Netherlands Journal of Agricultural Science

VOLUME 14 NO. 2 MAY 1966

Influence of daylength on vernalization of winter rye. II. Continued experiments with short-day vernalization in winter rye

TH. A. HARTMAN

Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen (I.B.S.), Wageningen, Netherlands

Summary

Experiments in which the effect of short-day in the period preceding the cold treatment was investigated at 25 °C show that even at this temperature short-day vernalization may induce accelerated development and early ear emergence.
The investigation of the effectiveness of short-day during the cold treatment showed that a short-day period may also lead to acceleration during protracted cold treatments provided the optimum for short-day vernalization is not exceeded.

1. Introduction

It was concluded from the investigation into the effect of short-day before, during and after cold periods of varying duration (HARTMAN, 1964) that the effects of cold and short-day are two independent processes. Under conditions in which cold and short-day may occur simultaneously (as in plant vernalization) the plant will be affected by both factors at once.
The short-day effect is due to "short-day vernalization"; as in the cold period, this is a *direct* effect (slowing down of growth) and an *indirect* or after effect (early ear emergence being due to more rapid differentiation of the primordia). The accelerated flowering of unvernalized winter rye as a result of a 6-week period of short days after sowing (GREGORY and PURVIS, 1937) is also to be attributed to short-day vernalization, not to short-day induction.
Short-day induction and short-day vernalization should be clearly distinguished. In both cases there is a photoperiodic after-effect or induction, but short-day induction refers to the influence of a short-day period on *short-day plants,* whereas short-day

Received for publication 25th April, 1965.

vernalization occurs in *long-day plants*. By short-day induction is meant giving short-day plants a sufficient number of short days to enable them to flower in the following period of *unfavourable* day-length (long day). In short-day vernalization a short-day treatment is applied to long-day plants which induces them to flower early in the subsequent period of *favourable* day-length (long-day). The short-day effect in non-vernalized winter rye is completely explained by short-day vernalization and there is no need to assume that winter rye begins as a short-day plant and later changes into a long-day one.
Independently of growth retardations due to the direct effect of low temperatures and short day, growth depressions occur which are inherent to certain phases of plant life, *i.e.* at the end of the vegetative phase and in the period of ultimate spikelet-number (WITTENROOD, 1959). The final outcome is therefore determined by the resultant of these retardations, and the accelerations by the indirect effect of the cold and the short day.

2. Theoretical

2.1. The effect of short-day preceding the cold period

In the above-mentioned investigation (HARTMAN, 1964) the effect of short-day in the pre-treatment (*i.e.* preceding the cold period) was determined in plants raised for 2 weeks in a greenhouse at 16 °C in continuous day (C.D.) and short-day (S.D.). The acceleration in flowering of the short-day treatments in the pre-treatment period compared with the continuous day treatments, especially in the vernalization classes with short periods of low temperature, were attributed to short-day vernalization. However, this may also be explained by assuming an interaction between temperature and day-length and that a temperature of 16 °C still has a vernalizing effect under short-day conditions. This possibility was investigated in the 1962 experiments.

2.2. The effect of short-day during the cold period

The effect of short-day during low temperatures was examined in continuous day (C.D.) and short-day (S.D.) treatments during cold periods of varying lengths (HARTMAN, 1964). However, since in this experimental design the short-day treatment also varied with the duration of the cold period, any possible differences in the optimal periods for short-day and cold treatments were ignored. In these experiments the short-day treatments in the vernalization classes with 8- and 6-week cold periods showed a retardation, whereas those with 4- and 2-week cold periods were accelerated. These results were explained by assuming that in the longer cold periods the short-day vernalization had exceeded its optimal period during the cold period. The induction to acceleration would then have reached its limit and from then onward there is only increased retardation, so that the ultimate result will be a retardation. If this explanation is correct, shorter short-day treatments in the vernalization classes with long cold periods should result in an acceleration. This was examined in the 1963 investigation.

3. Material and methods

As in the previous experiments, seeds of Petkus winter rye were germinated in mitscherlich pots. In the S.D. treatments the day-length was set at 8 h. before, during

and after the cold period by screening the plants.
The possibility was investigated that the S.D. effect in the pre-treatment period might be due to the interaction between temperature and day-length. The length of the pre-treatment and cold treatment periods was fixed at 4 weeks.
After sowing on November 22, 1961 half the treatments were exposed to 16 °C and the other half to 25 °C, a temperature that may be assumed to have no vernalizing effect, even under short-day conditions. The various treatments were exposed to short days for 4 weeks at different times. Except for the controls kept in C.D. throughout, the S.D. periods coincided with the pre-treatment, the last 2 weeks of the pre-treatment period and the first 2 weeks of the cold treatment, with the cold treatment, the last 2 weeks of the cold period and the first 2 weeks of the post-treatment period, and with the post-treatment.
Some treatments were also exposed to short days of 2 weeks for the last 2 weeks of the pre-treatment and the last 2 weeks of the cold period.
As the daylight is weak in the pre-treatment period from 22 November to 20 December, especially for the treatments exposed to 25 °C, additional light was supplied with high-pressure mercury vapour lamps with a fluorescent coating (Philips HPL, 400 W) during the 8-h. photoperiod. The S.D. treatments were then screened with black cloths, and from then onward the C.D. treatments were given additional light from fluorescent tubes (Philips TLF 33, 40 W, 1 per 1½ m^2).
The various treatments were periodically sampled from 2 weeks after sowing and analysed for fresh and dry weight. In the later samples the developmental stages of the growing point were determined by the Wittenrood scale, which expresses the development up to ear-formation by means of stages numbered 1—13 (WITTENROOD, 1953; HARTMAN, 1964). The observations were continued up to ear emergence, this stage being denoted by > 13 in the graphs illustrating the development.

