EFFECTS OF DAY LENGTH AND LIGHT INTENSITY ON GROWTH OF BARLEY

IV. GENETICALLY CONTROLLED VARIATION IN RESPONSE TO PHOTOPERIOD

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Summary

Apical growth, floral development, stem elongation, tillering, and dry weight at ear emergence were compared for 10 varieties of barley (*Hordeum vulgare* L.) growing in a range of photoperiods. All the varieties could be described as quantitative long-day plants but there was a wide range of response to the photoperiod. In all the varieties and over all photoperiods, apical primordium production was linked with floral organogenesis, suggesting a common mechanism of photoperiodic influence on the two processes. The control of internode elongation, however, varied between different varieties, commencing at a much earlier stage of floral organogenesis in some varieties than in others. Tillering appeared to be controlled more by the amount of energy available for photosynthesis than by any photoperiodic process, and this was also an important factor in shoot dry weight at ear emergence.

I. INTRODUCTION

Previous papers in this series (Aspinall and Paleg 1963, 1964; Paleg and Aspinall 1964) have described the photoperiodic response of one variety of barley (Prior) in some detail. It has been shown that the length of the photoperiod affects a variety of plant attributes, many deriving ultimately from the response of the apical meristem. Considerable differences in the photoperiodic responses of cereal varieties have been recorded (Chinoy and Nanda 1951; Best 1959; Takahashi and Yasuda 1960; Griffiths 1961), and varieties of barley have been described to be practically day-neutral (Takahashi and Yasuda 1960), quantitatively long-day (Guitard 1960), or obligate long-day plants (Takahashi and Yasuda 1960). These varietal comparisons have generally been conducted over only a few photoperiods with little control of other environmental factors and the emergence of the ear has been used as the sole criterion of photoperiodic effectiveness. Although such studies provide a useful guide to the field behaviour of different varieties, they are insufficient as a basis for an adequate exploration of the genetics and physiology of the photoperiodic response.

The present survey of the photoperiodic responses of 10 varieties of barley was initiated to investigate the generality of conclusions reached with the variety Prior and to form the basis of a study of the inheritance of photoperiodic response. A range of varieties was selected to include current Australian commercial varieties as well as others which may prove to be of importance in breeding programs.

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II. Experimental Methods

Plants were grown in controlled environments throughout (Aspinall and Paleg 1963) at a constant temperature of 18±1°C. The light source consisted of white fluorescent tubes (Philips TLF 80/33) supplemented with incandescent strip lamps (Osram, 24-in., 75 W), and was adjusted to give a mean illumination of 6·67 cal cm^{-2} hr^{-1} (2000 f.c.) fluorescent light and 5·69 cal cm^{-2} hr^{-1} (50 f.c.) incandescent light at plant level. Effects of photoperiods of 24, 16, 14, 12, and 8 hr on plant growth were compared, and of photoperiods of 14 hr with fluorescent light alone and of 12 hr

Table 1

Country of origin, parentage, and field behaviour of the barley varieties

Variety	Country of Origin	Parentage	Relative Flowering Date in the Field*
CI 3576	ex USDA, believed to be of Egyptian origin	Unknown	2
Noyep	South Australia	Farmer selection from Prior	1
Prior	South Australia	Believed to be farmer selection from Chevallier type	3
Piroline	Bavaria	Weihenstephaner Mildew Resistant × Morgenrot	4
Volla	Bavaria	Wisa × Haisa I	5
Research	Victoria	Plumage Archer × Prior	4
Freja	Sweden	Victory × Opal	5
CI 5611	ex USDA, believed to be of Turkish origin	Unknown	7
Proctor	United Kingdom	Plumage Archer × Kenia	6
Pioneer	United Kingdom	Spratt Archer × Tschermaks two-row winter	No flowering

* Scored in order of ear emergence in a field trial conducted at Clinton, S. Aust., in 1963, following a June sowing. Successive numbers do not indicate equal time intervals, only the relative order of flowering.

fluorescent light supplemented with a 2-hr night interruption (1·13 cal cm^{-2} hr^{-1}, 10 f.c. incandescent light). Two cabinets were employed in these experiments so that only two photoperiodic regimes were compared concurrently; experience has shown, however, that photoperiodic experiments with barley in these controlled-environment cabinets are accurately reproducible so that this factor should not seriously affect the validity of inter-treatment comparisons.

Ten barley varieties were compared (Table 1) covering a range of field flowering habits, countries of origin, and parentage. Seeds of these varieties were pregerminated in petri dishes for 48 hr at 20°C and were then planted out into 6-cm plastic pots containing a coarse sand : vermiculite (3 : 2) mixture. These were watered twice weekly with a complete nutrient solution (Aspinall 1961, 10% concentration), watering with distilled water being carried out at other times when required. Five pots of each variety were sown with six seeds and the plants were removed at intervals for apical dissections, a further five pots were sown with one seed and the tillering of

these plants was recorded twice weekly. In most experiments these single plants were carried through to ear emergence and were then harvested for dry weight determinations. The pots were randomized in five replicate blocks across the cabinet and were moved around daily in a regular manner within each block to minimize the effects of the minor gradients of light intensity present in the cabinet. The practice of initially sowing six plants in each pot and removing them one by one, which was unavoidable from space considerations, curtailed tillering but did not affect the flowering response as judged by a comparison of the time of ear emergence of these plants with those growing singly. The interval between successive samplings of these plants varied with the photoperiod, being longer at shorter photoperiods, in an attempt to so space the samples as to span the complete course of apical development.

Sampled plants were removed from the pot with as little disturbance to the remaining seedlings as possible, tillers were recorded, and the main axis was dissected to reveal the apical meristem. Numbers and developmental stages of leaves, leaf primordia, and floral primordia were recorded and the node of origin of any internode elongation was noted. In the final harvest, at ear emergence, the single plants were treated as above and then all the above-ground material was collected, the roots were recovered, and the plant material was dried at 80°C for 48 hr and weighed.

The stage of apical development was graded according to the scale previously devised (Aspinall and Paleg 1963) in which the score progresses from 1 (vegetative apex with a short dome) to 11 (ear in anthesis). A score of 3 indicates the stage of double ridges (the first visible sign of floral initiation) and one of 8 indicates the stage of stamen initiation (a late stage of floral organogenesis). In each case the development of the apex as a whole was equated with that of the most advanced primordium.

