EFFECTS OF DAY LENGTH AND LIGHT INTENSITY ON GROWTH OF BARLEY

III. VEGETATIVE DEVELOPMENT

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[Manuscript received April 6, 1964]

Summary

The effects of variations in light intensity, photoperiod, and light quality on shoot dry weight, tillering, and leaf growth of barley (cv. Prior) have been examined in controlled environments. The rates of tillering and of dry matter production were primarily dependent upon the total radiant energy incident upon the plants. Tillering was unaffected by changes in the photoperiod (independent of light energy) or in the spectral composition of the light which profoundly affected apical development. At low light intensities, tiller buds on the main axis only elongated, whereas at higher intensities secondary and higher-order tillers were produced. The largest number of tillers was associated with the coleoptile node, and tiller production declined regularly with each successive node up the main axis.

The rate of leaf emergence on the main axis was relatively insensitive to changes in light intensity. At higher intensities there was an accumulation of expanding but unemerged leaves as the formation of leaf primordia progressively outstripped the rate of leaf emergence. Mature leaf size and shape were determined by the interaction of two control systems: a heteroblastic change from node to node linked with apical development and hence indirectly affected by the spectral composition of the light source; and a direct effect of light intensity in the short photoperiod, probably mediated through carbohydrate supply.

I. INTRODUCTION

Variations in the light environment have a profound influence on apical development in barley (Aspinall and Paleg 1963; Paleg and Aspinall 1964) but also have many other physiological and morphological effects on plant growth. Some of these effects on vegetative growth are probably mediated through variations in the supply of carbohydrates, particularly with changes in light intensity. Dry matter accumulation (Friend, Helson, and Fisher 1962) and tillering (Mitchell 1953b) have been postulated to be controlled in this manner. However, many plant responses to light, particularly to variations in photoperiod or spectral content, are derived from other reaction systems. The action of these more direct photomorphogenic pathways, such as the phytochrome system, has been shown to control such vegetative growth responses as stem elongation (Downs 1959), leaf expansion (Liverman 1959), cotyledon expansion, and hypocotyl extension (Mohr 1962).

The growth of the plant in any one light environment will therefore be dependent upon the interaction of these several controlling mechanisms, and the complete elucidation of the growth of a plant in a natural environment is likely to be complex in the extreme. An approach to the problem of assessing the role of the various

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mechanisms can be made through the study of plants growing in controlled environments. The most complete study of cereal growth in different light environments has been made with Marquis wheat by Friend, Helson, and Fisher (1962a, 1962b, 1964), who coupled the techniques of growth analysis with more refined growth measurements in assessing the effects of a wide range of environments. The present paper reports on a similar study with barley (*Hordeum vulgare* L. cv. Prior), in which the effects of variations in light intensity, spectral distribution, and photoperiod on leaf growth, tillering, and dry matter accumulation have been measured.

Fig. 1.—Effect of light intensity on shoot dry weight with plants growing under a fluorescent source. A, 16-hr photoperiod; B, 10-hr photoperiod. × Light intensity 3·25 cal/cm²/hr; ○ 2·17; △ 1·67; ▽ 1·17.

II. EXPERIMENTAL METHODS

The data discussed in the present paper were obtained from a series of experiments described in detail elsewhere (Aspinall and Paleg 1963; Paleg and Aspinall 1964). Briefly, all plants were grown in constant environmental conditions at a temperature of 20±1°C with an ample supply of mineral nutrients. Treatments consisted of variations in the photoperiod (10 or 16 hr) and light intensity and light source—fluorescent light over a range 1·17–6·67 cal cm⁻² hr⁻¹ (or 500–2000 f.c.) together with incandescent light over a range 0–22·74 cal cm⁻² hr⁻¹ (or 0–300 f.c.).

Plants were sampled at intervals of a week or less, apices were dissected from the main axis, and vegetative measurements were made. The total number of emerged tillers and the node of origin of each one were recorded, a tiller being considered to have emerged as soon as it had elongated beyond the lamina base of the subtending leaf. The lengths and maximum breadths of the fully expanded leaf laminae on the main axis were then measured. These leaf measurements were continued in successive samples until leaf-tip senescence prevented an accurate assessment of length. In two experiments, the tillers and leaves were collected after the several measurements had been completed, dried at 80°C for 48 hr, and weighed.
III. Experimental Results

(a) Shoot Growth (Dry Weight)

The limited number of experiments in which shoot dry weight was measured provide a comparison of the rates of dry weight increase in different light intensities and photoperiods in fluorescent light (Fig. 1) and fluorescent with incandescent light (Fig. 2). In all environments, the relative rate of growth decreased with time and with any decrease in light intensity or photoperiod.