Two-week old plants, grown at 16 °C in C.D. and S.D. were exposed to cold treatments at + 6 °C for 8, 6, 4 and 2 weeks. During the vernalization periods the various treatments were exposed to varying day-length conditions, *viz.* C.D., S.D. and C.D. preceded by 2 and 4 weeks S.D. In the post-treatment, which began at the same time for the various vernalization classes by choosing the sowing dates accordingly, all treatments were exposed to C.D. at 16 °C. The treatments were periodically sampled from the beginning of the cold period onward and analysed for fresh and dry weight; later on the developmental stages of the growing point were also determined.

4. Results and discussion

4.1. Experiments in 1962

The coding of the treatments in the successive periods of pre-treatment/cold treatment/post-treatment indicates the length of the treatments at various temperatures and day-lengths (continuous day = C, short day = S). The number of days in the post-treatment period indicates the time the plant needs to reach the ear emergence stage after vernalization. The results are given in TABLE 1.
The growth trends of treatments $28C_{16}$ / $28C_6$ / $52C_{16}$, $28S_{16}$ / $28C_6$ / $44C_{16}$ and $28C_{25}$ / $28C_6$ / $61C_{16}$, $28S_{25}$ / $28C_6$ / $54C_{16}$, derived from the dry-weight increment of the plants, are shown in FIG. 1.
As might to be expected, the S.D. treatments are retarded compared with the cor-

TABLE 1. Cold and S.D. treatments of plants grown at 16 °C and 25 °C in the pre-treatment

Pre-treatment temperatures					
16 °C			25 °C		
$28C_{16}$ /	$28C_{6}$ /	$52C_{16}$	$28C_{25}$ /	$28C_{6}$ /	$61C_{16}$
$28S_{16}$ /	$28C_{6}$ /	$44C_{16}$	$28S_{25}$ /	$28C_{6}$ /	$54C_{16}$
$14C_{16}.14S_{16}$ /	$14S_{6}.14C_{6}$ /	$45C_{16}$	$14C_{25}.14S_{25}$ /	$14S_{6}.14C_{6}$ /	$56C_{16}$
$14C_{16}.14S_{16}$ /	$28C_{6}$ /	$49C_{16}$	$14C_{25}.14S_{25}$ /	$28C_{6}$ /	$60C_{16}$
$28C_{16}$ /	$28S_{6}$ /	$58C_{16}$	$28C_{25}$ /	$28S_{6}$ /	$65C_{16}$
$28C_{16}$ /	$14C_{6}.14S_{6}$ /	$14S_{16}.49C_{16}$	$28C_{25}$ /	$14C_{6}.14S_{6}$ /	$14S_{16}.57C_{16}$
$28C_{16}$ /	$14C_{6}.14S_{6}$ /	$57C_{16}$	$28C_{25}$ /	$14C_{6}.14S_{6}$ /	$71C_{16}$
$28C_{16}$ /	$28C_{6}$ /	$28S_{16}.39C_{16}$	$28C_{25}$ /	$28C_{6}$ /	$28S_{16}.48C_{16}$
$14C_{16}.14S_{25}$ /	$14S_{6}.14C_{6}$ /	$51C_{16}$	$14C_{25}.14S_{16}$ /	$14S_{6}.14C_{6}$ /	$45C_{16}$
$14C_{16}.14S_{25}$ /	$28C_{6}$ /	$56C_{16}$	$14C_{25}.14S_{16}$ /	$28C_{6}$ /	$44C_{16}$

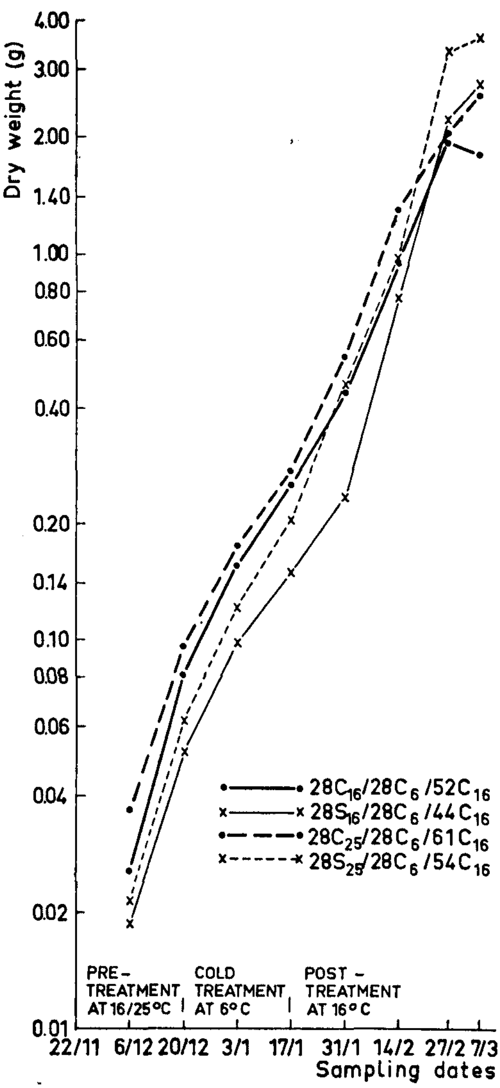


FIG. 1
Growth curves of treatments with C.D. and S.D. at 16 °C and 25 °C in the pre-treatment; 1962

