indication of reversal	dead
idem 21 sh. days	flowering finished, dying	since long dead

In my experiments the reversed inflorescences of *ocymoides* were different from those in *nankinensis*; the apical axis was equally elongated, the bract leaves became larger, but an entirely new shoot with normal leaves never developed; the lateral axes were similarly changed. A very striking fact, however, was that there were two inflorescences in each axil in serial order. The aspect of the plant with its densely foliated and numerous inflorescences was very luxuriant, as was the case in *nankinensis*, and varied widely from that of the control specimens; the aftereffect of one week short day treatment was therefore very considerable indeed.

We can draw the following comparison between *P. ocymoides* and *nankinensis*; see table 5:

TABLE 5. Effect of short day induction upon *P. ocymoides* and *nankinensis*.

	P. ocymoides	*P. nankinensis*
Effect of 7 short days	premature flowering, reversal and 2d flow.	no influence
Effect of 14 short days	premature flowering, reversal, death	premature flowering, reversal and 2d flowering
Effect of 21 short days	premature flowering, death	premature flowering, reversal and 2d flowering

We see that in *ocymoides* a smaller number of short days is sufficient to induce premature flowering, reversal and second flowering than in *nankinensis*; it seems as if the former is more sensitive to florigen and that a larger quantity hastens the end of its life cycle, whereas *nankinensis* needs this larger quantity in order to show the after-effects.

On October 15th 1941 I found another case of reversibility in the Botanical Garden at Leyden, viz. a branch of *Epilobium angustifolium* which had developed a large vegetative shoot after the flowering period; see figure 4. A not quite similar case has been described by FRICKE (18, pag. 286): „Im folgenden Herbst" (1925) „war im Garten des Instituts" (München) „Epilobium angustifolium vegetativ geworden. Sowohl die Hauptblütenstände als auch die seitlichen aller Pflanzen waren fast ausnahmslos in Laubtriebe übergegangen. Zwar standen in den Achseln dieser Blätter noch verkümmerte Blüten, aber offenbar waren die Infloreszenzen wieder vegetativ geworden unter dem Einfluss der milden Witterung."; page 287: „Wir stellten also fest: bei Pflanzen mit labil veranlagten Infloreszenzen bewirkt eine „Verdünnung" der organischen Substanzen die Umbildung der Infloreszenzen in Laubtriebe. Bei relativ. stabiler Potenzierung dagegen ist experimentell höchstens die Bildung von Laubsprossen aus den Achseln der Hochblätter zu erreichen." FRICKE's interpretation dates from a time when photoperiodism was still unknown; therefore we need not discuss it here. The reversal of *Epilobium* has nowhere else been described as far as I could ascertain. I do not know if the phenomenon is rare; last autumn I found a large number of plants in the Zuiderpark, the Hague, where most specimens showed it more or less distinctly, though none so well as the one on figure 4. The weather conditions of 1942 were perhaps favorable for its production; in the Botanical Garden at Leyden it was also common, whereas in 1941 I observed it on one branch only.

Up till now I have never succeeded in obtaining other cases of reversibility in my experiments, nor have I observed them in nature. BORMANN mentions a fairly great number of them, most of which were not grown experimentally though. In older publications (18, 22, 32, 56 and the literature cited there) many cases are mentioned which are not yet explained, but in which photoperiodism is certainly an important factor, if not the only explanatory one.

How the equilibrium of a plant can be upset by a few days of photoperiodic induction was a.o. neatly demonstrated by *Scrophularia nodosa.* As this long day plant formed inflorescences I transported specimens to a dark compartment in order to induce the reaction of reversibility. This did not succeed and contrary to any expectation the blossoming was hastened by the treatment and the more so the younger the inflorescences were. The most striking feature was presented by some very young spikes which were only about 10 mm high. The flower buds were of course tiny and utterly immature; nevertheless, after not more than 8 short days they swelled and took on a dark violet colour; one flower opened a day later and another after three days; their size was normal and therefore quite out of proportion with the small spikes which by that time had elongated to 15 mm. Still three days later the inflorescences were dead.

