EFFECTS OF DAY LENGTH AND LIGHT INTENSITY ON GROWTH OF BARLEY

V.* RESPONSE BY PLANTS IN THE FIELD TO NIGHT INTERRUPTION

By L. G. PALEG† and D. ASPINALL†

[Manuscript received February 18, 1966]

Summary

Four varieties of barley (Prior, Noyep, CI 3576, and CI 5611) were grown in field plots and subjected to varying intensities of incandescent light as a 2-hr night interruption.

The light treatment accelerated spikelet development, primordium production, and stem elongation and reduced the number of leaves on the main stem and of grains on the ear. These effects were most pronounced in the variety CI 5611 where illumination commenced prior to floral initiation but were also manifest in the other varieties which were not illuminated before initiation, demonstrating the photoperiodic sensitivity of barley in the later stages of development.

The data are discussed in relation to the control of apical morphogenesis in cereals, the use of night interruption in plant breeding, and the investigation of the effects of the environment on cereal growth.

I. INTRODUCTION

Apical morphogenesis in cereals has been demonstrated to be under the control of photoperiod, and the majority of barley and wheat varieties have been classified as quantitative long-day plants. A promotion of floral development by night interruption with low energies of light frequently (Aspinall 1966), though not invariably (Evans, Borthwick, and Hendricks 1965), accompanies floral initiation in response to a long photoperiod. This characteristic has been of great experimental value in investigations of the physiology of floral initiation but the potentialities of the response in other areas have been little explored.

In view of the low energies and the brief periods of illumination required for this response, it would appear that manipulation of cereal development on a field scale by these means is at least feasible. This could be of benefit both in investigations of the development of the plant in the field (in relation to the environment) and in the control of flowering date in high-value crops such as breeding material. It is also tempting to speculate on various other field responses that might be obtained with such an effect if efficient, inexpensive, and effective light sources could be developed.

† Department of Plant Physiology, Waite Agricultural Research Institute, University of Adelaide.
This paper describes the results of an experiment designed to test, under field conditions, the responses of four barley varieties to night interruption with low energy light, and to provide information on the effects of such treatment on apical morphogenesis and grain yield. The four varieties investigated provided a range of photoperiodic response types and growth patterns (Aspinall 1966).

II. Experimental Methods

The experiment was laid out in a randomized block design on an area fallowed in the previous season. Seed of four barley varieties, Prior, Noyep, CI 3576, and CI 5611 (for a description of these varieties see Aspinall 1966) were sown using an experimental plot drill (Finlay 1963) on July 19. Each block (Fig. 1) had marginal guard plots sown with Prior barley. Seedling emergence was completed within 2 weeks, and the light treatments were imposed 4 weeks after sowing (August 17). Two hours of illumination each night (11 p.m.–1 a.m.) was given with three 500-W incandescent-filament floodlamps (Philips Altrilux 13104E/99) mounted 10 ft above ground level 20 ft from the end of the treatment plots (Fig. 1). The lamps were directed at the centre of the first plots, the two areas further away from the lamp also receiving some illumination. Even illumination was not achieved by this means but the major gradient in light intensity was from the front to the rear of the plots. Similar plantings sown behind the lamps were utilized as a control series; no detectable illumination from the lamps was received by these plants.

Each experimental plot consisted of three 8-ft rows of plants, hence the number of plants available for sampling was strictly limited. In order to overcome the effects of the light gradient, the plots were divided into three equal sections at different distances from the light source. Every week one plant was sampled at random from within a different section in each block. One plant from each control block was obtained at the same time.

The sampled plants (removed with a small portion of the root system) were dissected to reveal the apex of the main axis and the following data were collected: stage of development (Aspinall and Paleg 1963), apex length, number of primordia, number of leaves, internode length, and number of tillers. In the final sample the number of grains on the ears on the main stems was also recorded. The remaining plants were harvested when fully ripe and the number of grains per ear, mean grain weight, and grain weight per ear were determined on the composite sample (main stems and tillers) so obtained.