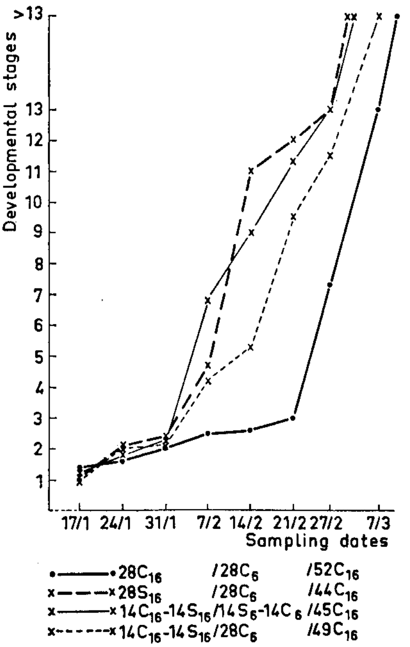


FIG. 2a
Development curves of plants grown at 16 °C in the pre-treatment; 1962

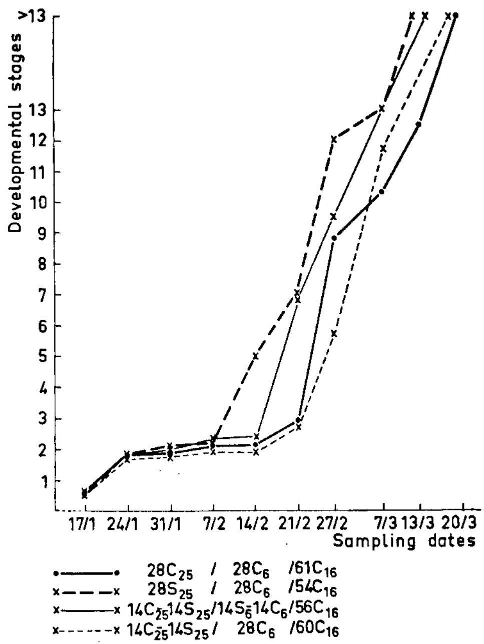


FIG. 2b
Development curves of plants grown at 25 °C in the pre-treatment; 1962

responding C.D. treatments. On the other hand, the development trend illustrated in FIG. 2a and 2b shows that the S.D. treatments have a clear lead. The other treatments in these figures, *viz.*:

$14C_{16} . 14S_{16} / 14S_6 . 14C_6 / 45C_{16}$, $14C_{16} . 14S_{16} / 28C_6 / 49C_{16}$

and: $14C_{25} . 14S_{25} / 14S_6 . 14C_6 / 56C_{16}$, $14C_{25} . 14S_{25} / 28C_6 / 60C_{16}$

also show an accelerated development as a result of the various S.D. periods. These results clearly show that in the pre-treatment period an S.D. treatment will accelerate differentiation of the primordia even at 25 °C. Accelerated ear emergence as a result of S.D. in the pre-treatment at 16 °C is therefore not to be explained by assuming an interaction between temperature and day-length, resulting in a vernalizing effect at 16 °C and hence an extension of the vernalization period, but by the S.D. effect.

As already mentioned, this effect is determined by a *direct* component, *i.e.* retardation due to growth inhibition, and an *indirect* component, *viz.* acceleration due to more rapid differentiation of the primordia.

Comparison of the various growth curves in FIG. 1 shows that both the C.D. and the S.D. treatments exposed to 25 °C show a higher growth rate in the first two weeks of the pre-treatment than exposed to 16 °C. These differences are maintained during the cold treatment and practically throughout the post-treatment period.

In former experiments (HARTMAN, 1964) a difference in growth was also observed in the C.D. treatments after using different light-sources for lengthening the day. The treatments given additional light from incandescent lamps showed a higher growth rate than those given supplementary light from fluorescent tubes, resulting in earlier

ear emergence.
However. this does not seem to apply to the accelerated growth rate due to a higher temperature. In the samples taken at the beginning of the post-treatment (17 January) the plants raised at 25 °C in the pre-treatment were at an earlier stage of development than those raised at 16 °C (FIG. 2a, b; FIG. 3a, b and FIG. 4a, b). But, as will be demonstrated by the subsequent development, this cannot be explained by assuming a *greater cold requirement after a preceding period of higher temperature* (anti-vernalization, BARENDSE, 1964). The retardation at the beginning of the post-treatment is soon compensated and development runs almost paralel up to 6 weeks after (27 February). It is only then that the 25 °C treatments are inhibited, resulting in a retardation of 9 days in ear emergence for

$28C_{25}$ / $28C_{6}$ / $61C_{16}$ compared with $28C_{16}$ / $28C_{6}$ / $52C_{16}$ and of 10 days for $28S_{25}$ / $28C_{6}$ / $54C_{16}$ compared with $28S_{16}$ / $28C_{6}$ / $44C_{16}$.

In the treatments $28C_{16}$ / $28S_{6}$ / $58C_{16}$ *vs.* $28C_{25}$ / $28S_{6}$ / $65C_{16}$ (FIG. 3a, b) and $28C_{16}$ / $28C_{6}$ / $28S_{16}$. $39C_{16}$ *vs.* $28C_{25}$ / $28C_{6}$ / $28S_{16}$. $48C_{16}$ (FIG. 4a, b) the same rate of development is observed up to 4 and 7 weeks after the beginning of the post-treatment. Since the conditions during the cold and the post-treatments are the same for each set, and the day-lengths are also the same in the pre-treatment, subsequent differences in the development pattern must be due to the temperature of 25 °C in the pre-treatment period. The results of the following treatments also show this trend.

