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Flowering in Lentil (*Lens culinaris* Medic.): The Duration of the Photoperiodic Inductive Phase as a Function of Accumulated Daylength above the Critical Photoperiod

E. H. ROBERTS*, R. J. SUMMERFIELD*, F. J. MUEHLBAUER† and R. W. SHORT†

**University of Reading, Department of Agriculture, Plant Environment Laboratory, Shinfield Grange, Cutbush Lane, Shinfield, Reading, Berks RG2 9AD and †USDA, ARS, Grain Legume Genetics and Physiology, 215 Johnson Hall, Washington State University, Pullman, WA 99164, USA*

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ABSTRACT

The durations from emergence to the appearance of first flower buds and to first open flowers were recorded in three genotypes of lentil (*Lens culinaris* Medic.) when plants were transferred from short days (either 8 or 10 h) to long days (16 h), or *vice versa*, after various times from emergence. These results were compared with those of control treatments in which plants remained in either short or long days throughout. Four developmental phases were identified: pre-emergence, pre-inductive, inductive and post-inductive. The first two phases and the last are insensitive to photoperiod, but are probably sensitive to temperature. The duration of the inductive phase, which has to be completed before flowering can occur at the end of the post-inductive phase, can be predicted by assuming that its reciprocal is a linear function of both photoperiod and temperature. It follows that the critical photoperiod decreases with increase in temperature and that the duration of the inductive phase can be calculated from a summation of the amounts by which successive daylengths exceed the critical photoperiod until a value ('the photoperiodic sum') characteristic of the genotype is reached. The implications of these findings for predictive field models of time to flowering in lentils are discussed.

Key words: *Lens culinaris* Medic., lentil, flowering, critical photoperiod, photoperiodic sum, temperature, developmental phases, field models.

INTRODUCTION

Lentils (*Lens culinaris* Medic.) are traditionally seeded after autumn rains throughout the Mediterranean region, so that vegetative crops experience progressively lengthening days and warming temperatures, or after the monsoon rains in India and Pakistan, to emerge into shortening days and cool, or even cold, conditions (Summerfield, Muehlbauer and Short, 1982). Not surprisingly, times to flowering (f) vary appreciably between genotypes, locations and seasons, and timely flowering is important in the adaptation of the crop to its traditional and novel environments (Summerfield, 1981) – as it is in most annual crops (Bunting, 1975).

Relative responsiveness to three factors – vernalization, post-vernalization mean temperature and photoperiod – modulates rate of progress towards flowering ($1/f$) in this quantitative long-day species (Summerfield *et al.*, 1985). But, there remains a possibility that genotypes differ in relative sensitivity to photo-thermal conditions throughout the vegetative period. Although a pronounced 'juvenile' (or 'basic vegetative') phase, during which plants are insensitive to normally inductive conditions, has not previously been reported in lentils, field observations have revealed that plants of several genotypes come into flower only after a minimum number of leaves (about 11)

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have been expanded (M. C. Saxena, pers. comm.). And so, the vegetative period could comprise two distinct phases – a juvenile (or basic vegetative) period followed by a photoperiod-sensitive one (and see Vince-Prue, 1975; Bernier, Kinet and Sachs, 1981). In rice, for example, these two phases are apparently under separate genetic control and the basic vegetative period can vary in duration from about 10 to about 60 d (Vergara and Chang, 1976).

Clearly, it is essential to determine whether or not a juvenile period exists in lentils and, if it does, whether the duration of this photoperiod-insensitive phase differs appreciably between genotypes relatively early or late to flower or between those which are insensitive or variously sensitive to photoperiod. Such information would allow not only the more effective screening of germplasm for relative sensitivity to photo-thermal effects on flowering but also rational interpretations of subsequent studies undertaken either to investigate the genetic control of these responses or to develop predictive models for application in the field (see Summerfield *et al.*, 1985).

MATERIALS AND METHODS

General comments

Two, almost identical, experiments were undertaken in glasshouses. The initial investigation was conducted using a facility equipped with only modest photo-thermal controls (described by Summerfield and Muehlbauer, 1982), whereas the second investigation involved glasshouses with more precise and automatic regulation of both photoperiod and day and night temperatures (Roberts *et al.*, 1979). The original investigation had to be terminated prematurely after 110 d from sowing as it became progressively more difficult to regulate the intended artificial climate under glass; as a consequence, complete results for only one early flowering genotype were salvaged from this investigation.