The data taken at the successive samplings in each experiment allowed estimates to be made of the time required for the plants to reach particular stages of floral development. No valid statistical significance can be placed on these estimates of rate of floral development as they were derived by interpolation in smoothed curves drawn through experimental values, but the uniformity of rates of apical development was high with little variation between replicate plants dissected at the same time. An exception must be made, however, in the case of the variety Research which demonstrated a high degree of heterogeneity in the long photoperiods (24 and 16 hr) but much less in short photoperiods.

III. Results

(*a*) *Apical Development*

All the varieties, apart from Pioneer which requires vernalization, formed double ridges within the period of the experiments (Fig. 1) but several varieties did not form stamen initials in the shortest photoperiod before the experiment was terminated.

The varieties showed little increase in the time taken to reach double-ridge initiation with a drop in photoperiod from 24 to 16 hr, compared with the effects of further reduction in the photoperiod to 8 hr. The time taken to form double ridges in continuous light varied from 9 days (Noyep, Prior, Research, and Volla) to 17 days (CI 3576) and a reduction to a 16-hr photoperiod increased this time by 1 (CI 3576,

CI 5611) to 5 days (Proctor). The effects of further reduction in photoperiod below 16 hr followed two basic patterns. Some varieties (Noyep, Prior, Piroline, Freja)

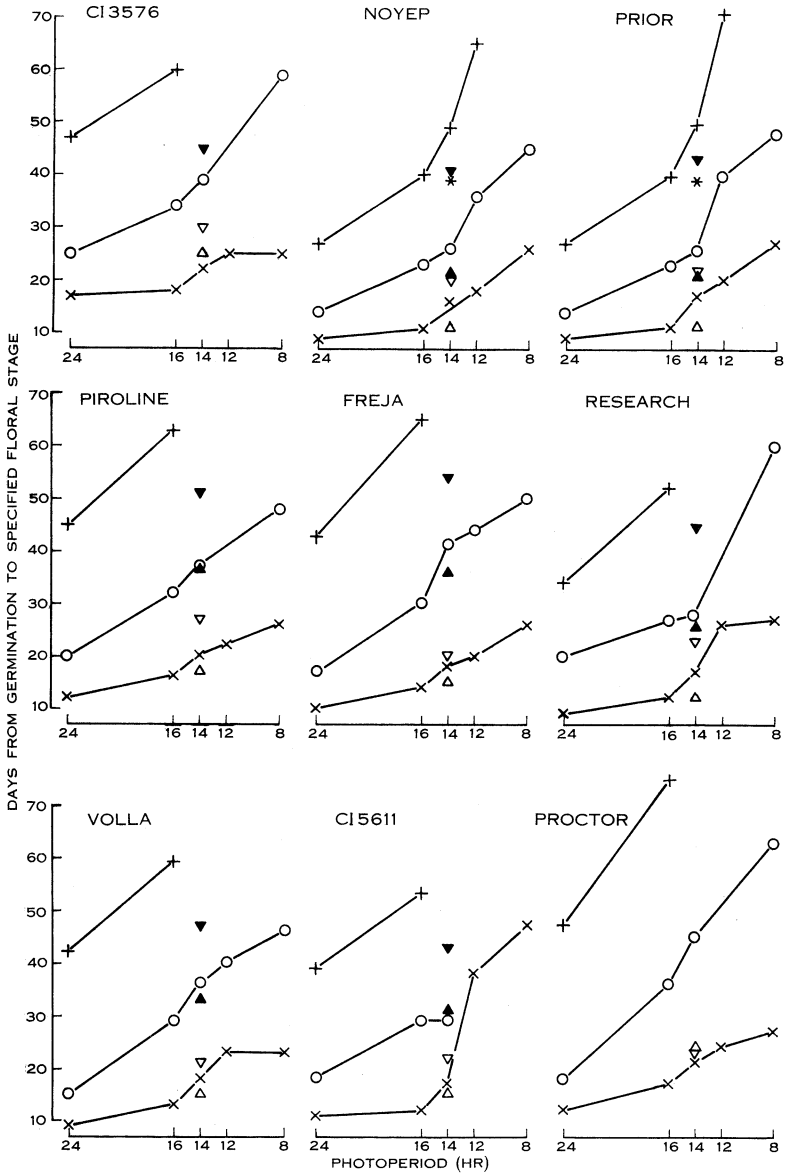


Fig. 1.—Effect of photoperiod on the rate of floral development. Double-ridge stage (×), stamen-initiation stage (○), and ear emergence (+) in various photoperiods of mixed fluorescent and incandescent light. Double-ridge stage (△), stamen-initiation stage (▲), and ear emergence (*) in 12-hr photoperiod with night interruption. Double-ridge stage (▽) and stamen-initiation stage (▼) in 14-hr photoperiod of fluorescent light alone.

showed a linear increase in this period with decreasing photoperiod down to 8 hr. The remaining varieties showed less increase in time to form double ridges between

a 12- and an 8-hr photoperiod than between a 16- and a 12-hr photoperiod. Indeed, CI 3576, Volla, and Research formed double ridges almost as rapidly in 8- as in 12-hr photoperiods. All the varieties are clearly quantitative long-day plants, demonstrating an increasing time to form floral initials with decreasing photoperiod, but no clearly critical photoperiod. CI 3576 approached most closely to a day-neutral condition with a 16-hr decrease in photoperiod resulting in only an 8-day increase in the time to floral initiation. At the other extreme, CI 5611 had an almost obligate day-length requirement as the same decrease in photoperiod increased the time to form double ridges by 36 days, the greatest increase occurring between 14 and 12 hr.

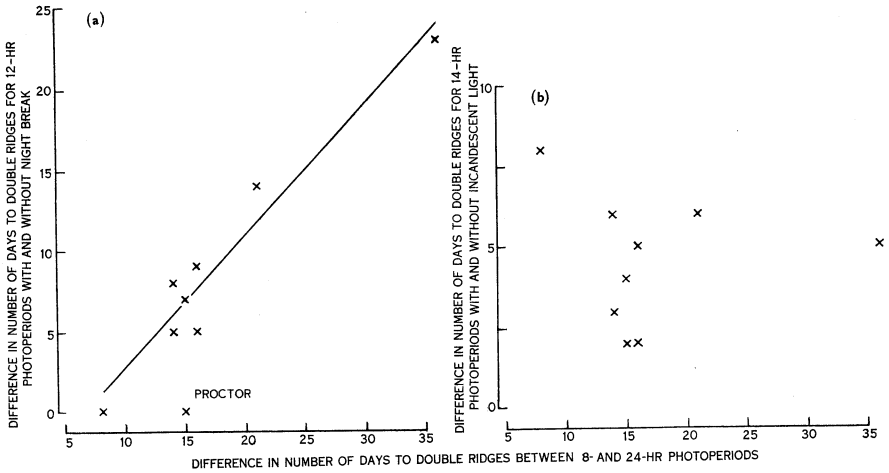


Fig. 2.—Relationship between photoperiodic response and response to (*a*) night interruption and (*b*) inclusion of incandescent light in the light source.