When we consider these and various other consequences which can be determined by a photoperiodic induction, even when it is a short one, abnormalities in the several stages of the reproductive organs (2, 6a-b-c, 15, 21, 23, 27, 30a-b-c, 37), reversal of sex (40,49, 53, 54), reversal from vegetative into generative phase and vice versa (8, 14, 16, 20, 24, 26, 30e-f, 31, 35, 36, 41, 42), cleistogamic instead of chasmogamic flowers (4), etc. (17, 25, 33, 43b-c-d, 44), we may safely admit that further experiments in this direction and more extensive observations in the field will certainly add valuable material to the physiology of flowering and to what I would call the experimental photo-teratology.

SUMMARY.

According to their reactions to different photoperiodic treatments plants can be divided into 4 groups; a definition of these groups is given on page 393.

Anthemis tinctoria is a long day plant and belongs to group I. A long blue day, that means natural day light from 7.— a.m. till 3.— p.m. supplemented by blue light from sunrise till 7.— a.m. and from 3.— p.m. till sunset, suppresses the formation of reproductive organs in seedlings as well as in older plants. In seedlings, moreover, it

checks the vegetative development whereas older plants grow normally under these conditions.

Iberis amara is a long day plant and belongs to group IV. The variety investigated in 1941 reacted principally in the same way as the one of 1938 at Ghent, but the blossoming times in the various compartments were shifted closer together; the retardation in "red" and "dark", which was as much as 45 and 90 days at Ghent, was reduced to about 20 and 30 days; this is perhaps due to a greater production of florigen.

Glycine hispida, G. hispida var. *nigra* and *G. soja* are short day plants, but a somewhat higher temperature during the night is a stronger stimulation for the flowering and especially for the ripening of the fruits than the 8 hour day. The three varieties belong very distinctly to group I.

Hedera amurensis hort. and *H. colchica* Koch forma *arborea* are short day plants and very typical for group I.

Sedum: all species investigated are extreme long day plants. *S. Kamtschaticum* belongs to group I; *S. Aïzoon* to group II; *S. Telephium* is transitional between II and IV; *S. Selskianum* belongs to group IV with perhaps a slight tendency towards II; *S. spectabile* and probably also *S. lividum* are to be classed in group IV. *Sedum* offers the first examples of plants belonging to group IV which are not *Cruciferae.*

Perilla ocymoides and *P. ocymoides* var. *nankinensis*: both varieties, but especially *nankinensis* are extreme types of short day plants belonging to group II. In natural day length they remain vegetative till the end of September. When the natural illumination is interrupted in May by a small number of short photoperiods they blossom in the middle of the summer and afterwards they show the reaction of reversibility, that is, the axes of the inflorescences resume their vegetative growth; towards the end of the season a second flowering stage follows. There seems to exist an equilibrium between the formation of florigen during short days and of auxins during long days. A large quantity of florigen, due to a great number of short photoperiods, checks the formation of auxins with the consequence that after the first flowering stage growth is not resumed and the life cycle comes to an end. *Ocymoides* is more sensitive in this respect than *nankinensis*; in the former 7 short days determine the premature flowering, reversal and second flowering; 14 short periods induce premature flowering, but prevent the reversal, the plants die; in the latter variety 7 short days have no influence, but 14 determine the onset of flowering, reversal and second reproductive stage.