Based on the responses of this genotype and especially on subsequent research involving a range of diverse genotypes in widely different photo-thermal regimes (Summerfield *et al.*, 1985), the second investigation included a trio of genotypes (Table 1) known to differ appreciably in both relative earliness to flower in the same strongly inductive photoperiod (16 h) and in relative sensitivity to sub-optimal photoperiods (to as short as 10 h).

TABLE 1. *Origin and selected characteristics of lentil genotypes used*

Germplasm accession number*	Name	Country of origin	Relative earliness to flower†	Relative sensitivity to photoperiod‡
ILL 4400	Syrian Local large	Syria	Late	Acute
ILL 4349	Laird	Russia	Late	Moderate
ILL 4605	Precoz	Argentina	Early	Slight

* Accession number of the world lentil germplasm collection maintained at the International Centre for Agricultural Research in the Dry Areas (ICARDA) at Aleppo in Syria.

† In the same most-inductive photo-thermal regime (16 h and $\bar{t} = 21{\cdot}8$ °C) of the wide range investigated (Summerfield *et al.*, 1985).

‡ Relative delay in flowering in 10 cf. 16 h days (Summerfield *et al.*, 1985).

Plant husbandry and culture

Techniques in both investigations were based on those developed for tropical grain legumes in general (Summerfield, Huxley and Minchin, 1977) and subsequently modified for lentils as described in detail elsewhere (Summerfield and Muehlbauer, 1982). In both cases, the seeds of each accession (Table 1) were weighed individually and only those from the median range of each stock were used. They were immersed in 50 per cent ethanol for 30 s, surface sterilized for 2 min in 0·2 per cent mercuric chloride in 0·01 M HCl and washed three times in sterile distilled water. Seeds of many *Microsperma* (small-seeded) lentil land-races and, depending on the time of harvest and conditions during storage, even those of improved cultivars may imbibe only poorly unless scarrified (Summerfield, 1981). Because of this, the graded stocks were soaked in aerated distilled water at room temperature and only those seeds which were plump after 4 h (the typical duration to maximum imbibition, determined by preliminary trials) were selected. These seeds were blotted dry and either sown immediately (original investigation) or soon after inoculation with strain of *Rhizobium* SL 13 [a broadly effective strain from the collection maintained at the International Centre for Agricultural Research in the Dry Areas (ICARDA), at Aleppo in Syria] using standard procedures (Summerfield *et al.*, 1977).

Four (original investigation) or three seeds were sown to each 15 cm diameter (0·75 l capacity) or 12 cm square (1·5 l capacity) plastic pot containing, respectively, either a mixture of field soil, peat, sand and 0·6 cm gravel (5:5:5:1, v/v) or vermiculite, sand, gravel and loamless peat compost without fertilizer (4:2:4:1, v/v) and soaked 24 h beforehand with deionized water. After sowing, the seeds were covered with a 2 cm layer of the respective rooting medium, all components of which had been steam-sterilized at 96 °C and 3 kg cm^{-2} for between 10 and 20 min.

Pots were not irrigated until 10 d after sowing, when the seedlings of all three genotypes were well established. Thereafter, sufficient nutrient solution containing either 200 or 20 mg l^{-1} inorganic nitrogen for non-nodulated and nodulated plants, respectively (Summerfield *et al.*, 1977), was applied either manually or delivered automatically up to four times each day so that drainage through the pots occurred at every application in both investigations. The non-nodulated plants were obviously dependent solely on inorganic nitrogen; we expect the nodulated ones will have derived a large proportion of their nitrogen from symbiotic dinitrogen fixation, but this has yet to be confirmed.

Three or five replicate pots of all genotypes were sown (on 1 May 1981 and on 17 May 1984, respectively) for each experimental treatment. Seedlings were thinned after 10–20 d to leave single uniform plants in each pot. At thinning, all pots were given a surface dusting of Captan, as an effective precautionary measure against seedling pathogens which may otherwise lead to 'damping-off'.