Further information on the photoperiodic response of these varieties is obtained by consideration of the effects of a night interruption and of omitting incandescent light (the major source of far-red light) from the light panel. In two varieties, CI 3576 and Proctor, the night interruption was ineffective, the plants behaving as if in a 12-hr photoperiod. All the other varieties showed some response to the night interruption, although the extent of the decrease in time to flower initiation varied. The magnitude of this response to the night interruption bore a close relationship to the response of the variety to photoperiod [Fig. 2(*a*)]. Proctor was the only variety which departed markedly from a linear relationship between these two quantities. This suggests that the response of a barley variety to night interruption may be a good indication of the nature of its photoperiodic response.

In all varieties omission of the incandescent lights increased the time taken to form double ridges. This response was also variable, however, varying from 2 (Freja) to 8 (CI 3576) days and apparently unrelated to the response to increasing day length [Fig. 2(*b*)]. This response would appear to be due to the spectral composition of the light received during the photoperiod rather than its total energy (Paleg and Aspinall 1964) and it is of interest that varietal differences in response to length of the photoperiod are not directly related to this factor.

Further floral development to the stage of stamen initiation was also more rapid in longer photoperiods and there were large effects of the genotype (Fig. 1). There was less evidence of a levelling of the response between the 12- and 8-hr photoperiods, since even those varieties which initiated double ridges at the same time in the two photoperiods showed an increase in the time taken to form stamen initials. Similarly, there was a greater difference between 24- and 16-hr photoperiods in their effect on stamen initiation than on double-ridge formation. This could indicate that further development following the initiation of double ridges is more susceptible to control by the availability of the products of photosynthesis than is the initiation of double ridges itself. It must be noted, however, that a night interruption generally decreased, and omission of the far-red component from the light source generally increased, the time taken to initiate stamens. In some cases (e.g. Noyep and Prior) the effects of these treatments were greater on stamen initiation than on double-ridge formation. This would argue that stamen initiation is under photoperiodic as well as photosynthetic control.

CI 3576 and Proctor, the varieties exhibiting least effect of photoperiod on double-ridge formation, showed a pronounced effect on further development. Noyep, Prior, and Piroline showed the least effect on this later period of development, although even here there was some 14–16 days difference in the time from double ridge to stamen initiation as between 24- and 8-hr photoperiods. The data for stamen initiation is incomplete for the variety CI 5611 since in the 12- and 8-hr photoperiods the experiment was terminated before the plants had initiated stamens. However, in the 8-hr photoperiod the state of the apices on the final dissection indicated that stamen initiation was considerably delayed (in excess of 150 days). In this respect also, this variety approaches most closely to an obligate response to photoperiod.

Data on ear emergence is much more restricted as there was insufficient time to carry all varieties through to ear emergence in the shorter photoperiods. The time from stamen initiation to ear emergence was at least as long, and sometimes considerably longer, than the time from germination to the initiation of stamens (Fig. 1). In Prior and Noyep, for which the most complete data is available, there was an almost exponential increase in the time to ear emergence with decreasing photoperiod, accentuating still further the divergence between the effects of photoperiod on double-ridge formation and on further floral development. Night interruption decreased the period to ear emergence even more than the period to stamen initiation, indicating that development even at this late stage is apparently responsive to photoperiodic stimulation.

(*b*) *Primordium Production at the Apex*

The total number of nodes (including those bearing leaves, spikelets, and undifferentiated primordia) produced by the main axis was counted at each sampling date as a measure of the activity of the apical meristem (Fig. 3). All the data (with the exception of Pioneer—cf. Fig. 4) could be fitted by sigmoid rather than linear functions with time as was previously demonstrated with Prior barley growing under a mixed light source (Paleg and Aspinall 1964). In the longer photoperiods, the initial rate of primordium production was higher but the total number of primordia produced was less than in the intermediate photoperiods, although there was an

indication in some varieties (e.g. Piroline, Proctor) that both the rate of primordium production initially and the final number of primordia were reduced at the shortest day length (8 hr). There was considerable genotypic variation in the effects of photoperiod on these parameters. Noyep and Prior demonstrated a considerable photo-