III. Experimental Results

(a) Development of Floral Primordia

The experiment was begun comparatively late in the season, and night-interruption treatments were not initiated until 4 weeks after sowing. As a result, the two early varieties, CI 3576 and Noyep, and some of the plants of Prior, had already initiated double ridges (stage 3) when the light treatment began (Fig. 2). Nevertheless, all four varieties demonstrated an acceleration in the rate of floral development as a result of illumination. Clearly, the stages of development subsequent to floral initiation are also subject to photoperiodic control as indicated by the general appearance of the plants 8 weeks after sowing (Plate 1).
Effect of night interruption on the four barley varieties growing in the field, 8 weeks after sowing. Reading from left to right in each group: C, no night interruption; I₃, night interruption with low-intensity light (1 f.c. or less); I₂, night interruption with median-intensity light (1–3 f.c.); I₁, night interruption with high-intensity light (5–10 f.c.).

CI 5611, the variety showing the slowest rate of development in the natural environment, demonstrated the most pronounced promotion by night interruption. Even plants receiving the lowest intensity of illumination (considerably less than 1 f.c.) were significantly more advanced than control plants.

In all varieties there was an apparent convergence of the stage of development of the apex in the various treatments towards the end of the experiment. This was primarily due to inadequacies of the numerical scale used to assess development, since it did not allow sufficient discrimination between stages after the initiation of stamens (stage 8). The time to ear emergence, a more objective measure of ear
development at the later stages of growth, was advanced up to a maximum of 3 weeks in CI 5611 and 1 week in the other varieties by the most intense night illumination.

(b) Formation of Primordia on the Apex

With the exception of CI 5611, night interruption did not significantly promote the rate of primordium production on the main apex (Fig. 3), and in CI 5611, only the highest level of illumination was effective. This more rapid rate was linked to an earlier cessation of primordium formation, and hence a lower maximum number. This tendency was also evident in the other varieties.

The numbers of primordia on the apex paralleled the rate of primordium production in that they reached a maximum and then declined. Once primordium formation on the apex ceased, a variable number of the more apical primordia lost turgor.

![Graph showing effect of night interruption on apical development.](image-url)
and became senescent. Although the process began earlier (particularly in CI 5611), as a result of the light treatment, there was no consistent effect of light interruption on the number of apical primordia which degenerated (Table 1). Several basal primordia (about four, including the collar) formed infertile florets, and this number was also unaffected by the light regime. However, the number of fertile florets on

Fig. 3.—Effect of night interruption on the production of primordia on the main axis. ○ No night interruption (control); ×, +, Δ, light treatments I₁, I₂, I₃, respectively, as defined in Figure 2.

the apex shortly after anthesis was considerably affected (Fig. 4) by the light treatment (also reflected in the yield data which follows). This response can be traced back primarily to the earlier cessation of primordium production caused by the night interruption.
The total number of primordia produced by the apex can be subdivided into those developing into leaves, and those remaining on the apex and ultimately differentiating into floral primordia. The criterion used to distinguish a leaf primordium was the presence of a lamina initial at least 1 mm in length. On this basis CI 5611 had a total of nine leaves and leaf primordia at the first sample and the other varieties each had 10. With the exception of CI 5611 there was no appreciable increase in this number (Fig. 5), but rather a decrease with night illumination. This suggests that a few primordia which initiate growth in the direction of leaf formation ultimately

### Table 1

**Number of Apical Primordia Degenerating in the Later Stages of Apical Development**

Values obtained by difference between maximum primordium number recorded and number at final harvest.

<table>
<thead>
<tr>
<th>Light Treatment</th>
<th>Prior</th>
<th>Noyep</th>
<th>CI 3576</th>
<th>CI 5611</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>12</td>
<td>10</td>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>$I_1$ (high intensity)</td>
<td>10</td>
<td>13</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>$I_2$ (median intensity)</td>
<td>14</td>
<td>7</td>
<td>10</td>
<td>17</td>
</tr>
<tr>
<td>$I_3$ (low intensity)</td>
<td>9</td>
<td>10</td>
<td>11</td>
<td>14</td>
</tr>
</tbody>
</table>

Fig. 4.—Influence of night interruption on the number of fertile spikelets on the ear of the main axis. Control (no night interruption); $I_1$, $I_2$, $I_3$, light treatments as defined in Figure 2.
form floral organs where the environment promotes rapid floral development. A similar change in the development of individual primordia has been noted previously in barley (Paleg and Aspinall 1964) and by Gott, Gregory, and Purvis (1956) in Petkus rye. The treatment effects were not large in any of the varieties but CI 5611 demonstrated the greatest decrease. The significant response in Noyep and CI 3576 resulted from illumination after the plants had initiated flowers, indicating the transitional state of the lower undifferentiated primordia at this time.