Records were made on individual plants of the times from sowing until the appearance of the first flower bud and to first open flower (corolla colour visible).

Environmental conditions and experimental treatments

Plants in the original investigation at Pullman, Washington, USA were grown within two large, opaque enclosures constructed from sheets of black polythene supported on wooden frames and covering individual benches each 7 m long and 1 m wide within a glasshouse equipped with semi-automatic top ventilation and conventional fan-wet pad cooling. A mixture of three 300 W incandescent lamps (with domed, white enamel reflectors) and banks of Sylvania 'Cool White' fluorescent tubes (with 135 °C internal reflectors) were used to illuminate the plants for 8 h each day in one enclosure (from 0800 to 1600 h Pacific Daylight Time). A long photoperiod of 16 h was imposed in the

second enclosure in which the incandescent lamps remained switched on for longer each day (i.e. from 0400 to 2000 h). The illuminance provided by the incandescent lamps alone varied from about 4000 lux at a distance 30 cm below them to about 1000 lux at bench level, and so was well above the value needed to saturate the photoperiodic response in the genotypes investigated (Summerfield, Muehlbauer and Roberts, 1984).

Plants in the second and principal investigation were grown in fully-automated glasshouses during the summer months at Reading, UK (a facility described in detail elsewhere; Roberts *et al.*, 1979). They received natural light only from either 0400 until 2000 h (16 h d) or from 1000 until 2000 h (10 h d).

Thermograph records were taken continously in each of the polythene enclosures in which daily maximum and minimum air temperatures averaged 29·7/15·0 °C and 27·6/13·3 °C in the 8 and 16 h photoperiods, respectively. In the second investigation, day temperature was maintained to within ± 1 °C of the required value of 30 °C by automatic ventilation with cool external air, and rose slightly above this value on less than 5 per cent of the days during the investigation. Plants were supported on two trolleys which were automatically drawn into and out of 'night' compartments at the appropriate times. A night temperature of 15 °C was maintained to within ± 0·5 °C by heating elements and cooling fans operating in tandem, with little or no lag between the day/night temperature transition. Photoperiods of either 10 or 16 h duration were imposed.

In both investigations, replicate plants of each genotype experienced either short (8 or 10 h) or long (16 h) days throughout (the control treatments), or were transferred between the short and long day regimes at 4-d intervals during the first 40 d after emergence. They experienced, therefore, different durations of either weakly or strongly inductive photoperiods before being transferred into the respective alternative regime until they came into flower, at which times the plants were discarded.

In the principal investigation at Reading and, we believe, improving the original experimental design, the different photoperiod treatments were confounded with solar radiation receipt. (The reasons for this approach have been discussed elsewhere; Hadley *et al.*, 1983). But, so that photoperiods were not confounded with temperature, plants grown in the long-day regime experienced a temperature of 15 ± 1 °C for the first 6 h (0400 until 1000 h) each day. Thus, mean diurnal air temperature in all treatments was close to 21·25 °C (i.e. [(14 h × 15 °C) + (10 h × 30 °C)]/24), compared with estimated average values of 20·5 and 22·2 °C in the long and short day enclosures in the original investigation.

RESULTS

General comments

This paper reports the results of an experiment carried out in carefully controlled and precisely regulated glasshouses at Reading, and where three genotypes of lentil were subjected to 20 different photoperiodic treatments in which plants were transferred from short to long photoperiods, or *vice versa*, at different times from emergence (reciprocal transfer treatments). These treatments were compared with controls in which plants remained in either 10 or 16 h photoperiods throughout. The results of a preliminary experiment carried out at Pullman, Washington, USA on one of the genotypes subsequently used at Reading are also reported; in this case, however, photoperiods of 8 h and 16 h were used. By comparing the two sets of results, for nodule-dependent or nitrate-dependent plants exposed either to only natural or to only artificial light in the UK and USA, respectively, we hoped to validate and extend the conclusions drawn from the principal investigation. Details of the treatments imposed and their consequences for flowering are shown in Figs 1–4.