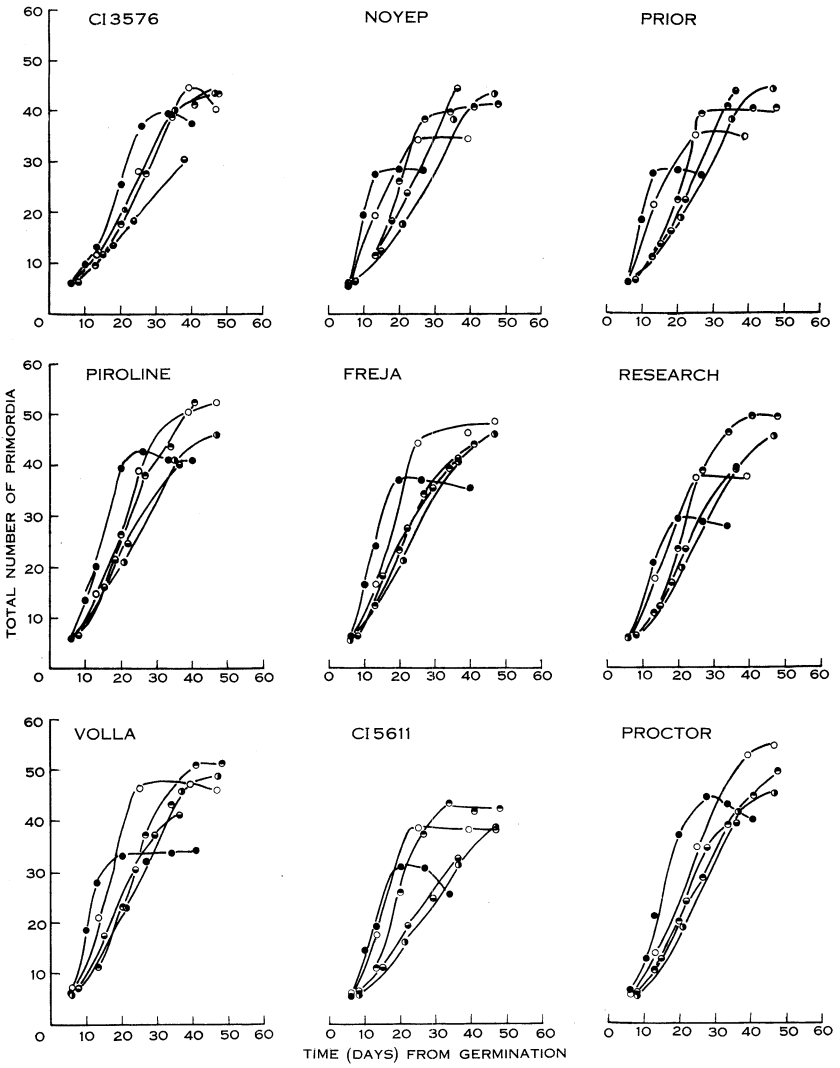


Fig. 3.—Effect of photoperiod on primordium production on the main axis: ● 24 hr, ○ 16 hr, ◓ 14 hr, ◒ 12 hr, and ◑ 8 hr.

periodic influence on both the rate of production and the final number of primordia, but there was much less effect of photoperiod in CI 3576.

The data for the vernalization-requiring variety, Pioneer, indicate that primordium production at the apex was continuing at a rate constant with time in all environments. These rates were calculated (from linear regressions) and show an

almost linear decrease with decreasing photoperiod between 24 and 14 hr but thereafter a constant rate down to an 8-hr photoperiod (Fig. 4). The introduction of a night break or omission of the incandescent light source had little effect on these relationships. There are two possible explanations for this result. Firstly, apical growth may be limited by the supply of photosynthate at the apex over the range of photoperiods above 14 hr. Below this the plant may compensate for a further reduction in the assimilate supply by a limitation in the growth of other sinks (e.g. tiller buds). Alternatively, the pattern of growth rates may be a resultant of two opposing

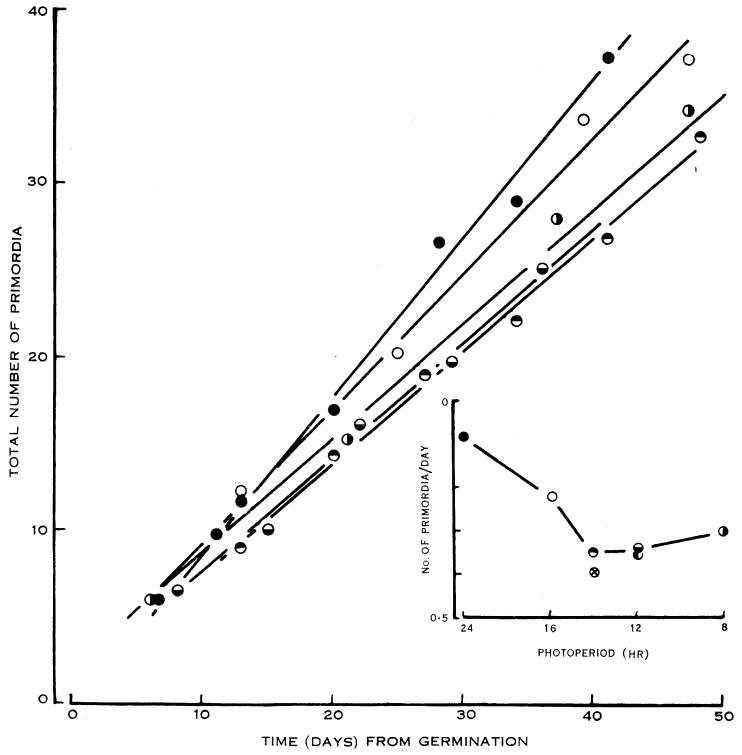


Fig. 4.—Effect of photoperiod on primordium production in the variety Pioneer. Symbols as in previous figure; in addition, ◐ 12 hr plus night interruption, ⊗ 14 hr (fluorescent light only).

influences; assimilate supply and short-day "vernalization" (Chujo 1962) in the shorter photoperiods. Whatever the mechanism, however, it is of interest that the other varieties show a similar trend in that the *relative* rates of primordium production calculated over the first 3–4 weeks of growth show a much larger fall between the 24- and 16-hr day lengths than between the 16 and 8 (e.g. in Prior this relative rate was 0·22, 0·09, and 0·06 in the 24-, 16-, and 8-hr photoperiods respectively).

A comparison between the data on primordium production and that on apical development (Fig. 1) leads to the conclusion that there is a general relationship between these two parameters. Thus CI 3576 which shows the least effect of photoperiod on apical development also exhibits the least effect on primordium initiation. It is difficult to obtain unequivocal single representative values for these variables to

evaluate the relationship between them. In the present case the number of primordia present on two occasions (12 and 24 days post-germination) have been plotted against the number of days taken to form double ridges (Fig. 5) the necessary values being obtained by interpolation on the relevant graph where required. It can be seen that there is a reasonably close curvilinear relationship between these measures—none of the varieties showing significant systematic departures from the curve. Even with these relatively crude estimates of the rates of the two processes it is evident that there is a good degree of correlation between them over a wide range of photoperiods