![Graph showing the effect of fluorescent light intensity on shoot dry weight with plants growing under a mixed fluorescent and incandescent light source in a 16-hr photoperiod.](image)

In order to determine whether these results may be interpreted solely in terms of the light energy available for photosynthesis, the logarithm of dry weights for the fluorescent-grown plants have been plotted against the summated light energy available to the plants in each treatment (Fig. 3A). The light energy has been computed from 7 days after sowing, as there were no treatment effects up to that time, and possible complications due to substrate reserves in the endosperm and seedling emergence from the soil are minimized. The data from the various energy levels and photoperiods form a family of similar curves when plotted in this manner, and
quadratic functions \((\log w = a + b_1 l + b_2 l^2)\), where \(w\) is shoot dry weight and \(l\) is summated light energy) have been computed to fit the data (Table 1). The trend of the coefficients in these functions indicates that decreasing the photoperiod or lowering the light intensity initially increased the efficiency of light utilization (increase in \(b_1\)); in other words, it required less light energy to achieve the same plant weight. However, decreasing light intensity or photoperiod also heightened the progressive reduction in efficiency of light utilization (decrease in \(b_2\)), such that, as the plants grew, light utilization became less efficient at low than at high light intensities.

The data from the plants grown under a mixed light source have not been considered in this manner because it is difficult to compute the relative efficiencies of the two light sources in promoting photosynthesis. The absolute energy measurements (cal cm\(^{-2}\) hr\(^{-1}\)) include, in the case of the incandescent lamps, a very large component of emission in the infrared region of the spectrum which is not present in the fluorescent emission and plays no part in photosynthesis. Measurements in terms of foot-candles, although approximating more closely to the effective photosynthetic spectrum, would also conceal major differences in the emission spectra of the two light sources. The incandescent light at this intensity (5.69 cal cm\(^{-2}\) hr\(^{-1}\) or approximately 50 f.c.) appears, however, to have had but little effect on dry weight gain. At comparable intensities of fluorescent light (1.17–3.25 cal cm\(^{-2}\) hr\(^{-1}\) or approximately 500–1500 f.c.), the rates of dry weight increase were very similar with
or without the additional incandescent light (Figs. 1 and 2). At the end of the experiments, 6 weeks from sowing, the log dry weight of the shoots was linearly related to the total fluorescent light energy received per day (Fig. 3B) over all treatments. Although there were some departures from the regression line, the fit is sufficient to demonstrate the dominating role of available light energy in determining the rate of dry matter accumulation.

### Table 1

**Coefficients of Regression of Shoot Dry Weight on Incident Light Energy**

Regressions are calculated as \( \log_{10} w = a + b_1 l + b_2 l^2 \), where \( w \) = shoot dry weight (mg) and \( l \) = summed light energy (cal/cm\(^2\)).

<table>
<thead>
<tr>
<th>Photo-period (hr)</th>
<th>Light Intensity (cal/cm(^2)/hr)</th>
<th>( b_1 )</th>
<th>Standard Error of ( b_1 )</th>
<th>( b_2 )</th>
<th>Standard Error of ( b_2 )</th>
<th>( a )</th>
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<tbody>
<tr>
<td>16</td>
<td>3.25</td>
<td>+0.16903</td>
<td>0.01195</td>
<td>-0.00013</td>
<td>0.00063</td>
<td>1.366</td>
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<tr>
<td>16</td>
<td>2.17</td>
<td>+0.19634</td>
<td>0.01483</td>
<td>-0.00734</td>
<td>0.00113</td>
<td>1.380</td>
</tr>
<tr>
<td>16</td>
<td>1.67</td>
<td>+0.26859</td>
<td>0.01575</td>
<td>-0.01468</td>
<td>0.00141</td>
<td>1.283</td>
</tr>
<tr>
<td>16</td>
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<td>+0.29902</td>
<td>0.02024</td>
<td>-0.01910</td>
<td>0.00428</td>
<td>1.266</td>
</tr>
<tr>
<td>10</td>
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<td>+0.19173</td>
<td>0.01501</td>
<td>-0.00733</td>
<td>0.00127</td>
<td>1.436</td>
</tr>
<tr>
<td>10</td>
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<td>+0.22350</td>
<td>0.01625</td>
<td>-0.01273</td>
<td>0.00205</td>
<td>1.342</td>
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<tr>
<td>10</td>
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<td>+0.30733</td>
<td>0.02236</td>
<td>-0.02805</td>
<td>0.00387</td>
<td>1.290</td>
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<td>10</td>
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<td>+0.28885</td>
<td>0.02880</td>
<td>-0.02874</td>
<td>0.00674</td>
<td>1.398</td>
</tr>
</tbody>
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**Tiller Numbers**