$14C_{16}$. $14S_{16}$ / $14S_{6}$. $14C_{6}$ / $45C_{16}$ *vs.* $14C_{16}$. $14S_{25}$ / $14S_{6}$. $14C_{6}$ / $51C_{16}$
$14C_{16}$. $14S_{16}$ / $28C_{6}$ / $49C_{16}$ *vs.* $14C_{16}$. $14S_{25}$ / $28C_{6}$ / $56C_{16}$
and :
$14C_{25}$. $14S_{25}$ / $14S_{6}$. $14C_{6}$ / $56C_{16}$ *vs.* $14C_{25}$. $14S_{16}$ / $14S_{6}$. $14C_{6}$ / $45C_{16}$
$14C_{25}$. $14S_{25}$ / $28C_{6}$ / $60C_{16}$ *vs.* $14C_{25}$. $14S_{16}$ / $28C_{6}$ / $44C_{16}$

FIG. 3a
Development curves of plants grown at 16 °C in the pre-treatment; 1962

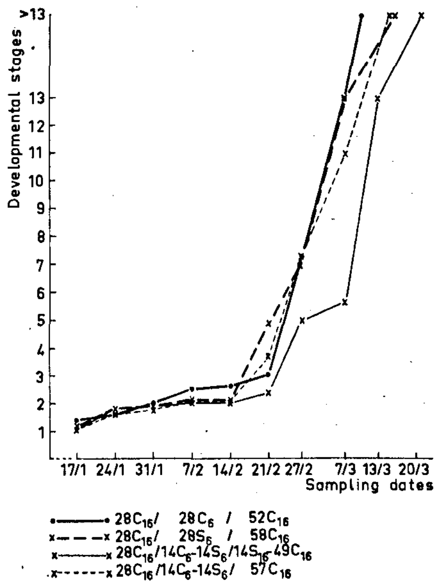


FIG. 3b
Development curves of plants grown at 25 °C in the pre-treatment; 1962

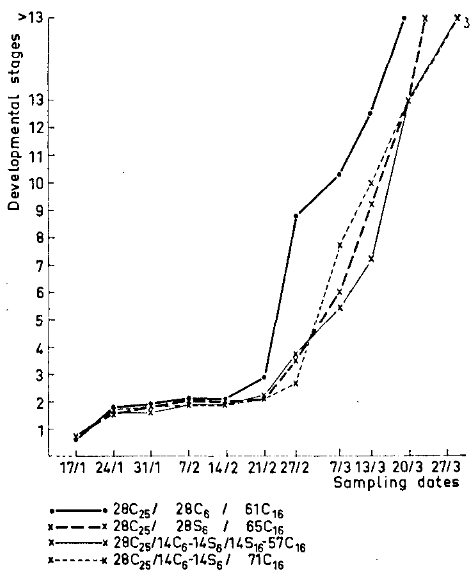


FIG. 4a
Development curves of plants grown at 16 °C in the pre-treatment; 1962

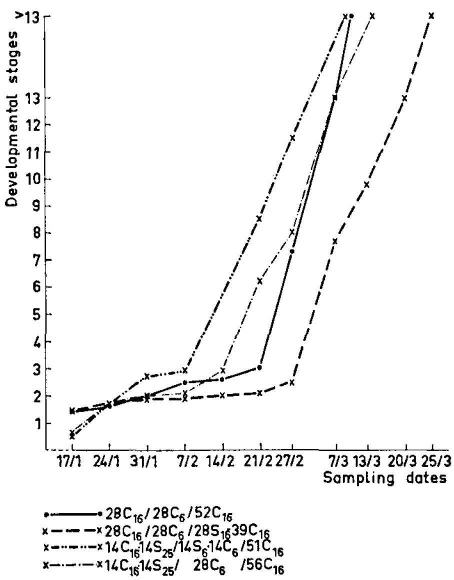
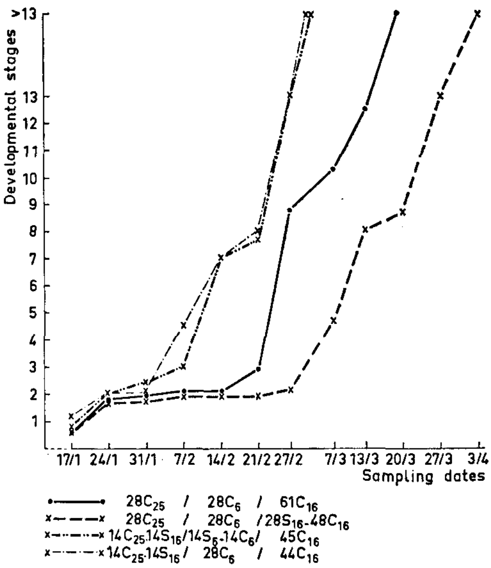


FIG. 4b
Development curves of plants grown at 25 °C in the pre-treatment; 1962



These retardations cannot be understood without a further study of the developmental physiology of these plants. For the time being it may suffice to observe that 25 °C compared to 16 °C in the pre-treatment period retarded ear emergence 9 days, as is shown by comparing
$28C_{16}$ / $28C_6$ / $52C_{16}$ with $28C_{25}$ / $28C_6$ / $61C_{16}$. The divergent results of the S.D. treatments are due to the S.D. effect.

4.2. Experiments in 1963

The influence of 2- and 4-week S.D. periods during cold treatments of 8, 6, 4 and 2 weeks was observed in 2-week old plants grown at 16 °C in C.D. and S.D. The experimental design and results are given in TABLE 2. Compared with the controls, the plants of the 8- and 6-week vernalization classes with an S.D. treatment throughout the cold period are retarded both in the C.D. and the S.D. group, unlike the 4- and 2-week vernalization classes, where the C.D. group show a retardation, but the S.D. group an acceleration. It would seem likely that in the vernalization classes with long cold periods, therefore long S.D. treatments, the optimum period of S.D. vernalization is exceeded. The induction to acceleration has then reached its limit and continuation of the treatment will only increase the retardation due to growth depression in S.D. The resultant of retardation and acceleration will ultimately produce a retardation.