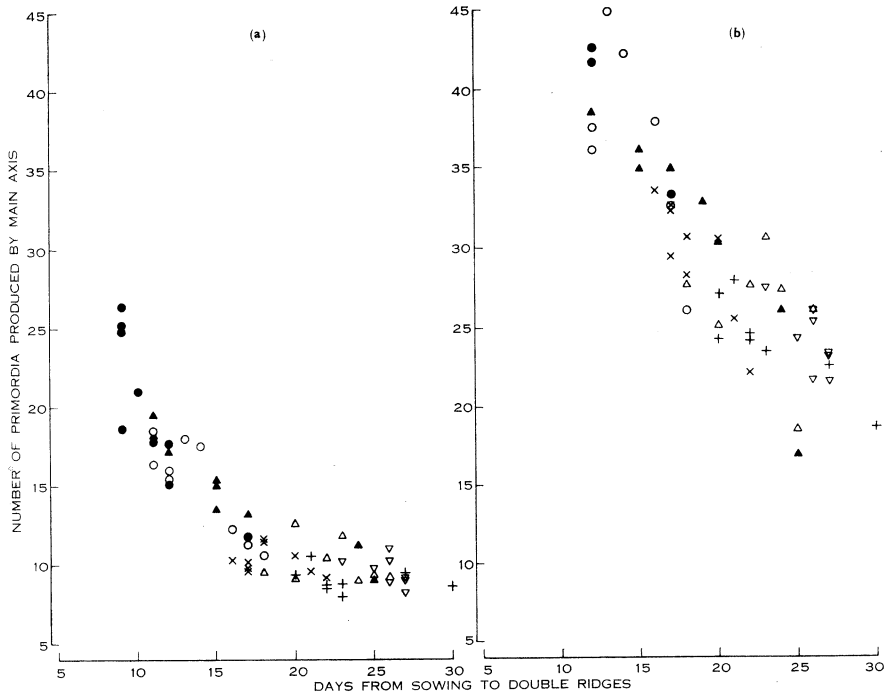


Fig. 5.—Relationship between the rate of floral development and the rate of primordium formation on the main axis (*a*) 12 days after germination, (*b*) 24 days after germination for photoperiods of ● 24 hr, ○ 16 hr, × 14 hr, △ 12 hr, + 8 hr, ▲ 12 hr plus night interruption, ▽ 14 hr (fluorescent light only).

and genotypes. This supports the earlier claim that primordium production and floral development in barley are rate-limited by a similar photoperiodic process (Paleg and Aspinall 1964).

The initiation of lateral organs by the apex has so far been considered as a whole, but the eventual products of apical activity are leaves and fertile spikelets. Genotypic and photoperiodic influences on primordium production are reflected in both of these variables. The data for the numbers of fertile spikelets (Table 2) are incomplete, values for all varieties being obtained only in the 24-, 16-, and (12+2)-hr photoperiods. It is evident, however, that a reduction in the photoperiod results in an increase in the size of the ear and that there are considerable varietal differences. Thus Volla had relatively few fertile spikelets in continuous light and twice as many in a 16-hr

photoperiod, Noyep had the same number as Volla in continuous light but fewer in the shorter photoperiod, and Proctor had more fertile spikelets than either variety in both photoperiods. In those varieties where the comparison is possible it can be

TABLE 2

NUMBER OF FERTILE SPIKELETS IN THE MATURE EARS OF THE BARLEY VARIETIES IN RESPONSE TO DIFFERENT PHOTOPERIODS

Variety	No. of Spikelets in Response to Photoperiods (hr) of:					
	24	16	14	12	8	12+2
CI 3576	13·3	12·9	22·5	—	—	15·0
Noyep	11·9	18·8	21·5	27·7	29·0	19·0
Prior	10·6	18·6	21·0	26·9	26·8	20·2
Piroline	20·5	25·7	—	—	—	24·7
Freja	16·6	26·8	—	—	—	28·0
Research	11·9	22·7	28·0	—	—	25·1
Volla	11·5	22·6	—	29·7	—	28·1
CI 5611	12·5	18·8	—	—	—	24·1
Proctor	20·0	31·0	—	—	—	33·4

seen that the introduction of a night interruption reduced the number of potential grains on the ear. It is likely, therefore, that the main determinant of fertile spikelet number in these experiments was photoperiodic rather than photosynthetic in origin.

TABLE 3

MEAN NUMBER OF LEAVES ON MAIN AXIS OF EACH BARLEY VARIETY IN RESPONSE TO DIFFERENT PHOTOPERIODS

Variety	Mean No. of Leaves* in Response to Photoperiods (hr) of:						
	24	16	14	12	8	12+2	14†
CI 3576	9·5	10·3	10·4	—	12·9	9·9	10·2
Noyep	7·0	8·0	8·4	10·1	13·5	7·3	10·5
Prior	7·0	7·8	8·7	10·4	12·4	7·8	11·1
Piroline	9·0	9·6	10·5	12·1	14·0	11·7	13·6
Freja	7·4	9·0	11·3	—	13·3	10·4	12·2
Research	7·1	8·3	9·3	10·6	12·4	8·7	11·7
Volla	7·2	8·9	9·7	11·0	13·4	9·8	11·2
CI 5611	7·1	8·7	8·8	—	19·4	10·5	10·6
Proctor	8·6	9·9	12·6	—	14·5	12·2	13·4

* Significant difference ($P = 0{\cdot}05$) = 0·9. † No incandescent light.

It has been stated (Gott, Gregory, and Purvis 1955) that the most unequivocal measure of a photoperiodic response is the number of leaves formed prior to the production of a terminal flower. Doubt has recently been expressed on the validity of this conclusion (Friend, Fisher, and Helson 1963) but leaf number remains a useful summary parameter of photo-induction. The leaf numbers in the present series of experiments (Table 3) serve to confirm the previous conclusions regarding the effects

of photoperiod and genotype on flowering, and there was, in fact, a close linear relationship between leaf number and number of days from sowing to double ridges ($b = +0{\cdot}307$, $P < 0{\cdot}001$). The range of leaf numbers in continuous light was not great but the difference between varieties increased in shorter photoperiods.