![Graph showing the influence of night interruption on the final number of leaves on the main axis. Control (no night interruption); I₁, I₂, I₃, light treatments as defined in Figure 2.]

(c) Apex Length

The length of the apex (from the base of the primordium above the last distinguishable leaf primordium to the apex tip) was measured in the later samples (Fig. 6) and illustrates the accelerated rate of development due to night interruption. When first measured, the apex was much longer in illuminated plants, but tended to cease elongation earlier, manifesting a shorter final length. Apex elongation appeared to cease just prior to ear emergence in each case. CI 5611, the late-flowering variety, again showed the greatest effect of night interruption.
(d) Vegetative Growth

The number of tillers formed in each variety differed, ranging from six (CI 5611) to three (Prior) but there were no consistent effects of night interruption on this aspect of growth. Internode elongation, however, was markedly affected by the light regime (Fig. 7). Elongation began earlier in illuminated plants but ceased earlier, and control plants in all but the variety Noyep eventually demonstrated the longest internodes. CI 3576 plants were shorter than the other three varieties but showed very similar trends. This pattern of earlier commencement and cessation of internode elongation induced by night interruption was correlated with the effect of the light treatment on apical development (Aspinall 1966).

(e) Yield Data

The yield of grain from the small plots was generally decreased by night interruption (Table 2). In Prior and CI 3576 the treatments followed a logical order,
with each increase in light intensity further decreasing yield. In Noyep and CI 5611, however, although the highest yield came from the control plots, the lowest came from the plants receiving least illumination. This may have been due to an interplay between the effects of illumination in advancing development, and of some other environmental factor, such as water stress.

Only Prior demonstrated even a marginal (8%) effect of treatment on mean grain weight. The number of grains per ear was sensitive to night interruption, however, showing similar trends to the data for the number of spikelets on the main axis ears (Fig. 4). The ear size of treated plants was generally smaller, due to the inclusion of tiller ears, but in every case the ears of control plants contained the largest number of grain.
IV. Discussion

The accelerating effect of lengthened photoperiod (Paleg and Aspinall 1964) or night interruption (Aspinall 1966) on the initiation of spikelets in cereals has been reported previously. In the present work, however, only one variety (CI 5611) was

Table 2
DATA FROM FINAL HARVEST AT MATURITY

<table>
<thead>
<tr>
<th>Light Treatment</th>
<th>Prior</th>
<th>Noyep</th>
<th>CI 3576</th>
<th>CI 5611</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>40·3</td>
<td>40·8</td>
<td>47·4</td>
<td>44·7</td>
<td>43·4</td>
</tr>
<tr>
<td>I₁</td>
<td>37·1</td>
<td>40·6</td>
<td>47·9</td>
<td>44·4</td>
<td>42·5</td>
</tr>
<tr>
<td>I₂</td>
<td>38·6</td>
<td>36·2</td>
<td>48·2</td>
<td>45·5</td>
<td>42·1</td>
</tr>
<tr>
<td>I₃</td>
<td>39·9</td>
<td>40·4</td>
<td>48·9</td>
<td>41·1</td>
<td>42·6</td>
</tr>
<tr>
<td>Mean</td>
<td>39·0</td>
<td>39·5</td>
<td>48·1</td>
<td>43·9</td>
<td></td>
</tr>
</tbody>
</table>