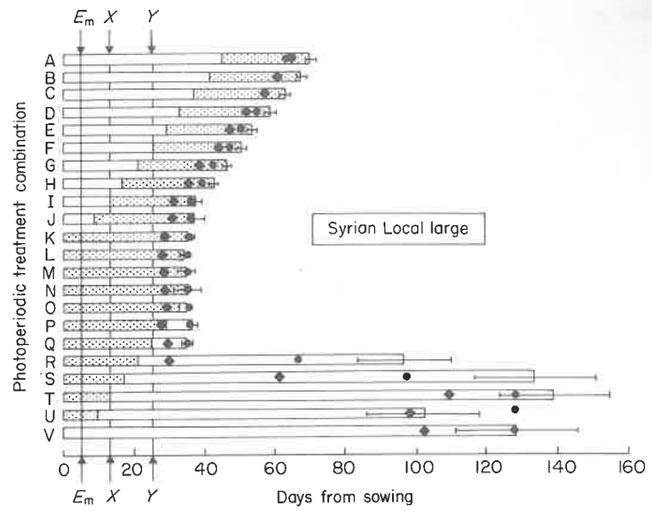

FIG. 1. Effects of various photoperiodic treatments (**A** to **V**) on days from sowing to the appearance of first flowers (complete histograms) and first flower buds detectable by eye (◆) in the lentil landrace Syrian Local grown at a mean temperature of 21·25 °C. Open and stippled areas within individual histograms are 10 and 16 h photoperiods, respectively. Horizontal lines spanning times to first flowers are standard deviations (for clarity, those for times of appearance of first flower buds have been omitted but were of similar relative magnitude, or smaller, in respective treatments). *Em* and *X* denote seedling emergence and the end of the pre-inductive phase, respectively; *Y* marks the end of the inductive period in continuous 16 h photoperiods (see text). Theoretical times from sowing to first flower (days from emergence to first flower + 5 d) calculated according to the method described in the text are shown as ● within or adjacent to individual histograms.

Photoperiod sensitivity

As expected in this quantitative long-day species, plants of all genotypes took the longest time to come into flower (55–128 d after sowing) when grown in continuous short days and they flowered most rapidly in continuous long days (after 36–54 d) – see treatments **V** and **K**, respectively, in Figs 1–4. Differences in time to flower between these two control treatments confirmed previous data on relative photoperiod sensitivity (Summerfield *et al.*, 1985): the Syrian Local landrace was most sensitive (Fig. 1); cultivar Laird, released in Canada from germplasm introduced from Russia, was intermediate (Fig. 2); and Precoz, an 'early' cultivar from Argentina, was least sensitive to photoperiod (Figs 3 and 4). However, relative earliness is very much affected not only by genotype but also by environment: it depends not only on photoperiod sensitivity but also on responsiveness to vernalization and to post-vernalization average air temperature (Summerfield *et al.*, 1985). Furthermore, photoperiod sensitivity, when defined in terms of the difference in days to flower between two different photoperiods, is itself also markedly affected by temperature (Summerfield *et al.*, 1985). Nevertheless, the large differences in relative sensitivity under the temperature regime imposed (30 °C day; 15 °C night) are indicative of the widely different origin and selection history of the genotypes tested.

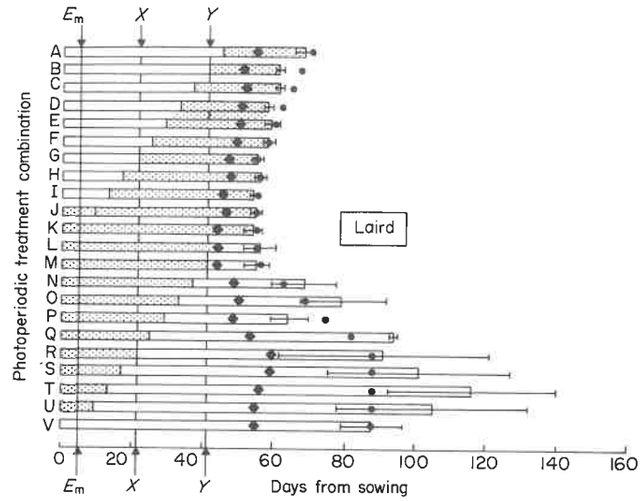

FIG. 2. Effects of various photoperiodic treatments on the lentil cultivar Laird. Other details as for Fig. 1.