A case of reversibility in *Epilobium angustifolium* is reported; this

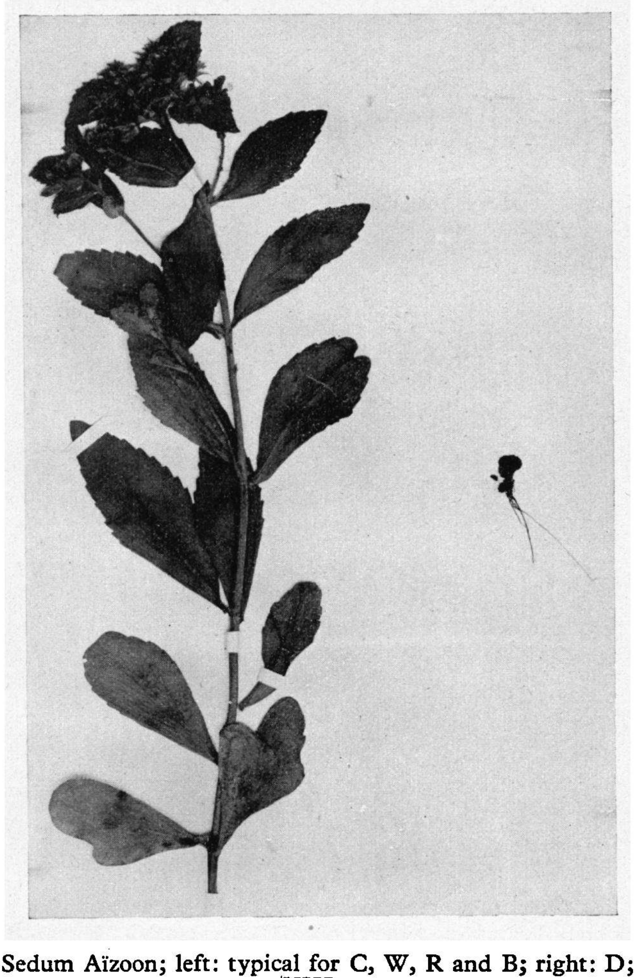

Fig. 1. Sedum Aïzoon; left: typical for C, W, R and B; right: D; Leyden, 20/VIII-1942.

TAB. II

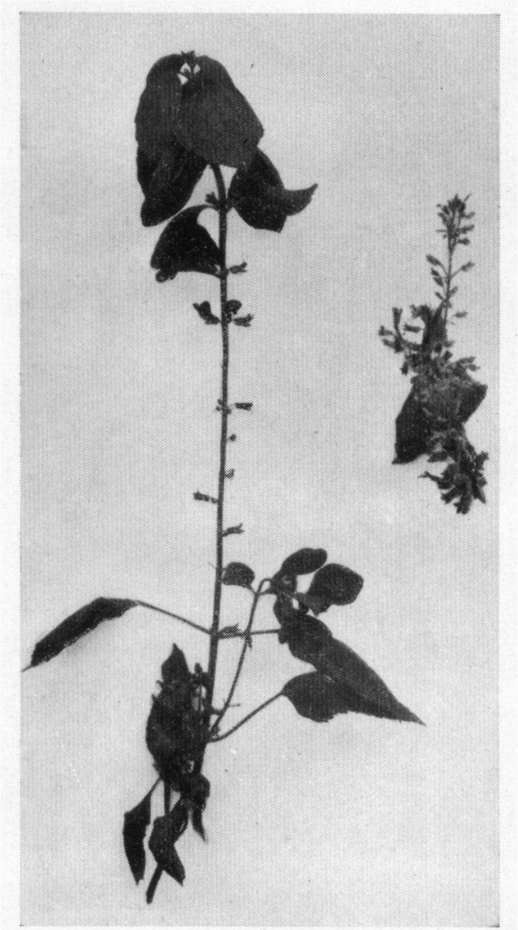

Fig. 2. Perilla nankinensis; left reversed and right control inflorescence, both from a grafted plant; Leyden, 3/IX-1941.
(*Cliché De Natuur, by courtesy of the Hofstaddrukkerij. the Hague*).