In suitable light environments tillering was continuous throughout the 6-week growing period (Figs. 4 and 5). There was no decline in tillering rate with time except where tillering was initially very rapid, and mineral nutrients probably became limiting in the final week (Aspinall 1961). Tiller numbers per plant showed an almost exponential rise with time in the more favourable environments, but were considerably reduced by a decrease in light intensity or photoperiod (Fig. 4). At the lower tillering rates the increase with time was more irregular, owing to the partial synchronization of tiller emergence between individual plants. At higher rates, the larger numbers obscured this synchronization. As well as lowering the tillering rate, a reduction in light intensity or photoperiod delayed the emergence of the first tiller. In favourable conditions this tiller was visible within 10–14 days of sowing the grain, whereas with a 10-hr photoperiod at a light intensity of 1.17 cal/cm\(^2\) hr\(^{-1}\), no tillers appeared within 42 days.

Contrasting with these marked effects of total light intensity on tillering, varying the intensity of the incandescent light alone in a mixed source had virtually no effect in either a short (Fig. 4B) or a long (Fig. 5A) photoperiod. Thus plants exhibiting very different flowering responses (Paleg and Aspinall 1964) produced identical tillering patterns even though the development pattern of the tillers following emergence also differed widely. In the high-intensity incandescent treatments
the tiller apices rapidly produced floral initials and the internodes elongated, whereas in a low-intensity treatment the tillers remained vegetative.

The reverse of this situation was produced where plants were illuminated with varying intensities of fluorescent light in the presence of a constant, high (5.69 cal cm\(^{-2}\) hr\(^{-1}\) or 50 f.c.) intensity of incandescent light (Fig. 5B). In this experiment the general level of tillering was inexplicably lower than in previous experiments (compare the upper curve in Fig. 5B with that in Fig. 5A where the intensities of incandescent and fluorescent light sources were similar). This may have been due to unknown soil factors, but if attention is confined to comparisons within the experiment the absolute level of tillering is less important. Tillering was considerably depressed by a reduction in fluorescent light intensity, although these light conditions had no major effect on the flowering of the plants (Paleg and Aspinall 1964).

(ii) Tiller Position

The tillers on a cereal plant can be classified either according to the node of origin of the parent tiller on the main axis or according to their relationship with the original axis: thus primary tillers arise directly on the main axis, secondaries on the

Fig. 4.—Light intensity and tillering. A, 16-hr photoperiod: ○ light intensity 6.67 cal/cm\(^2\)/hr (fluorescent only); × 3.25; ○ 2.17; ▲ 1.67; ▼ 1.17. B, 10-hr photoperiod. ◆ light intensity 6.67 cal/cm\(^2\)/hr (fluorescent only); + 3.25; ● 2.17; ▲ 1.67; ▼ 1.17. ○ 1.92 cal/cm\(^2\)/hr fluorescent light plus 22.74 cal/cm\(^2\)/hr incandescent light. F.I., floral initiation.
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primaries, and so on. On either system, it can be demonstrated that the incandescent content of the light source had no effect on plant form. Thus similar numbers of tillers arose at similar positions on the plant.