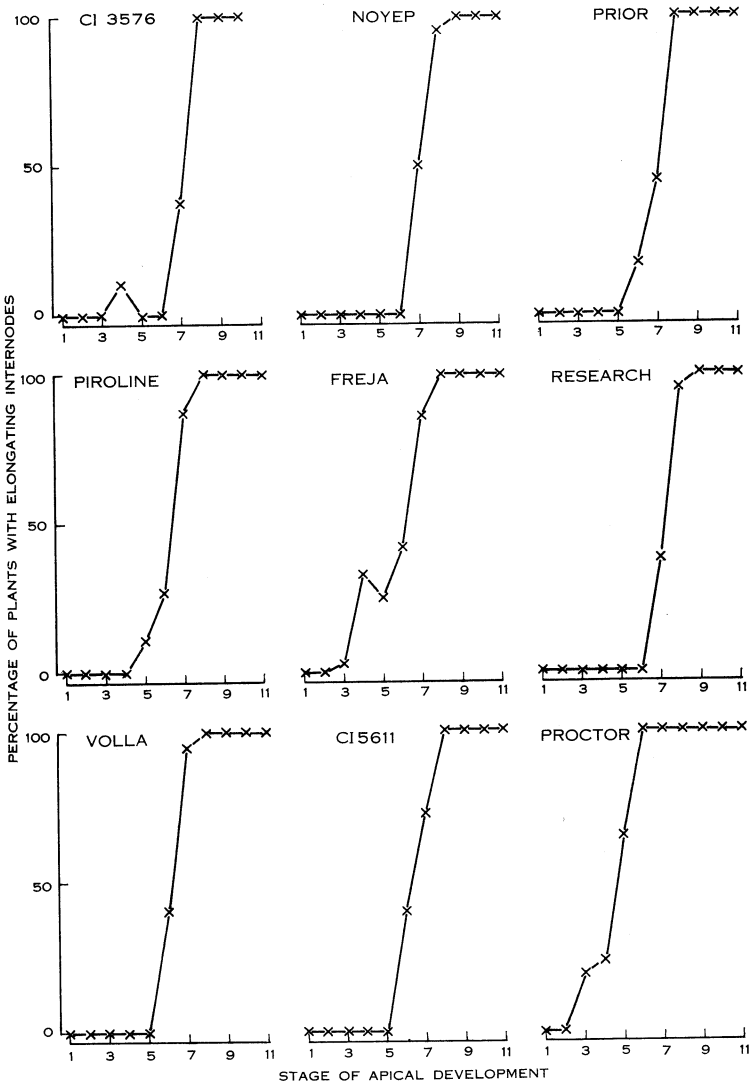


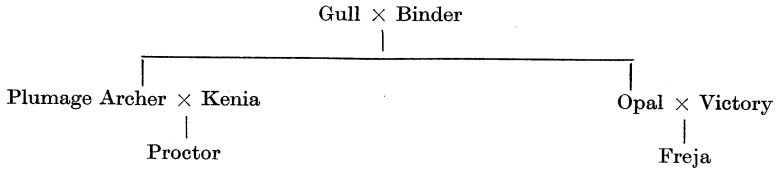
Fig. 6.—Internode elongation and floral development.

(c) *Elongation of the Stem Internodes*

No records were taken of internode lengths but the presence or absence of visible (>2 mm) internode elongation and the internodes involved was noted for each plant when dissected. It has been reported (Nicholls and May 1964) that the onset of internode elongation in Prior barley, particularly within the ear, is correlated with

the formation of stamen initials. The present data allowed a far wider survey of this possible correlation over a range of photoperiods and varieties. The proportion of plants with elongating internodes in each developmental class has been plotted for each variety (summed over photoperiods) in Figure 6. The varieties appear to fall into two distinct categories: in the first group (CI 3576, Noyep, Prior, Piroline, Research, Volla, and CI 5611) there was little or no internode elongation until the apex reached the stage of initiating lateral spikelets (5) and all plants had commenced internode elongation by the stage of stamen initiation (8). This group of varieties, hence, tends to substantiate the claim for a correlation between elongation and apical development but indicates that the critical developmental stage occurs earlier than the initiation of stamens.

In the remaining two varieties (Freja and Proctor), however, internode elongation commenced in some plants with the formation of double ridges (3) and, in Proctor, all plants were elongating when glumes were initiated (6). In this connection, it is of interest to note that Proctor and Freja share common ancestors in the varieties Gull and Binder which do not appear in any of the other tested varieties. The data from these two varieties indicates that the relationship between



apical development and internode elongation is not fixed and that the physiological mechanism which initiates elongation may not be as closely correlated with a particular stage of apical development as was conceived. In continuous light internode elongation was initiated in these two varieties at the time of glume formation and all plants were elongating by the stage of lemma initiation (7). A similar relationship was observed in the 16-hr photoperiod but in all shorter photoperiods, internode elongation was initiated earlier [at the double-ridge or advanced double-ridge stage (stages 3 and 4 respectively)] in at least a proportion of the plants. In the other varieties internode elongation was delayed until lateral spikelet formation even in the short photoperiods.

The lowest node above which internode elongation took place also varied with the photoperiod and the variety. In CI 3576 and Proctor, parallelling their relative insensitivity to photoperiod, there was little change in the position of this node between different day lengths (extreme difference nodes 4–5, in Proctor). In all other varieties, and particularly CI 5611 (extreme difference nodes 3–7), internode elongation commenced at a lower position on the stem in longer day lengths. This parameter also would appear to be under photoperiodic control.

(*d*) *Tillering*

Data on the tillering behaviour of the plants growing singly and of those growing six to the pot were collected but only the former will be presented here. Competition from the companion plants reduced tillering in the plants sampled for

apical dissections and the differences in sampling interval between different experiments complicates consideration of the tillering patterns.

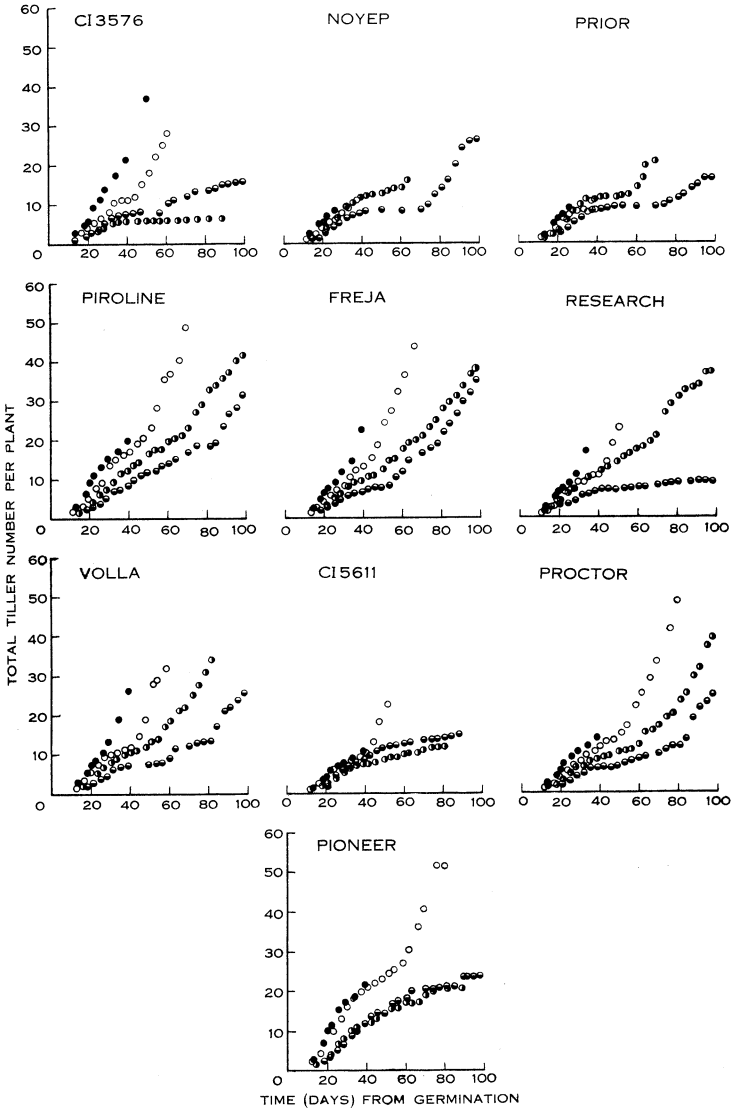


Fig. 7.—Effect of photoperiod on tillering: ● 24 hr, ○ 16 hr, ◑ 12 hr, and ◒ 8 hr.