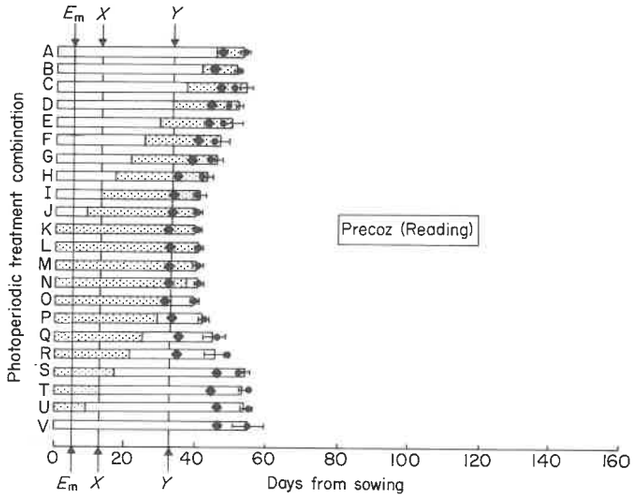

FIG. 3. Effects of various photoperiodic treatments on the lentil cultivar Precoz. Other details as for Fig. 1.

Responsiveness to photoperiod

Since, in the temperature regime used at Reading, the Syrian Local landrace was clearly the most sensitive to photoperiod, we have chosen to analyze the responses of this genotype first. Attention will then focus on minor differences in this pattern with those observed in the cultivars Laird and Precoz.

After sowing, there is an initial pre-emergence phase, *g*, during which the seedlings experience darkness and so cannot be subject to photoperiodic stimulation. In Syrian Local this phase ended after 5 d, at emergence (E_m in Fig. 1). Then followed a period

of about 8 d after emergence (i.e. from time E_m to *X* in Fig. 1) during which photoperiod had no significant effect on the time taken to flower: compare the similarity of the results of treatments **I** and **J** (which had either no long days (**I**) or only 4 long days (**J**) during this period) with those of treatments **K** to **Q** (in which this first phase consisted entirely of long days). We shall refer to this period, starting at emergence and finishing at time

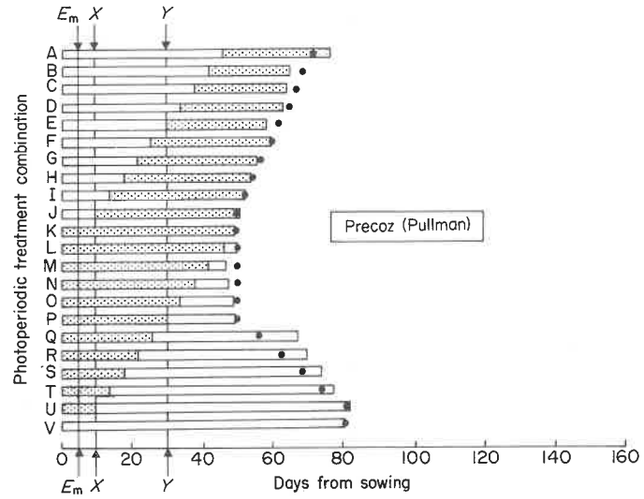

FIG. 4. Effects of various photoperiodic treatments on the lentil cultivar Precoz grown at a mean temperature of 20·5 °C combined with 16 h photoperiods (stippled areas) or 22·2 °C combined with 8 h photoperiods (open areas). Times of reciprocal transfers were slightly different to those shown in Figs 1 to 3 (see text), otherwise details as for Fig. 1.

X, as the 'pre-inductive phase', *j*, and define it as an initial period when plants are relatively insensitive to photoperiod; it is presumably equivalent to what is sometimes referred to in the literature as the juvenile or basic vegetative phase. The reciprocal transfer technique is not sufficiently sensitive for us to conclude whether or not the plants are *completely* insensitive to photoperiod during the pre-inductive phase because, although there were no significant differences between the individual treatments **I** to **N**, there does seem to be a continuous trend in decreasing time to the appearance of the first flower bud (denoted by ◆) throughout the sequence of treatments **A** to **L**. For this reason we prefer to think of the pre-inductive phase as a period of relative insensitivity to photoperiod, but we accept the possibility remains that plants could be completely insensitive to photoperiod during part or all of this phase of their development.