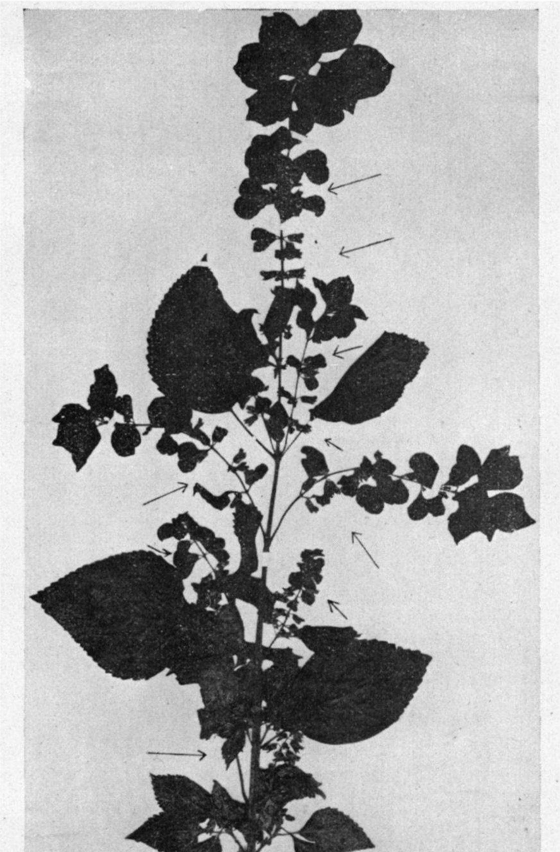

Fig. 3. Perilla nankinensis; short day from 28/V till 18/VI; before and afterwards long day; apical and lateral inflorescences reversed; arrows indicate flowers; Leyden, 14/VIII-1942.

TAB. IV

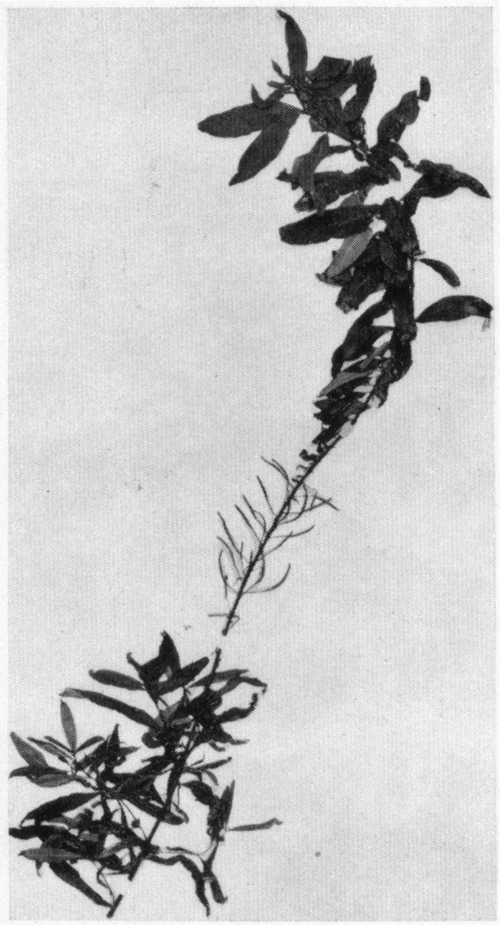

Fig. 4. Epilobium angustifolium; reversed inflorescence; Leyden, 15/X-1941. *(Cliché De Natuur, by courtesy of the Hofstaddrukkerij, the Hague).*

is also most probably due to photoperiodic induction. It is suggested that closer observation in nature and more experiments can add valuable material to the physiology of flowering and to the experimental phototeratology.

I want to express my heartfelt thanks to everyone in the Botanical Institute, the National Herbarium and the Botanical Garden at Leyden who helped me to carry out these researches.

Leyden, Botanical Institute. December 1942.

LITERATURE.