There were considerable varietal differences in tillering (Fig. 7). Some varieties produced many tillers under all the photoperiodic regimes (Piroline, Proctor, Pioneer, Volla, and Freja), others produced relatively many in long but few in short days (CI 3576, Research). In all varieties there was a general decline in the initial rate of tillering from long to short photoperiods. The simplest explanation of this response would appear to be that in these environments the effects of photoperiod on tillering

are mediated mainly through the photosynthetic system and the general availability of metabolites to support tiller expansion (Aspinall and Paleg 1964). This is further supported by the general lack of influence of the imposition of a 2-hr night interruption on the 12-hr photoperiod (in only four varieties was there any effect and this is a marginally significant decrease in the tillering rate). If the early tillering rate was dependent upon the rate of assimilation then it is evident that varieties differed considerably in efficiency of converting the available assimilate into new

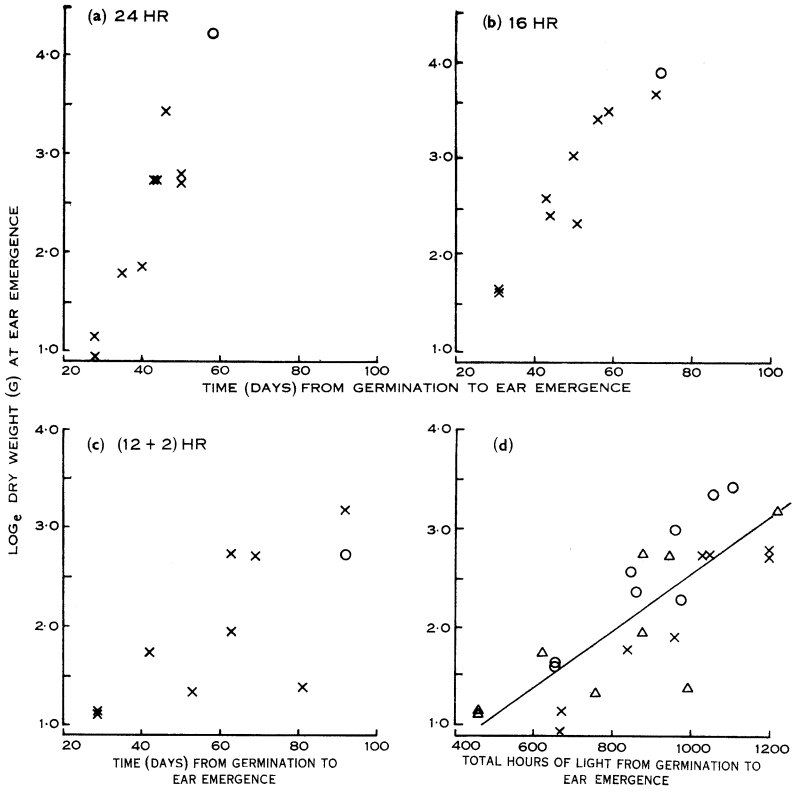


Fig. 8.—Relationship between shoot dry weight at ear emergence and the time of ear emergence for photoperiods of: (*a*) 24 hr; (*b*) 16 hr; (*c*) 12 hr plus night interruption. ○ Pioneer (taken prior to ear emergence); × all other varieties. (*d*) Shoot dry weight for three photoperiods plotted against hours of light received by the plants prior to ear emergence: × 24-hr photoperiod; ○ 16-hr photoperiod; △ 12-hr photoperiod plus 2-hr night interruption.

growing shoots. Thus CI 5611 showed only a doubling of the tillering rate with a threefold increase in the photoperiod whereas Piroline gave a fourfold increase in tillering rate in the same circumstances. All varieties tillered slowly in the 8-hr photoperiod and much larger differences in tillering rate were observed in continuous light. These differences were undoubtedly complex and dependent upon such parameters as assimilation rate, leaf area, leaf disposition, translocation, and intraplant competition. In connection with this last suggestion, it is of interest that Pioneer, which did not initiate flowers in any environment until well after 25 days, had the

highest rate of tillering in all environments. The apices of these plants were growing more slowly than those of any of the other varieties and presumably would have had a lower requirement for nutrients.

The pattern of tillering from germination to anthesis also varied with photoperiod and variety. The mineral nutrient supply was renewed weekly in all of these experiments and continuous tillering would be expected under these circumstances (Aspinall 1961). In many cases this was true (e.g. Freja and Piroline, all photoperiods) but in other cases there was a definite period of reduced tillering rate between an initial and a final high rate, in some cases (e.g. Noyep, 8-hr photoperiod) tillering ceased entirely for a short period. In all varieties, tillering was continuous in continuous light and tended to become more pronouncedly phasic with decreasing photoperiod. The period of reduced tiller-bud elongation may mark a phase of high intraplant competition for the products of photosynthesis, possibly associated with internode elongation and apical organogenesis which are occurring contemporaneously. A similar explanation has been advanced for identical tillering patterns which can be induced by manipulation of the supply of mineral nutrients to the plant (Aspinall 1961).

(*e*) *Dry Weight*

Dry weights of the roots and the shoots were taken separately at ear emergence of the single plants in the 24-, 16-, and (12+2)-hr photoperiods and for some varieties in the 12-hr photoperiod (Noyep, Prior, Piroline, and Volla). In any one photoperiod, the total dry weight of the plant at ear emergence depended very largely on the length of the period between germination and ear emergence for that particular variety [Figs. 8(*a*), 8(*b*)]. The difference in slope in this relationship as between the various photoperiods could be due to the total light available for photosynthesis and allowance can be made for this factor by plotting the data against the hours of light received by the plants [Fig. 8(*d*)]. However, the data do not show a good fit to a linear regression ($P<0\cdot05$) and although the total amount of light energy available for photosynthesis between the times of germination and ear emergence was of considerable importance, varietal- and photoperiodically induced characteristics affecting the efficiency of assimilation must have also influenced the total dry weight. Differences in plant height suggest themselves as an obvious varietal characteristic which would affect efficiency. In this connection, it is of significance that the most pronounced varietal differences in this parameter occurred in the interrupted-night treatment [Fig. 8(*c*)] where an increase in photoperiodic stimulation was not linked to a comparable increase in energy for photosynthesis.