Mean grain weight (mg)*

<table>
<thead>
<tr>
<th>Light Treatment</th>
<th>Prior</th>
<th>Noyep</th>
<th>CI 3576</th>
<th>CI 5611</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>19·7</td>
<td>20·3</td>
<td>16·6</td>
<td>18·3</td>
<td>18·7</td>
</tr>
<tr>
<td>I₁</td>
<td>16·7</td>
<td>16·6</td>
<td>14·3</td>
<td>15·6</td>
<td>15·8</td>
</tr>
<tr>
<td>I₂</td>
<td>18·5</td>
<td>18·6</td>
<td>13·4</td>
<td>14·0</td>
<td>16·1</td>
</tr>
<tr>
<td>I₃</td>
<td>18·7</td>
<td>15·1</td>
<td>15·1</td>
<td>14·1</td>
<td>15·6</td>
</tr>
<tr>
<td>Mean</td>
<td>18·4</td>
<td>17·6</td>
<td>14·9</td>
<td>15·5</td>
<td></td>
</tr>
</tbody>
</table>

Number of grains per ear†

<table>
<thead>
<tr>
<th>Light Treatment</th>
<th>Prior</th>
<th>Noyep</th>
<th>CI 3576</th>
<th>CI 5611</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>78·2</td>
<td>83·9</td>
<td>76·9</td>
<td>82·7</td>
<td>80·4</td>
</tr>
<tr>
<td>I₁</td>
<td>61·7</td>
<td>66·7</td>
<td>65·2</td>
<td>70·5</td>
<td>66·0</td>
</tr>
<tr>
<td>I₂</td>
<td>65·9</td>
<td>65·3</td>
<td>65·4</td>
<td>60·3</td>
<td>64·2</td>
</tr>
<tr>
<td>I₃</td>
<td>74·1</td>
<td>57·2</td>
<td>71·7</td>
<td>57·6</td>
<td>65·2</td>
</tr>
<tr>
<td>Mean</td>
<td>70·0</td>
<td>68·3</td>
<td>69·8</td>
<td>67·8</td>
<td></td>
</tr>
</tbody>
</table>

Grain yield (g per plot)‡

* Significant difference (P = 0·05) between variety means = 3·8. Light treatment and interaction means not significantly different.

† Significant difference (P = 0·05) between variety and between light treatment means = 1·7. Interaction means not significantly different.

‡ Significant difference (P = 0·05) between light treatment means = 7·0. Variety and interaction means not significantly different.

subjected to night interruption at a sufficiently early stage of development to unequivocally demonstrate this response (Fig. 1). In view of the fact that night-interrupted CI 5611 plants initiated spikelets 1 week after night interruption was begun (2 weeks sooner than control plants), the response was pronounced.
The photoperiodic sensitivity of floral morphogenesis subsequent to spikelet initiation in grasses has been the subject of some discussion (Evans 1960; Guitard 1960). In the present work, clear evidence was obtained of night-interruption-induced acceleration of floral development, substantiating earlier indications (Aspinall 1966) that, in barley, further development of spikelet initials and differentiation of floral organs is markedly influenced by the prevailing photoperiodic regime. In field experiments, where the natural photoperiod is a continuous variable, it is difficult to quantitate this effect, and in the present work the effects of night interruption on floral morphogenesis were probably reduced because the natural photoperiod was itself increasing, during ear differentiation, at the rate of approximately 20 min per week. Similar considerations may help to explain the data of Bean (1965) in which limited periods of night interruption were given mainly before floral initiation. The treatment accelerated floral initiation but decreased the rate of post-initiation development in Timothy (Phleum pratense). In this case, the treatment resulted in the initiation of flowers at a time of shorter natural photoperiods which presumably delayed later development.

Effects on differentiation of the floral organs appear to be central to all the other subsequent effects of photoperiod on plant growth. Thus the changes in stem elongation, primordium production, and the cessation of apical meristematic activity can each be correlated with the progress of the differentiating ear. The processes controlling the production of primordia at the tip of the ear are particularly interesting in view of the influence they exert on the number of grain in the mature ear and hence on yield. In general it has been shown that the longest ears and greatest number of grain are produced in short photoperiods (e.g. Haensel 1951). The mechanism of this effect has been discussed by Ryle (1965) for perennial ryegrass in which a decrease in photoperiod increased the number of spikelet sites on the apex before spikelet initiation as well as increasing the number produced after spikelet initiation. The effects on spikelet numbers were attributed to the pre-initiation photoperiod as transfer at initiation was without effect. In this respect perennial ryegrass appears to differ from barley as there is clear evidence in the present experiment of an effect of post-initiation photoperiod on spikelet numbers in at least three of the four varieties.