The pre-inductive phase was followed by a period during which the plants became very sensitive to photoperiod, and which we describe as the 'inductive phase', *i*. This phase immediately follows the pre-inductive phase and therefore begins at time*X*. Its duration depends on the photoperiod(s) experienced after time *X* but in a continuous succession of 16 h photoperiods the inductive phase is completed at time *Y*. And so, in Fig. 1 the inductive phase in treatments **I** to **Q** is from *X* to *Y*. This can be seen by noting the similarity of the results of treatment **Q** (in which 12 d of 16 h photoperiodic cycles immediately following the pre-inductive phase were sufficient to minimise the time taken for Syrian Local to come into flower) with those of treatments **I** to **P** (in which the

number of 16 h cycles after the pre-inductive phase were continued beyond time Y in Fig. 1). It is therefore clear that 12 d of 16 h photoperiods satisfy the inductive phase in this genotype. This conclusion is substantiated by the fact that when 10 h cycles were substituted for 16 h ones during the period X to Y then flowering was delayed dramatically (compare treatments **R, S** and **T** with treatment **Q**).

Although 12 d of 16 h photoperiods are required to induce flowering in the shortest time when they immediately follow the pre-inductive phase, a flower bud takes time to develop and open and so there is a delay after the induction phase is completed before the first flower appears. The duration of this 'post-inductive phase', d, can be estimated by calculating the time taken to the appearance of the first flower after the inductive phase has been completed. This is most clearly seen in those treatments where the pre-inductive phase was immediately followed by 12 cycles of 16 h photoperiods, i.e. in treatments **I** to **Q** in Fig. 1. In all these treatments the post-inductive phase (which started at time Y) was of almost exactly the same duration, viz. 10 d, and despite large variations amongst the treatments in the number of 10 h and 16 h photoperiodic cycles given during this final phase. We therefore conclude that the duration of the post-inductive phase is not affected by photoperiod.

To summarize these arguments, four phases can be discerned which combine to give the flowering responses observed in different photoperiodic treatments: first there is a pre-emergence phase during which the seed germinates and its shoot reaches the surface; this together with the pre-inductive and a final post-inductive phase are unaffected by photoperiod so that their respective durations remain constant across treatments (at least within a given temperature regime); and, sandwiched between the later two phases, there is an inductive phase which *is* sensitive to photoperiod and which varies in duration, as we describe below, in a rational way depending on the photoperiods experienced during this period.

In a previous paper (Summerfield *et al.*, 1985) we reported a factorial experiment in which several lentil genotypes were grown in widely different combinations of daily mean temperature and photoperiod, and in which both of these factors remained constant with time. It was shown that the number of days from sowing to the appearance of the first flower, f, could be described by the following equation:

$$1/f = a + b\bar{t} + cp \tag{1}$$

in which $\bar{t}$ is mean temperature (°C), p is photoperiod (h), and a, b, and c are values which remain constant for a genotype (but which vary between genotypes).

The value f in eqn (1) comprises the pre-emergence phase, g, the pre-inductive phase, j, the inductive phase, i, and the post-inductive phase, d, described above. The pre-emergence phase could not be affected by photoperiod since the seedlings are then in the dark; we have also shown here that j and d are not affected by photoperiod and so photoperiodically modulated variations in f must be the result of treatment effects on the duration of i.

Most of the pre-emergence phase is occupied by germination, the rate (i.e. the reciprocal of the time) of which is linearly related to mean temperature (Covell *et al.*, 1986). As yet, we have no information about the effects of temperature on j and d. But, on general physiological grounds and also because the reciprocal of the time taken to flower in photoperiod-insensitive plants of other species (i.e. in plants without a photoperiod inductive phase, i) is linearly related to temperature (e.g. Hadley *et al.*, 1983), we postulate that temperature affects both j and d as well as i, and in a similar manner. If these postulates are accepted, then phases g, j and d would each have constant durations at a given temperature in all photoperiods, but all would vary with temperature. And so all the variation in f with photoperiod at a given temperature is due to variation in i.