The partitioning of this dry weight as between shoots and roots was considerably affected by both photoperiod and variety (Table 4) but caution must be used in interpreting these results. The plants were grown in small pots throughout (6 cm diam.) and the restricting effect of this reduced volume for root extension would become progressively more pronounced as ear emergence was delayed. Nevertheless some of the varietal and photoperiodic effects on the shoot/root ratio are of such a magnitude as to appear to be indisputably real. Thus in continuous light the variety CI 5611 had a shoot/root ratio which was four times greater than that of any other variety and yet in shorter photoperiods was close to the mean of the varieties. This

reduction in shoot/root ratio with decreasing photoperiod in this variety is interesting in that it is the reverse of the trend in all the other varieties and the reverse of what might be anticipated to be the result of progressive root restriction as ear emergence was delayed. It is possible that this shift in the shoot/root ratio is a further manifestation of the extreme photoperiodic sensitivity of this as compared with the remaining varieties. Even apart from this one variety it is evident that there is considerable variation in the partitioning of dry matter between shoots and roots and that this is an extremely plastic parameter with both genotypic and environmentally determined variations.

TABLE 4

SHOOT/ROOT DRY WEIGHT RATIOS AT EAR EMERGENCE OF EACH BARLEY VARIETY FOR DIFFERENT PHOTOPERIODS

Variety	Shoot/Root Dry Weight Ratios for Photoperiods (hr) of:			
	24	16	12	12+2
CI 3576	1·3	4·7	4·0*	6·1
Noyep	1·8	3·4	3·3	4·9
Prior	2·6	3·2	2·9	4·9
Piroline	0·9	1·3	7·0	3·6
Freja	2·0	1·2	5·6*	5·8
Research	3·8	4·3	5·3*	4·4
Volla	2·0	1·8	5·1	4·9
CI 5611	12·1	4·8	2·0*	5·7
Proctor	1·5	1·7	6·0*	5·0
Pioneer	0·2*	0·8*	6·8*	3·1*

* Determined before anthesis.

IV. DISCUSSION

In general, the data obtained from these 10 varieties supports the conclusions previously reached from a study of the responses of the variety Prior alone (Aspinall and Paleg 1963, 1964; Paleg and Aspinall 1964). Thus there was a close correlation between primordium production and apical organogenesis, floral initiation (but not necessarily stamen initiation) occurred before internode elongation, incandescent light had a marked influence on the photoperiodic response, and tillering appeared to be controlled by the photosynthetic rate. Some aspects of the photoperiodic response in the barley plant have been clarified by this study, however, and some questions raised.

In all varieties there was evidence that all the stages of development — including the emergence of the ear — were accelerated by the photoperiodic treatment. As the treatments were continuous, however, this does not necessarily mean that the later stages of growth were accelerated by the contemporary photoperiod. Guitard (1960) has shown with two other barley varieties that the photoperiod between germination and stem elongation and that between stem elongation and earing both affect the rapidity of development following stem elongation. There is evidence, therefore, that in the barley plant floral initiation does not mark the sole event controlled by photoperiod but that the process (or processes) influenced by photoperiod is present and exerts an influence during a considerable period of

morphological development at the apex. In fact the effects on the rates of post-initiation development may be of greater magnitude than those on initiation (Fig. 1) although, of course, the means of assessing development are imperfect, being necessarily qualitative rather than quantitative in nature.

The nature of the photoperiodic response appeared to be very similar in these barley varieties although the quantitative reaction to specific photoperiods differed widely. All the varieties gave some response to a night interruption and the extent of the response was a reasonable measure of the photoperiodic responsiveness of the variety. Similarly, all of the varieties gave a response to the exclusion of incandescent light from the light source, emphasizing the generality of this effect. The effects of incandescent light were only investigated at one photoperiod and temperature in this case and it may well be that these two environmental factors may influence the response — it is known that at least for Prior barley the effect is much greater at a 16-hr rather than 10-hr (Paleg and Aspinall 1964) or 14-hr (Fig. 1) photoperiod. It is also significant that neither the night interruption nor the omission of incandescent light from the light source had any influence on the rate of primordium production in the non-vernalized but vernalization-requiring variety Pioneer, suggesting that both of these factors are affecting a photoperiodic process, blocked in the case of Pioneer by the failure to provide the prerequisite vernalization.

Any practical benefit to be derived from a study of the physiology and genetics of photoperiodism in barley will depend ultimately on the relationships between photoperiodic behaviour and field response on the one hand and flowering date and yield on the other. In the southern Australian environment the optimal earing date is governed principally by the onset of soil moisture stress in spring. The early stages of earing are particularly vulnerable to the effects of drought (Aspinall, Nicholls, and May 1964) which places a premium on early flowering in any cereal variety. This has led to the general adoption of varieties which are early by European standards (Prior, Research) and the search for still earlier varieties (Noyep) for areas where moisture stress is likely to occur early in spring.

There is no direct simple relationship between flowering date in the field and photoperiodic response. CI 3576 tends to flower slightly earlier than Prior in the field (Table 1) and yet Prior has a marked response to photoperiod and CI 3576 a very small response (Fig. 1). The photoperiodic response can be used to predict how varieties are likely to behave in a new area — for instance it can be seen why Prior will flower so rapidly in a European environment with much longer photoperiods (Bell 1939), and on the other hand it can be predicted that European varieties (e.g. Proctor) will be late in coming to head by Australian standards. The seasonal pattern of day length during the growth of the cereal crop in southern Australia is such that the barley crop is sown when the day length is approximately 10 hr increasing to a maximum of $13\frac{1}{2}$ hr by the time plants become relatively insensitive to photoperiod subsequent to earing (Guitard 1960). Depending upon the season and the cropping program, barley may be sown before or after the shortest day and hence the plants may be subjected to a variable period of relatively short photoperiods during early development. The effect of this on earing date could be expected to depend on the photoperiodic response of the variety. Thus a variety showing a marked photoperiodic response (e.g. Prior) would be delayed by the short photo-

period in early growth but accelerated by increasing photoperiod later in growth such that the influence of sowing date on earing date would be minimized. In contrast, a variety with less photoperiodic response (e.g. CI 3576) may show a more marked effect of sowing on earing date. A more detailed examination of the reasons for varietal differences in flowering date in the field would require more information on the interaction of other environmental factors (e.g. temperature) with the photoperiodic response on the one hand and data on apical development before ear emergence in field-grown crops on the other.

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