Reducing the total light intensity, and hence tiller numbers, affected the proportion of tillers in the various classes. At low light intensities only tillers arising directly on the main axis were present (Fig. 6A) whereas at higher intensities large numbers of secondary and higher-order tillers also elongated. In this variety, at higher light intensities the tiller at the coleoptile node generally produced the largest group of

\[ \begin{align*}
\text{Fig. 5.} & \quad \text{Variations in spectral composition of the light source and tillering.} \\
& \quad \text{A, uniform intensity of fluorescent light (1.92 cal/cm}^2\text{/hr) with varying intensity of incandescent light: } \times 8.04 \text{ cal/cm}^2\text{/hr}; \ O 1.19; \ \Delta 0.40; \ \nabla 0.13. \\
& \quad \text{B, uniform intensity of incandescent light (5.69 cal/cm}^2\text{/hr) with varying intensity of fluorescent light: } \times 2.46 \text{ cal/cm}^2\text{/hr}; \ O 1.79; \ \Delta 1.21; \ \nabla 0.88. \\
& \quad F.I., floral initiation. 
\end{align*} \]

daughter tillers, and other nodes on the main axis gave rise to progressively fewer tillers in order of their position (Fig. 6B). A reduction in light intensity consistently reduced the difference between the sizes of the first few tiller groups but had no other effects. As with changes in tiller numbers, the influence of the photoperiod was similar to that of light intensity, reductions in day length and in light intensity having analogous effects.

(c) Leaf Growth

(i) Leaf Numbers

The rate of production of leaf primordia on the apex of the main axis was determined by factors influencing the growth and development of the apex, as previously discussed (Aspinall and Paleg 1963; Paleg and Aspinall 1964). The
expansion of these primordia to form leaves and their emergence from within the enveloping sheaths of the older leaves were only slightly affected by the range of light environments covered in these experiments. A maximum treatment difference of only one mature leaf per main shoot was recorded at the end of the 6-week growing period: that is, between plants growing at a high light intensity in a long photoperiod (8 leaves) and those at a low intensity in a short photoperiod (7 leaves). The rate of leaf appearance was therefore comparatively constant.

(ii) Leaf Area

The areas (A) of the individual leaves were estimated from the product of leaf length (L) and maximum width (B) as, assuming no marked change in shape, $A = f(LB)$ (Lal and Subba Rao 1951). In the present case, a different relationship was utilized for the first leaf than for the subsequent ones, as this leaf was the only one showing a consistent departure from the function fitted to sample data from all the leaves. Serial measurements demonstrated that there was no change in lamina area once the base (auricle and ligule) was fully exposed. Measurements of mature
leaves from the same node on the main axis but from different times of sampling therefore have been pooled to obtain a mean mature area for each leaf.

There was a marked parallelism between the effects of the light environment on floral development and those on leaf area (Fig. 7A). In all environments the area of successive leaves increased from leaf 1 to leaf 3; thereafter, in less floral-inductive conditions (e.g. low incandescent light intensity) leaf area was greater or remained constant in higher leaves. In highly inductive conditions (e.g. high incandescent light intensity), the area of each successive leaf was reduced from leaf 3 or 4 onwards and the flag leaf, the ultimate leaf, was very small. In the one experiment where plants were grown in a short photoperiod with high incandescent illumination in addition to fluorescent, leaf areas increased in successive leaves to leaf 8 and were larger than in any other treatment (Fig. 10A).
The intensity of fluorescent light incident upon the plants was without effect on leaf area in the long photoperiod, either with (Fig. 8A) or without (Fig. 9A) simultaneous illumination from incandescent lamps. In the short photoperiod, however, a reduction in fluorescent light intensity resulted in a reduction in the area of all leaves above leaf 1 (Fig. 10A). At the lowest intensity, 1.17 cal cm\(^{-2}\) hr\(^{-1}\), in the short photoperiod leaf 2 was the largest on the main axis, and leaf size declined progressively node by node up the main axis above that leaf.

(iii) Leaf Shape

A measure of changes in leaf shape can be derived from a consideration of variations in length and maximum width and of the ratio between them. Although
this ignores certain changes in shape, such as the position of maximum width, it does reveal major variations.