1. Abakumova, M., *C. R. Ac. Sc. U.R.S.S.*, **18**, 105 (1938), „On the problem of photoperiodical and temperature after-effects".
2. Biddulph, O., *Bot. Gaz.*, **97**, 139 (1935), „Histological variations in Cosmos in relation to photoperiodism".
3. Blaauw, A. H., *Proc. Kon. Ned. Ac. Wet. Amst.*, **44**, 684 (1941), „On the relation between flower-formation and temperature II (Bulbous Irises)".
4. Borgström, G., *Nature*, **144**, 514 (1939), „Formation of cleistogamic and chasmogamic flowers in wild violets as a photoperiodic response".
5. Bormann, J., *Planta*, **29**, 679 (1939), „Untersuchungen über die künstliche Umwandlung von Blütenständen in Laubsprosse".
6. Borthwick, H. A. and Parker, M. W., (a) *Bot. Gaz.*, **99**, 825 (1938), „Influence of photoperiods upon the differentiation of meristems and the blossoming of Biloxi soy beans"; (b) *ibid.*, **100**, 245 (1938), „Effectiveness of photoperiodic treatments of plants of different age"; (c) *ibid.*, **100**, 374 (1938), „Photoperiodic perception in Biloxi soy beans"; (d) *ibid.*, **101**, 341 (1930), „Photoperiodic responses of several varieties of soy beans"; (e) *ibid.*, **101**, 806 (1939), „Floral initiation in Biloxi soy beans as influenced by age and position of leaf receiving photoperiodic treatment".
7. Bouslova, E. D. et Lubimenko, V. N., *C.R. Ac. Sc.U.R.S.S.*, **14**, 143 (1937), „Influence de l'induction lumineuse sur le développement de Perilla ocymoides I".
8. Burkholder, P. R., *Bot. Rev.*, **2**, 1 and 97 (1936), „The role of light in the life of plants".
9. Cajlachjan, M. C., *C.R. Ac. Sc. U.R.S.S.*, (a) **1**, (**10**), 89 (1936), „On the mechanism of photoperiodic reaction"; (b) *ibid.*, **3** (**12**), 443 (1936), „On the hormonal theory of plant development"; (c) *ibid.*, **4** (**13**), 79 (1937), „New facts in support of the hormonal theory of plant development; (d) *ibid.*, **16**, 227 (1937), „Concerning the hormonal nature of plant development processes"; (e) *ibid.*, **18**, 607 (1938), „Motion of blossom hormone in girdled and grafted plants"; (f) *ibid.*, **27** (1940), „Translocation of flowering hormones across various plant organs" I p. 160, II p. 255, III p. 373.
10. Cajlachjan, M. C. and Yarkovaja, L. M., *C.R. Ac. Sc. U.R.S.S.*, **15**, 215 (1937), „New facts in support of the hormonal theory of plant development II".