Equation (1) implies a linear relation between $1/f$ and photoperiod but, given that a component of f (i.e. $g+j+d$) is invariable with respect to photoperiod, it would follow that the relation between $1/i$ and photoperiod could not then be strictly linear. Conversely, if in fact $1/i$ were a linear function of photoperiod, then $1/f$ could not be. We suggest that the latter relation is the more probable. If it is, then over the range of conditions which have so far been quantitatively investigated (viz., photoperiods of 10–16 h), and within the degree of accuracy of the data obtained, the theoretical curvature of the relation between photoperiod and $1/f$ would not be easily detectable.

For the present, therefore, we will assume that the relation between photoperiod and $1/i$ at any given temperature is linear and so can be described as follows:

$$1/i = k + c'p \tag{2}$$

in which k and c' are constants. This equation is analogous to that of the effect of mean temperature on the rate of progress towards flowering and on the rates of other developmental processes which have been discussed recently (Summerfield *et al.*, 1985), but in which a term $\bar{t}$ (for mean temperature) is substituted for p.

A very useful concept follows from, and is dependent upon, the linear relation between mean temperature and rates of developmental processes, i.e. the concept of day-degrees or thermal time as discussed, for example, by Monteith (1977). In this case, the event (e.g. flowering) takes place after a certain number of day-degrees above a base temperature have been accumulated. By analogy with those arguments, in circumstances where eqn (2) applies it is possible to develop the concept of photoperiodic inductive units, or daily hours of light in excess of a critical photoperiod.

In this case, the duration (h) of the critical photoperiod, p_c, i.e. that photoperiod at or below which no progress towards flowering occurs, is given by:

$$p_c = -k/c'. \tag{3}$$

It is only the hours of light each day in excess of p_c which are inductive, and the number of these hours of light which have to be accumulated in order to induce flowering, i.e. the photoperiodic sum, p_f is given by:

$$p_f = 1/c'. \tag{4}$$

We have used this approach to see whether the results of the transfer experiments described here can be simply explained. In order to clarify the approach a sample calculation using the data obtained for Syrian Local (Fig. 1) is undertaken below.

First of all, the durations of the pre-emergence phase, g, the pre-inductive phase, j, and the post-inductive phase, d, were estimated according to the arguments already explained and, from these, the durations of the inductive phase, i, in both control treatments – continuous long days (treatment **K**) and continuous short days (treatment **V**)–were then calculated: $i = f-(g+j+d)$. The durations of the pre-emergence phase, 5 d, the pre-inductive phase, 8 d, and post-inductive phase, 10 d, were subtracted from f, 35 d, to give an inductive phase of 12 d when a photoperiod of 16 h was imposed throughout. A similar calculation for plants maintained in a 10 h photoperiod gave an inductive phase of $128-(5+8+10) = 105$ d. Applying these values in eqn (2) enabled the values of the constants k and c' to be calculated, $-0{\cdot}113491$ and $0{\cdot}012302$, respectively, by simultaneous equations. And so the critical photoperiod (eqn 3) is 9·23 h and the photoperiodic sum (eqn 4), i.e. the accumulated number of hours of light in excess of p_c which is necessary to complete flower induction, is 81 h. Having calculated the critical photoperiod and photoperiodic sum, it is now possible to calculate the expected durations of the induction periods in treatments where the photoperiods do not remain constant, e.g. in the reciprocal transfer treatments. For example, in treatment

A (Fig. 1), in which the plants were transferred from a 10 to a 16 h photoperiod 45 d after sowing, the first 13 d will have occurred during the pre-emergence and pre-inductive phases and so will have no effect, leaving 32 d of 10 h photoperiods which would have been inductive. To calculate their contribution to the required photoperiodic sum, the value of p_c (i.e. 9·23 h) has to be subtracted from the experienced photoperiod. Thus, the total contribution of inductive hours of light to the photoperiodic sum will have been

TABLE 2. *Components of the photoperiodic response necessary for calculating the expected times to flower in lentils grown at a mean temperature of 21 ± 1 °C*