Floral initiation and subsequent development of the main shoot apex was accompanied by a considerable change in the shape of the leaves along the axis (Fig. 7B). In a long photoperiod with high incandescent light intensity, leaves 1–3 were progressively narrower but subsequent leaves were progressively broader. This

![Diagram](image-url)

Fig. 9.—Light intensity and leaf growth in a 16-hr photoperiod, fluorescent light. A, leaf area. B, leaf shape. C, leaf length. D, leaf breadth. × Light intensity 3.25 cal/cm²/hr; O 2.17; △ 1.67; ▽ 1.17. was primarily due to a corresponding change in leaf length (Fig. 7C), leaf breadth being constant to leaf 7 and then falling (Fig. 7D). In a short photoperiod (Fig. 10B) or in the absence of incandescent light (Fig. 9B), leaf shape changed only slightly above leaf 3.

Superimposed upon this change in leaf shape, and possibly linked to apical development, was an effect of light intensity modified by the photoperiod. In the long photoperiod, leaves had a generally lower length/breadth ratio in higher light intensities (Figs. 8B and 9B), particularly in fluorescent light alone. This was due to changes in both components, as leaf breadth was increased (Fig. 9D) and length decreased (Fig. 9C) by an increase in light intensity. In the short photoperiod, light intensity had no consistent effect on leaf shape (Fig. 10B) as both length and breadth were
decreased by a reduction in light intensity (Figs. 10C and 10D). The major difference between the growth of the leaves in the two photoperiods hence appears to be the response of leaf length to light intensity. In the long photoperiod, reduction in light intensity increased leaf length, whereas in the short photoperiod it decreased leaf length.

Fig. 10.—Leaf growth in a 10-hr photoperiod. A, leaf area. B, leaf shape. C, leaf length. D, leaf breadth. × Fluorescent light intensity 3·25 cal/cm²/hr; ○ 2·17; △ 1·67; ▽ 1·17. ● 1·02 cal/cm²/hr fluorescent light plus 22·74 cal/cm²/hr incandescent light.

IV. Discussion

It has frequently been noted that light energy utilization for dry matter production is more efficient at low than at high light intensities. In whole plant studies this is generally attributed to a relatively low light saturation value for the photosynthetic process, together with reflection and scattering of incident radiation. The present data suggest that, in this cereal plant, the initial superior efficiency at lower light intensities was not maintained and that, later in growth, light energy utilization may actually have been more efficient at higher intensities. This was probably due to
differential changes in plant form including leaf disposition and height. These differences cannot have been large as, even where the flowering behaviour of the plant was radically affected, there was little departure from a linear relationship between log shoot dry weight after 6 weeks' growth and the light energy incident upon the plants per day (Fig. 3B). Certainly, larger differences in efficiency would have become apparent if the plants had been grown beyond 6 weeks, for large treatment differences in plant height, for instance, would have developed. However, some caution must be exercised in the interpretation of these data, as root dry weight was not measured and Friend, Helson, and Fisher (1964) have demonstrated in wheat that the light environment can influence the root/shoot dry weight ratio.

The major component in these changes in total shoot dry weight was the tillering behaviour of the plants, the number of tillers increasing as the total illumination from a fluorescent source increased. It is clear that tillering was unaffected by the far-red content (730 mµ) of the light source, either by the absolute intensity or by the ratio
of intensities of light of this wavelength and of light in the red region of the spectrum (660 m), as variations in the incandescent component of the light source, which has the major effect of altering the intensity of light in the far-red region of the spectrum, were without influence on the tillering response. It is possible that the total intensity of red light (660 m) may have been operative in controlling tillering, as this would have varied directly with the total fluorescent light intensity. The more likely interpretation, however, would appear to be that light intensity controlled tillering through its effects on carbon assimilation, the incandescent component of the light source having no effect as it contributed comparatively insignificant amounts of energy in the region of the spectrum effective in photosynthesis. This would explain the relationship between the number of tillers formed by the plant and the light energy received by the plant each day (Fig. 11).

Tillering in cereal plants has been shown to be affected by several factors of the environment, and no simple hypothesis of the control mechanism will suffice. It has been demonstrated that both the rate and pattern of tillering can be controlled by the supply of mineral nutrients (Aspinall 1961) but in the present series of experiments the mineral nutrient supply apparently did not become limiting except, possibly, after the fifth week of growth at a very high light intensity. This was due to the high initial supply and the short duration of the experiments, the plants being in the early tillering phase of growth throughout (Aspinall 1961). There is adequate evidence, on the other hand, that tillering was here limited by the supply of assimilates, as affected by the total light energy incident upon the plants. The development and growth of the terminal shoot apex was without effect on tillering, which throws further doubt on the relevance of a direct auxin-mediated apical dominance system in barley (Aspinall 1963). The extreme manipulations of apical development achieved by altering the incandescent component of the light source would be expected to radically affect apical auxin synthesis, and yet tillering was unaffected. It is possible that, were the light and mineral nutrient factors at an optimal level, a direct effect of apical development modified by the photoperiod would be demonstrable.