A substantial number of terminal spikelets are lost in the final stages of ear differentiation and a few of the lower spikelets are sterile. The fate of these spikelets is apparently decided at an early stage of differentiation as Nicholls and May (1963) have shown that these peripheral spikelets show a markedly lower rate of differentiation throughout development. The loss of these spikelets does not appear to have contributed to the difference in grain numbers per ear between the various treatments since approximately the same number were lost in all treatments (Table 1). Ryle (1965) has suggested that competition for assimilates limits the number of florets per spikelet and a similar mechanism may be operating here, assimilate being channelled into the more advanced central spikelets. At the stage when spikelet deterioration commences, however, the apical meristem as a whole is comparatively small and it is difficult to conceive of the growth of the apex being limited by a lack of assimilates since later in development, when the inflorescence is much larger, there is not evidence of a comparable effect.
The largest single factor in the determination of ear size in the present experiment was the earlier cessation of primordium production induced by the night-interruption treatment. The number of primordia on the apex at the time of spikelet differentiation was only of consequence in the variety CI 5611 where night interruption occurred before initiation. In this case, the difference between the size of the apices at spikelet differentiation (8.7 primordia in high intensity treatment, 14.7 in control) fully accounted for the difference in grain numbers in the mature ear (Fig. 4). In the other varieties, however, the number of primordia at initiation was constant and the differences in final grain numbers can be attributed to the earlier cessation of primordium production with night interruption.

The fact that there is an effect of photoperiodic regime on both primordium production and spikelet differentiation leads to speculation on possible relationships, if any, between the two processes. Two hypotheses can be advanced:

1. The rate of spikelet differentiation and of primordium production are both affected by the photoperiod but primordium production is less affected than spikelet differentiation.

2. The cessation of primordium production at the apex is correlated with or initiated at a particular stage of morphogenesis in the central spikelets on the ear.

These two possibilities together could account for treatment effects on both the size of the apex at spikelet differentiation (CI 5611 above; Ryle 1965), and the time of cessation of primordium production (all varieties above; Aspinall and Paleg 1963; Ryle 1965). Evidence supporting the first of these hypotheses is difficult to acquire due to the uncertainties inherent in comparing the rates of entirely different processes. A comparison of the rates of development of spikelets and of primordium production in the present work (Figs. 2 and 3) would appear to support this conclusion, however. Similarly, a strict test of the second hypothesis would also require more exact data than that presented here. However, neither the present work nor any data previously presented for barley (Aspinall and Paleg 1963) is incompatible with the conclusion that cessation of primordium production occurs at or about the stage of stamen initiation in central spikelets.

These conclusions have some practical significance in that the yield of grain from plants in a breeding program may well be considerably reduced by an attempt to accelerate flowering with an artificial photoperiod extension. As Haensel (1951) suggests, the yield of grain may be improved without an undue delay in flowering by subjecting the plants to short photoperiods for the first few weeks of growth and then transferring them to long photoperiods to accelerate flowering. Similarly, it would appear that the number of grain per ear produced on commercial crops of barley would be, at least in part, a function of the latitude of the planting site, the date of planting, and the photoperiodic sensitivity of the variety sown.

The ease with which plant development in the field can be influenced by a simple night interruption suggests the use of this treatment as a tool in exploring the interaction between the plant and the field environment. In cases where the stage of plant development has been shown to influence the response of the plant to the environment—e.g. water stress (Aspinall, Nicholls, and May 1964), this system would seem to offer possibilities for direct exploration of the response in the field.
V. Acknowledgments

The authors are particularly indebted to Dr. K. W. Finlay, Agronomy Department, University of Adelaide, for arranging the sowing of the seeds for the experiment. Miss Felicia H. Smith provided technical assistance. The project was supported by the Barley Improvement Trust Fund.

VI. References