However, other factors may also affect earlier or later ear emergence. The "optimal earliness", *i.e.* the minimum number of days a treatment requires up to ear emergence, is not only affected by S.D., but also and simultaneously by cold. This induces an acceleration as well as a retardation, the latter being due to growth depression caused

TABLE 2. Effect of 2- and 4-week S.D. during vernalization periods of varying length preceded by 2-week C.D. and S.D. in the pre-treatment period

Day-length in the pre-treatment period	
S.D.	C.D.
$14C_{16}$ / $56C_6$ / $37C_{16}$	$14S_{16}$ / $56C_6$ / $37C_{16}$
$14C_{16}$ / $14S_6 . 42C_6$ / $36C_{16}$	$14S_{16}$ / $14S_6 . 42C_6$ / $34C_{16}$
$14C_{16}$ / $28S_6 . 28C_6$ / $37C_{16}$	$14S_{16}$ / $28S_6 . 28C_6$ / $35C_{16}$
$14C_{16}$ / $56S_6$ / $42C_{16}$	$14S_{16}$ / $56S_6$ / $39C_{16}$
$14C_{16}$ / $42C_6$ / $43C_{16}$	$14S_{16}$ / $42C_6$ / $39C_{16}$
$14C_{16}$ / $14S_6 . 28C_6$ / $42C_{16}$	$14S_{16}$ / $14S_6 . 28C_6$ / $39C_{16}$
$14C_{16}$ / $28S_6 . 14C_6$ / $44C_{16}$	$14S_{16}$ / $28S_6 . 14C_6$ / $39C_{16}$
$14C_{16}$ / $42S_6$ / $46C_{16}$	$14S_{16}$ / $42S_6$ / $42C_{16}$
$14C_{16}$ / $28C_6$ / $58C_{16}$	$14S_{16}$ / $28C_6$ / $52C_{16}$
$14C_{16}$ / $14S_6 . 14C_6$ / $61C_{16}$	$14S_{16}$ / $14S_6 . 14C_6$ / $49C_{16}$
$14C_{16}$ / $28S_6$ / $61C_{16}$	$14S_{16}$ / $28S_6$ / $50C_{16}$
$14C_{16}$ / $14C_6$ / $79C_{16}$	$14S_{16}$ / $14C_6$ / $76C_{16}$
$14C_{16}$ / $14S_6$ / $82C_{16}$	$14S_{16}$ / $14S_6$ / $68C_{16}$

by the low temperature. If as a result of the effect of the S.D. and the cold the condition of "optimal earliness" is reached during the cold period, the optimum period of cold vernalization will also have been reached and continuation of the cold treatment will not add anything to the acceleration, but only increase the retardation. However, the results of this investigation would not indicate that this applies to these treatments.

In addition to these accelerations and retardations due to S.D. and cold, there are independent retardations inherent to certain stages of plant development, *viz.* growth depressions occurring at the end of the vegetative phase and when the ultimate spikelet number has been reached.

In the C.D. group the development of the treatments receiving a S.D. treatment of shorter duration than the cold period is accelerated compared with that of the relevant controls, but when S.D. is given for the entire cold period development lags behind from the beginning of the post-treatment onward (FIG. 5a—8a). This is to be expected in the treatments with prolonged periods of cold (56 and 42 days) as the S.D. vernalization will exceed its optimum period, but it does not apply to the 2-week vernalization class (FIG. 8a) in which development is retarded because the effect of the S.D. treatment is too slight to outweigh the advantage of a higher growth rate obtained by the C.D. treatment. The same result would be expected with the 14-day S.D. treatment in the 4-week vernalization class, but here the development is slightly ahead of the control at a later stage (FIG. 7a). Since in both cases S.D. may be assumed to have induced the same degree of acceleration, there must have been less retardation due to growth depression. This is because after the S.D. treatment the plants remained in C.D. for 14 days at the same temperature (6 °C), whereas those in the 2-week vernalization class were immediately afterwards exposed to 16 °C in the C.D. post-treatment. This influence of the 6 °C C.D. period after the S.D. treatment in reducing the retardation caused by the growth depression in S.D. is clearly shown from the results of the treatments exposed to long periods of cold. In the 6-week vernalization class the 14 days' S.D. causes a marked acceleration compared with the control from the beginning of the post-treatment, this being due to the 28-day recovery period (FIG. 6a). This is also reflected in the treatment receiving a 56-day vernalization period, the plants remaining in C.D. for 42 days at 6 °C after the S.D. treatment (FIG. 5a). Yet these accelerations are not reflected in earlier ear emergence probably because of the growth depressions inherent in certain stages of plant development.

The 28-day S.D. treatments in the various vernalization classes show smaller differences, owing to the fact that with 28 days' S.D. there is greater retardation due to growth depression and the plants recover more slowly after this longer S.D. period. In this connection it is interesting to note that in the 8- and 6-week vernalization classes the treatments receiving 28 days' S.D. are retarded compared with the treatments exposed to a 14-day S.D. period (FIG. 5a and 6a). Yet the results of the 14-day S.D. treatments in the 2-week vernalization class and of the 14 and 28 days' S.D. during the 4-week cold period clearly show that the effect of 14 days' S.D. is less than that of 28 days' S.D. (FIG. 7a and 8a). This is also to be explained by the influence of the recovery period at 6 °C in C.D. after the S.D. treatment. In the 4-week vernalization class the reduction in the retardation caused by the growth inhibition in 14 days' S.D., is insufficient to outweigh the greater effect of the 28 days of S.D. treatment. But in the 6-week vernalization period the 14 days' S.D. is followed by a 28-day recovery period, compared with a 14-day recovery period in the treatment exposed to 28-days S.D., and in the 8-week vernalization class the recovery period is as long as 42 days after the 14 days' S.D. and 28 days after the 28-day S.D. treatment. The longer recovery periods after the 14-day S.D. treatments (28 and 42 days) reduce the retardations due to the growth depressions in S.D. to a greater extent than the 14- and 28-day recovery periods after the 28 days of S.D. treatment, so that the former show a distinctly better development than the latter. Moreover, this greater acceleration will be realised sooner, because the 14-day S.D. treatments are placed earlier in a photoperiodically favourable day-length (C.D.).