11. Cajlachjan, M. C. and Zdanova, L. P., (a) *C.R. Ac. Sc. U.R.S.S.*, **19**, 107 (1938) „Hormones of growth in formation processes I Photoperiodism and creation of growth hormones"; (b) *ibid.*, **19**, 219 (1938), „The role of growth hormones in form-building processes II Yarovization and formation of growth hormones"; (c) *ibid.*, **19**, 303 (1938), „id. III Effect of heteroauxin treatment of seeds upon growth and development of plants".
12. Canel, M., *Arch. Fitotécn. Uruguay*, **3**, 9 (1938), „Influencia del fotoperiodo y de la temperatura sobre el desarrollo del maiz" (*Biol. Abstr.*, **14**, No. 9376).
13. Denffer, D. von, *Jahrb. wiss. Bot.*, **89**, 543 (1941), „Über die photoperiodische Beeinflussbarkeit von Habitus und Sukkulenz bei einigen Crassulaceen-arten".
14. Eghis, S. A., *Mem. Inst. Agron. Leningrad*, **5**, 5 (1928), „Contribution to the question on photoperiodism with soy beans and corn" (Burkholder).
15. Eguchi, T., *Proc. Imp. Ac. Tokyo*, **13**, 332 (1937), „Effects of the day length upon the time of differentiation of flower bud and subsequent development to flowering".
16. Emerson, R. A., *Journ. Hered.*, **15**, 41 (1924), „Control of flowering in Teosinte" (Burkholder).
17. Ernst, H., *Ber. D. Bot. Ges.*, **59**, 351 (1941), „Die photoperiodische Reaktion bei autotetraploidem Antirrhinum majus L.".
18. Fricke, G., *Planta*, **2**, 249 (1926). „Über die Beziehungen der Hochblätter zu den Laubblättern und Blüten".
19. Funke, G. L., (a) *Biol. Jaarb.*, **3**, 225 (1936), „Proeven over photoperiodiciteit bij verschillend gekleurd licht I" (with a summary in English); (b) *ibid.*, **4**, 345 (1937), idem II; (c) *ibid.*, **5**, 404 (1938), idem III; (d) *ibid.*, **6**, 351 (1939), idem IV; (*e*) *C. R. Congrès A.F.A.S.*, **63**, 1003 (1939), „Le photopériodisme"; (f) *Proc. Kon. Ned. Ac. Wet. Amst.*, **44**, 989 (1941), „The photoperiodic responses of Anthemis tinctoria in different ranges of wave length".
20. Gardner, V. R., *Univ. Mo. Agr. Exp. St. Bull.* 57 (1923), „Studies in the nutrition of the strawberry" (Burkholder).
21. Gerhard, E., *J. Landw.*, **87**, 161 (1904), „Über die Entwicklung der Pflanzen unter dem Einfluss der Tageslänge und der Temperatur im Jugendstadium".
22. Goebel, K. von, (1908), „Einleitung in die experimentelle Morphologie der Pflanzen".
23. Hamner, K. C., (a) *Bot. Gaz.*, **99**, 615 (1938), „Correlative effects of environmental factors on photoperiodism"; (b) *ibid.*, **101**, 658 (1940), „Interrelation of light and darkness in photoperiodic induction".
24. Hamner, K. C. and Bonner, J., *Bot. Gaz.*, **100**, 388 (1938), „Photoperiodism in relation to hormones as factors in floral initiation and development".
25. Hamner, K. C. and Long, E. M., *Bot. Gaz.*, **101**, 81 (1939), „Localization of photoperiodic perception in Helianthus tuberosus".
26. Hamner, K. C. and Naylor, A, W., *Bot. Gaz.*, **100**, 853 (1939), „Photoperiodic responses of dill, a very sensitive long day plant".
27. Harder, R., *Ber. D. Bot. Ges.*, **58**, 70 (1940), „Scheinblüten und Blühhormonmenge".
28. Harder, R. und Gümner, G., *Biol. Zbl.*, **62**, 132 (1942), „Weitere Beobachtungen über Fernbeeinflussung der Blattform unter photoperiodischen Bedingungen".