The size of the vascular connections between the nutrient source (leaves or roots) and the various sinks (the tiller apices) should also contribute to the competitive success, and hence growth, of the emerging tillers. In both of these cases the age and position on the plant of the tiller apex would be expected to influence its growth; and it is significant that a reduction in light intensity, and hence presumably in the pool of assimilates available for growth, invariably first restricted the growth of buds in secondary positions or at higher nodes on the main axis. The tiller group developed at the coleoptile node was the only exception to this rule, as it was more severely affected by a reduction in light intensity than would be anticipated from its position. At low light intensities this tiller group was very variable in size, being completely absent from some plants. The presence of a tiller bud at this node is not invariable in this barley variety and its subsequent development can be greatly influenced by, among other factors, the depth of sowing; which suggests that this tiller group cannot be strictly compared with those further up the main axis.

The insensitivity of the rate of leaf emergence to the light environment was unexpected in view of several reports to the contrary (Mitchell 1953a; Friend,
The rate of initiation of leaf primordia was accelerated by an increase in light intensity (Aspinall and Paleg 1963) and there was a resultant accumulation of leaves in the pre-emergence state at the high intensities. It is possible that the growth of the lateral buds provided a compensating mechanism, as an increase in light intensity produced greater tiller development which must have been initially supported by photosynthesis in the main axis leaves. This additional sink may have absorbed much of the extra assimilate produced at the high light intensities, so that there was less available for leaf elongation.

The subsequent growth of the leaves has been considered in terms of the length and breadth of the mature leaves. These are arbitrary measures, but Borrill (1961) has demonstrated in *Lolium temulentum* that variations in leaf length are correlated with changes in epidermal cell length, whereas changes in leaf breadth involve changes in cell numbers. Similarly, leaf length in wheat is primarily dependent upon cell length (Borrill 1959).

Two distinct effects on leaf length have been demonstrated in barley. The first of these, a progressive increase in leaf length from node to node up the main axis followed by a decline, has been described in a number of grasses (Borrill 1959). It is linked with floral development but it is difficult to correlate the emergence of the longest leaf with floral initiation as proposed by Borrill (1959). In barley, floral initiation frequently occurred before the emergence of this leaf. Floral induction in *Chenopodium amaranticolor* is accompanied by a stimulation of leaf growth (Thomas 1961) but further floral development inhibits leaf development, resulting in heteroblastic changes in shape and size. A similar inhibition may operate in barley but there is no evidence for an initial stimulation. Successive leaves on the axis are initiated on an apex changing in both shape and size, the rate of change varying with the prevailing photoperiod. This alone will certainly influence their future development (Snow and Snow 1955).

Independently of the effect of leaf position, light intensity influenced both length and breadth of leaves (Figs. 9 and 10). In wheat grown in continuous light, Friend, Helson, and Fisher (1962b) have shown that increasing light intensity decreased leaf length but increased breadth. This is identical to the response of barley in a long photoperiod, but in a short photoperiod both were reduced by a decrease in intensity. A dual control of leaf growth is suggested, with a hormonal mechanism controlling leaf growth in long photoperiods, and carbohydrate supply determining leaf expansion in the short photoperiod, when photosynthesis is the rate-limiting process.

The effect of light intensity on leaf growth in the two photoperiods probably explains the differential effects of light intensity on apical growth, where the apical growth rate was more severely reduced by a reduction in available light energy in a short than in a long photoperiod (Aspinall and Paleg 1963, Fig. 5). In a short photoperiod the limitation on apical growth imposed by the rate of carbohydrate supply is rendered more acute by the reduction in assimilating leaf area resulting from a decrease in the light intensity. There is no such effect on leaf area in the long photoperiod with decreasing light intensity, and hence less limitation on apical development.
V. Acknowledgments

The authors wish to thank Miss Felicia H. Smith for technical assistance. The investigation was supported by the Barley Improvement Trust Fund.

VI. References