The treatments *in the S.D. group* show earlier ear emergence than the corresponding ones with C.D. in the pre-treatment; this was also observed in the previous years' experiments. This is clearly seen in the vernalization classes with cold treatments of 14 and 28 days, but the differences are also apparent in the case of the long vernalization periods (TABLE 2). The results of the various treatments compared with the respective controls show them to be both the result of S.D. in the pre-treatment period and of the S.D. treatment during the cold period.

In the treatments with S.D. throughout the 8- and 6-week cold period development lags behind the control until ear emergence (as is also the case with the C.D. group). This is also due to the fact that after the optimum for S.D. vernalization has been exceeded, retardation has increased to such an extent that the S.D. effect results in a retardation.

A distinct difference with regard to the effect of the S.D. during the cold period is shown by the treatments of the C.D. and S.D. groups in the 2- and 4-week vernalization classes. In the 2-week vernalization class the S.D. treatment of plants exposed to C.D. in the pre-treatment period results in a retardation in ear emergence compared with the control (FIG. 8a), but in an acceleration when preceded by S.D. (FIG. 8b). The main reason for this is that the S.D. treatment during the cold period induces acceleration to a greater extent, because the reaction has already started up in the S.D. period of the pre-treatment. The lower growth-rate of the plants grown

FIG. 5a
Development curves of plants in the 8-week vernalization class with C.D. in the pre-treatment; 1963

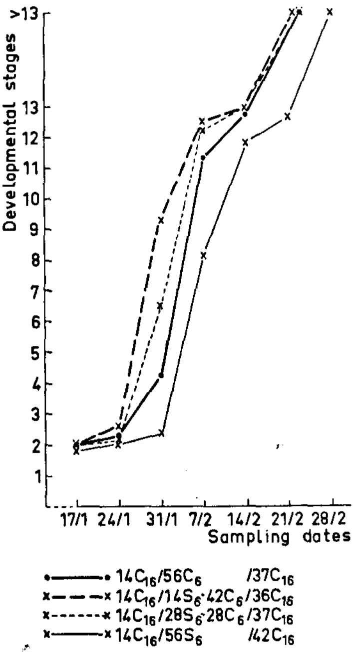
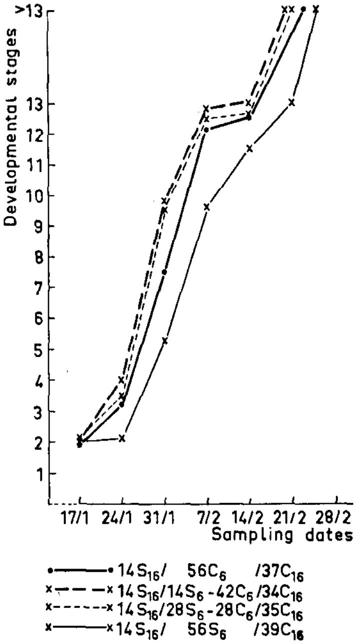


FIG. 5b
Development curves of plants in the 8-week vernalization class with S.D. in the pre-treatment; 1963



in S.D. from sowing-time onward, will also result in a lower growth depression compared with the control than if the plants were grown in C.D. Owing to these two factors the effect of the S.D. treatment during the cold will result in greater acceleration of the development. Ear emergence in the S.D. group was 8 days earlier than the control, but when exposed to C.D. in the pre-treatment (C.D. group) it showed a retardation of 3 days (FIG. 8a, b). The fact that S.D. treatment during the cold period with S.D. in the pre-treatment results in a greater acceleration than after a preceding C.D. period is also found in the 4-week vernalization class. The plants with 14 days' S.D. have a distinct lead over those of the control, while the corresponding plants in the C.D. group are only slightly accelerated at a later stage (FIG. 7a, b). The plants exposed to 28 days' S.D., however, react differently. Whereas in the C.D. group development is ahead of that of the control even at the beginning of the post-treatment, development in the S.D. group will first lag behind and only be in the lead at a later stage. Since the preceding results have sufficiently proved that the effect of S.D. during the cold in the S.D. group will result in a greater acceleration, this retardation would indicate an *additional* retardation. This is because the S.D. treatment in the S.D. group, due to greater acceleration and smaller retardation, will reach its optimum period sooner than in the C.D. group. In this case the optimum will already have been reached *during* the S.D. treatment, so that continuation of the S.D. treatment only increased the retardation, the acceleration remaining the same.