29. **Harder, R.** und **Störmer, I.**, *Landw. Jahrb.*, **83**, 401 (1936), „Über Entwicklungsbeschleunigung im Kurztag durch Kältenachwirkung".
30. **Harder, R.** und **Witsch, H. von**, (a) *Jahrb. wiss. Bot.*, **89**, 354 (1940), „Über den Einfluss der Tageslänge auf den Habitus, besonders die Blattsukkulenz, und den Wasserhaushalt von Kalanchoë Blossfeldiana"; (b) *Planta*, **31**, 192 (1940), „Über die Bedeutung des Alters für die photoperiodische Reaktion von Kalanchoë Blossfeldiana"; (c) *ibid.*, **31**, 523 (1940), „Über die Einwirkung von Kurztagblättern auf im Langtag befindliche Blätter und Stengelteile der gleichen Pflanze Untersuchungen zur Frage nach einem formbeeinflussenden Wirkstoff"; (d) *Gart. wiss.*, **15**, 226 (1940), „Wirkung von Photoperiodismus und Yarowisation auf die Blütenbildung von Kalanchoë Blossfeldiana"; (e) *Nat. wiss.*, **29**, 770 (1941), „Über die Bedeutung der Kohlensäure und der photoperiodischen Belichtung für die Blütenbildung bei Kalanchoë Blossfeldiana"; (f) *Nachr. Ak. Wiss. Gött., Math. phys. Kl*, **84** (1941), „Blühhormonleitung und Entstehung verlaubter Blütenstände (Untersuchungen an Kalanchoë Blossfeldiana)"; (g) *Planta*, **32**, 547 (1942), „Weitere Untersuchungen über die Veränderung der photoperiodischen Reaktion von Kalanchoë Blossfeldiana mit zunehmendem Alter der Pflanzen".
31. **Harder, R.**, **Witsch, H. von** und **Bode, O.**, *Jahrb. wiss. Bot.*, **90**, 546 (1942), „Über Erzeugung einseitig und allseitig verlaubter Infloreszenzen durch photoperiodische Behandlung von Laubblättern".
32. **Klebs, G.**, (a) (1903), „Willkürliche Entwicklungsänderungen bei Pflanzen"; (b) *Biol. Zbl.*, **24**, 257 (1904), „Über Probleme der Entwicklung"; (c) *Flora*, **111—112**, 128 (1918), „Über die Blütenbildung von Sempervivum".
33. **Kliucnikova, M. I.**, *C.R. Ac. Sc. U.R.S.S*, **14**, 219 (1937), „On the physiological characteristics of yarovised and non-yarovised Perilla".
34. **Knott, J. E.**, *Mem. Cornell Univ., Agric. Exp. St.*, No. 218 (1939), „The effect of temperature on the photoperiodic response of spinach" (*Biol. Abstr.*, **13**, No. 15741).
35. **Lang, A.**, *Biol. Zbl.*, **61**, 427 (1941), „Über die Bedeutung von Licht und Dunkelheit in der photoperiodischen Reaktion von Langtagpflanzen".
36. **Lang, A.** und **Meclhers, G.**, *Nat. wiss.* **29**, 82 (1941), „Über den hemmenden Einfluss der Blätter in der photoperiodischen Reaktion der Pflanzen".
37. **Loehwing, W. F.**, *Science*, No. 2346, 552 (1939), „Photoperiodic aspects of phasic development".
38. **Long, E. M.**, *Bot. Gaz.*, **101**, 168 (1939), „Photoperiodic induction as influenced by environmental factors".
39. **Lubimenko, V. N.** et **Bouslova, E. D.**, *C.R. Ac. Sc. U.R.S.S.*, **14**, 149 (1937), „Contribution à la théorie du photopériodisme II".
40. **Mc Phee, H. C.**, *J. Agr. Res.*, **28**, 1067 (1924), „The influence of environment on sex in hemp. Cannabis sativa L."
41. **Melchers, G.**, *Biol. Zbl.*, **57**, 568 (1937), „Die Wirkung von Genen, tiefen Temperaturen und blühenden Pfropfpartnern auf die Blühreife von Hyoscyamus niger L."
42. **Melchers, G.** und **Lang, A.**, *Biol. Zbl.*, **61**, 16 (1941), „Weitere Untersuchungen zur Frage der Blühhormone".
43. **Moshkov, B. S.**, (a) *C.R. Ac. Sc. U.R.S.S.*, **15**, 211 (1937), „Photoperiodism and a hypothesis as to hormones of flowering"; (b) *ibid.*, **19**, 751 (1938), „Photoperiodism and immunity"; (c) *ibid.*, **22**, 184 (1939), „Relationship between photoperiodism and drought resistance of peren-

nial plants"; (d) *ibid.*, **22**, 187 (1939), „Symbiosis of leguminous plants with nitrogen assimilating bacteria as determined by photoperiodism"; (e) *ibid.*, **22**, 456 (1939), „Minium intervals of darkness and light to induce flowering in short day plants"; (f) *ibid.*, **22**, 460 (1939), „Photoperiodic response of plants as determined by their ontogenesis"; (g) *ibid.*, **24**, 489 (1939), „Transfer of photoperiodic reaction from leaves to growing points"; (h) *Sovietskaja Botanika*, **4**, 32 (1940), russ. (*B.C.*, **177**, „Über kritische und optimale Photoperioden").