FIG. 6a
Development curves of plants in the 6-week vernalization class with C.D. in the pre-treatment; 1963

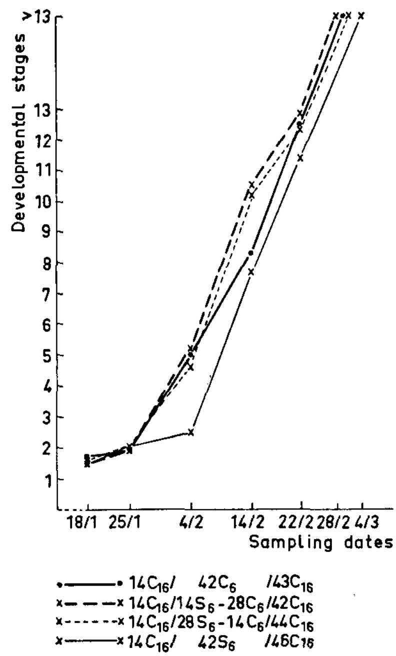
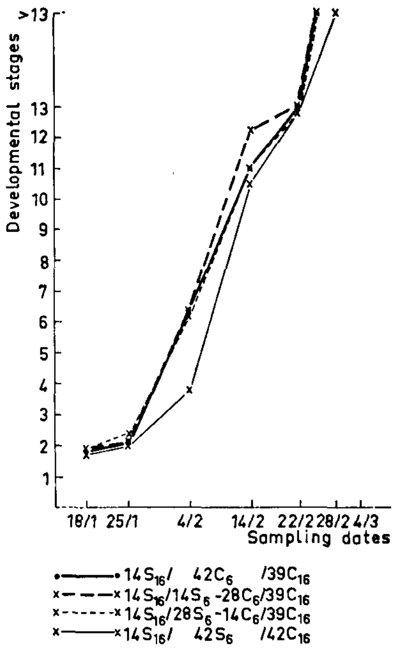


FIG. 6b
Development curves of plants in the 6-week vernalization class with S.D. in the pre-treatment; 1963



In plants receiving a 14-day S.D. treatment the shorter treatment time will result in lesser induction to acceleration. On the other hand no additional retardation will occur, as in view of the preceding the optimum period for S.D. vernalization may be put at between 14 and 28 days. Since the S.D. treatment is followed by a 14-day recovery period at 6 °C in C.D., the retardation due to the growth depression in S.D. will be reduced. The resultant of the effect of this S.D. treatment will thus show a greater acceleration than that of 28 days S.D. (FIG. 7b). The same phenomenon may be observed in the 6-week vernalization class; in the plants exposed to a 28-day S.D. period the optimum period of the S.D. vernalization is exceeded, so that the retardation is increased. But the influence of the 14-day recovery period after the S.D. treatment has reduced this increased retardation to a value equal to that of the acceleration, with the result that the development trend of this treatment coincides with that of the control (FIG. 6b). In the treatment with a 14-day S.D. period, however, the retardation due to the growth inhibition in S.D. is more reduced owing to the longer 28-day recovery period. For this reason and because of the absence of an additional retardation this treatment shows, despite the lesser induction to acceleration, a more accelerated development rate than that with 28-day S.D.
This is even more the case with the treatments in the 8-week vernalization class. The 28 days of S.D. are followed by a 28-day recovery period, as a result of which the reduction in the retardation is so much greater than in the relevant treatment

FIG. 7a
Development curves of plants in the 4-week vernalization class with C.D. in the pre-treatment; 1963

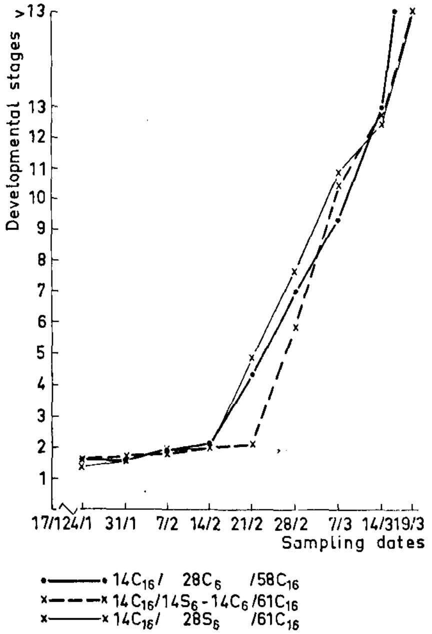


FIG. 7b
Development curves of plants in the 4-week vernalization class with S.D. in the pre-treatment; 1963

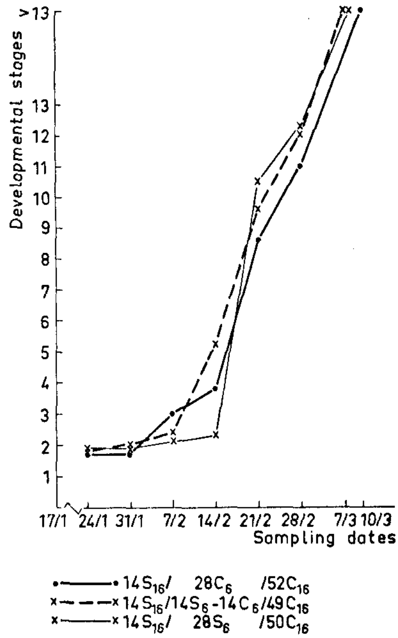


FIG. 8a
Development curves of plants in the 2-week vernalization class with C.D. in the pre-treatment; 1963

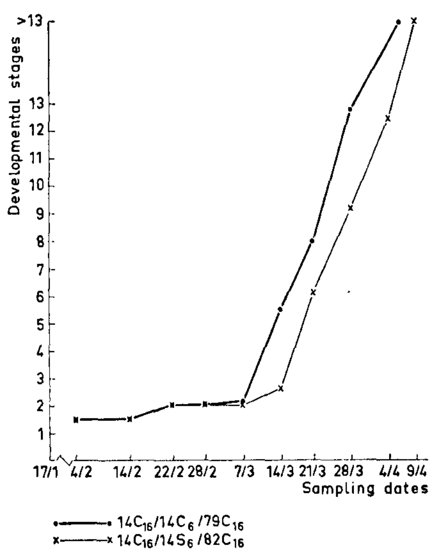
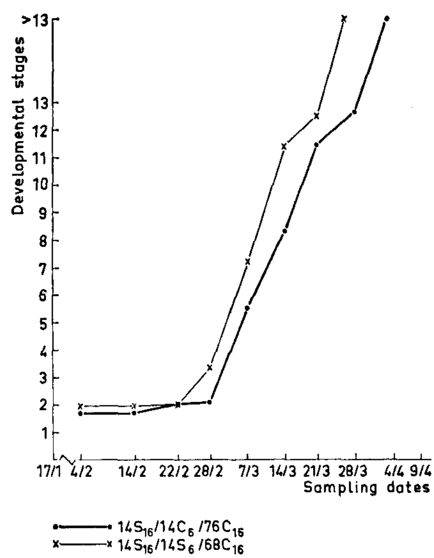


FIG. 8b
Development curves of plants in the 2-week vernalization class with S.D. in the pre-treatment; 1963



in the 6-week vernalization class, that the effect of the 28-day S.D. period results in an acceleration compared with the control. The plants exposed to 14 days' S.D. remain in C.D. for 42 days at 6 °C after the S.D. treatment. Owing to the absence of an additional retardation and the greater reduction in the retardation due to the longer recovery period, the development trend of these plants is more accelerated than those exposed to a 28-day S.D. period (FIG. 5b).

5. General discussion

The results of the 1962 investigation confirm the observations from the experiments in the previous years, *viz.* that an S.D. treatment in the period before the cold treatment may induce earlier ear emergence. But since in these previous experiments the S.D. treatments were applied at 16 °C, this S.D. effect may be due to an interaction between temperature and day-length. This means that under S.D. conditions a temperature of 16 °C would still have a vernalizing effect, so that the accelerated ear emergence would be the result of prolonging the cold vernalization.

HÄNSEL's observations (1951) on the distinct differences with respect to leaf and flower primordia in the growing cone after a cold and S.D. treatment would point already in the opposite direction. However, in the 1962 experiments this assumption was tested by applying the S.D. treatment in the pre-treatment period at a high temperature of 25 °C, which would obviously have no vernalizing effect, even under S.D. conditions. Yet the results of the plants exposed to an S.D. period in the pre-treatment at 25 °C clearly show that even at this high temperature the effect of S.D. is reflected in a more rapid differentiation of the primordia (FIG. 2b and FIG. 4a, b). These results confirm the assumption that cold vernalization and S.D. vernalization are two different reactions independently and simultaneously influencing the plant.

This was also found in the results of the 1963 experiments. In this investigation the effect of S.D. during the cold treatment was examined in a more detailed experimental design, as the results of the previous plant-vernalization experiments only showed an acceleration in ear emergence in the vernalization classes with a sub-optimal vernalization period. It might therefore be concluded that the length of the cold period determines the effect of S.D., in other words that the effect of S.D. is secondary to that of the cold treatment.

However, the observations made in 1963 showed that retardations due to S.D. during the cold in plants exposed to long vernalization periods are caused by exceeding the optimum period of S.D. vernalization. The S.D. effect is composed of a *direct* component, *i.e.* the retardation due to the reduced growth in S.D., and an *indirect* component, *i.e.* the acceleration due to faster differentiation of the primordia. After reaching the optimum period of the S.D. vernalization, continued S.D. treatment will increase the retardation but not the acceleration. Thus, after a long period the retardation will have increased to such an extent that the S.D. effect will result in a retardation.

It follows from what has been stated above that an S.D. treatment will lead to an acceleration even during long cold periods if the S.D. vernalization optimum has not been exceeded.

This is, in fact, the case with the plants in the 8- and 6-week vernalization classes which received an S.D. treatment of 14 and 28 days during the cold. In the plants exposed to C.D. in the pre-treatment period (FIG. 5a—8a) as well as those with preceding S.D. (FIG. 5b—8b), the development trend shows an acceleration compared with the controls.

6. Conclusions

1. S.D. vernalization also occurs when S.D. is applied at high temperatures (*i.e.* 25 °C).
2. Even with long cold treatments an S.D. treatment during the cold will lead to an acceleration, when the duration of the treatment does not exceed the S.D. vernalization optimum.

ACKNOWLEDGEMENT

The author is indebted to Drs. H. G. Wittenrood for his assistance in determining the developmental stages.

REFERENCES

BARENDSE, G. W. M. 1964 Vernalization in *Cheiranthus allionii* hort. *Meded. Landb.-hogesch. Wageningen. 64,* 14: 1—64.

GREGORY, F. G., and O. N. PURVIS 1937 Studies in vernalization of cereals. I. A comparative study of vernalization of winter rye by low temperature and by short days. *A. Botany. 1,* 4: 570—587.

HÄNSEL, H. 1951 Über die Wirkung des Kurztages auf Zeit des Ährenschiebens und auf Ährchenzahl pro Ähre bei Petkus Winterroggen. *Bodenkultur. 5,* 3: 305—312.

HARTMAN, TH. A. 1964 Influence of daylength on vernalization of winter rye. *Neth. J. agric. Sci. 12,* 2: 132—155.

WITTENROOD, H. G. 1953 Het verloop van de vernalisatie van zes wintertarwerassen bij novemberzaai op het veld. (The vernalization of six varieties of winter wheat sown in the open in November.) *Verslag Cilo 1952.* 161—170.

—— 1959 Correlatie tussen plant- en aargrootte ten tijde van de aar-aanleg bij tarwe. (Correlation between size of plant and ear — ultimate number of spikelets — at ear initiation in wheat.) *Meded. Inst. biol. scheik. Onderz. Landb.Gewass.* No. 84, 135—146.