44. MOSHKOV, B. S. and KOCHERZHENKO, I. E., *C.R. Ac. Sc. U.R.S.S.*, **24**, 392 (1939), „Rooting of woody cuttings as dependent upon photoperiodic condition".
45. PARKER, M. W. and BORTHWICK, H. A., (a) *Bot. Gaz.*, **100**, 651 (1939), „Effect of photoperiod on development and metabolism of the Biloxi soy bean"; (b) *ibid.*, **101**, 145 (1939), „Effect of variation in temperature during photoperiodic induction upon initiation of flower primordia in Biloxi soy bean".
46. ROBERTS, R. H. and STRUCKMEYER, B. E., (a) *Science*, **85**, 290 (1937), „The effect of temperature upon the responses of plants to photoperiod"; (b) *J. Agr. Res.*, **56**, 633 (1938), „The effects of temperature and other environmental factors upon the photoperiodic responses of some of the higher plants"; (c) *ibid.*, **59**, 699 (1939), „Further studies of the effects of temperature and other environmental factors upon the photoperiodic responses of plants".
47. ROODENBURG, J. W. M., (a) *Ber. D. Bot. Ges.*, **55**, 5 (1937), „Der Einfluss der Tageslänge in Zusammenhang mit der künstlichen Pflanzenbeleuchtung im Winter"; (b) *Rec. Trav. Bot. néerl.*, **37**, 301 (1940), „Das Verhalten von Pflanzen in verschiedenfarbigem Licht".
48. ROODENBURG, J. W. M. and TIDDENS, B. A., *Chron. Bot.*, **4**, 18 (1938), „The role of phytohormones in photoperiodism in strawberries".
49. SCHAFFNER, J. H., (a) *Bot. Gaz.*, **90**, 279 (1930), „Sex reversal and the experimental production of neutral tassels in Zea mays"; (b) *Am. J. Bot.*, **18**, 424 (1931), „The fluctuation curve of sex reversal in staminate hemp plants induced by photoperiodicity".
50. STEIN, E., (a) *Biol. Zbl.*, **59**, 59 (1939), „Über einige Propfversuche mit erblichen, durch Radiumbestrahlung erzeugten Varianten von Antirrhinum majus, Antirrhinum siculum und Solanum lycopersicm (Tomate König Humbert)"; (b) *ibid.*, **60**, 166 (1940), „Über die Blühfähigkeit von Antirrhinum siculum mut. sterilis".
50. STEINBERG, R. A. and GARNER, W. W., *J. Agr. Res.*, **52**, 943 (1936), „Response of certain plants to length of day and temperature under controlled conditions".
52. STRUCKMEYER, B. E. and ROBERTS, R. H., *Am. J. Bot.*, **26**, 694 (1939), „Effect of photoperiod and temperature upon the growth of seedlings and cuttings".
53. TIEDJENS, V. A., *J. Agr. Res.*, **36**, 721 (1928), „Sex ratios in cucumber flowers as affected by different conditions of soil and light."
54. TOURNOIS, J., *C.R. Ac. Sc. Paris*, **153**, 1017 (1911), „Anomalies florales du houblon japonais et du chanvre déterminées par des semis hâtifs".
55. VAKULIN, D. J., *C.R. Ac. Sc. U.R.S.S.*, **15**, 263 (1937), „Reaction of reversibility in Perilla ocymoides L. under natural conditions".
56. VÖCHTING, H., *Jahrb. wiss. Bot.*, **25**, 149 (1893), „Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen".
57. ZAKHAROV, B. S., *C.R. Ac. Sc. U.R.S.S.*, **15**, 369 (1937), „The problem of yarovization of Perilla".