	Genotype			
	Syrian Local	Laird	Precoz† (Reading)	Precoz‡ (Pullman)
Duration (d)				
Pre-emergence phase, *g*	5	5	5	5
Pre-induction phase, *j*	8	16	8	5
Post-induction phase, *d*	10	13	7	20
Photoperiod induction constants				
k	−0·113491	−0·029982	−0·007143	−0·010396
c′	0·012302	0·004850	0·003571	0·003775
Critical photoperiod (h) (i.e. $-k/c'$)	9·23	6·18	2·00	2·75
Photoperiod sum, $\Sigma\,(h > p_c)$, necessary for flowering (i.e. $1/c'$)	81	206	280	265

† Seed stock originating from ICARDA at Aleppo in Syria.
‡ Seed stock from crops grown in Pullman, USA.

$32 \times (10 - 9{\cdot}23) = 24{\cdot}6$ h. Since the required photoperiodic sum is 81 h this leaves 56·4 h to be contributed after transfer of the plants to the 16 h photoperiodic regime. The number of days required in this regime to complete flower induction is given by $56{\cdot}4/(16 - 9{\cdot}23) \approx 8$ d. Thus, the total number of days from sowing to first flower in this treatment is calculated by adding the following components: a pre-emergence phase of 5 d; a pre-inductive phase of 8 d; an inductive phase comprised of a combination of 32 d of 10 h photoperiods followed by 8 d of 16 h photoperiods, i.e. a total of 40 d; and a post-inductive phase of 10 d. Accordingly, the total calculated time to first flower is 63 d after sowing whereas the observed time in this case was 70 d (see treatment **A** in Fig. 1).

Adopting this same approach, the expected times to first flower were calculated for all transfer treatments in all genotypes using the photoperiod constants estimated from the respective control treatments in each case. Table 2 shows the essential components of the calculations while Figs 1–4 show the expected times to first flower calculated for all treatments using these data (denoted by ●), as well as the actual times observed.

It is clear that the majority of the theoretical values agree very well with the observed values (Figs 1–4), especially in treatments where plants were transferred from short to long days. When plants were transferred from long to short days, time of flowering tended to be much more variable (see standard deviations). The reason for this is unknown but it suggests that, after partial induction in long days, plants respond slightly less well to short days for the completion of induction. In spite of this minor discrepancy,

the model clearly accommodates the main features of the flowering response – whether plants are transferred from short to long days or *vice versa*. Furthermore, it is worth noting that in many systems of lentil production, the vegetative plants experience lengthening days – and in these circumstances the model appears to be particularly satisfactory.

DISCUSSION

In this paper we have concluded that, at any given mean temperature, the rate of the photoperiodic induction of flowering in lentils, $1/i$, is a linear function of photoperiod (eqn 2). This interpretation of the data is a necessary precondition for applying the concept of a critical photoperiod above which photoperiodically active hours of light, i.e. those in excess of the critical photoperiod each day, are accumulated until the sum reaches the value necessary to complete induction (the photoperiodic sum for flowering) and therefore induces flowering. Both the critical photoperiod and the photoperiodic sum required for flowering differ among genotypes.

A particularly attractive feature of this concept is that it allows the prediction of flowering in regimes where the photoperiod changes during the induction process. This was confirmed in the present experiments in which photoperiods were changed abruptly between extreme values (8 or 10 to 16 h and *vice versa*) during the course of induction. We therefore assume that there would be no difficulty in applying the concept to natural conditions where photoperiods change continuously, albeit gradually.

There are, however, two potential difficulties which need to be discussed before the method could be exploited in the field. The first is that in order for the values of the critical photoperiod (eqn 3) and the photoperiodic sum (eqn 4) to be determined accurately, it will be necessary to establish the durations of the pre-emergence, pre-inductive and post-inductive phases (g, j and d) so that the duration of the inductive phase, i, can be calculated. And so, photoperiodic reciprocal transfer experiments of the sort described here will be needed and at several temperatures in order to quantify the effects of temperature on g, j and d. Thus, the amount of work required on individual genotypes is considerable. In the meantime, it may be more attractive to accept a method which is somewhat less accurate but for which the data required would be more readily available.

Such an approach could involve the application of eqn (1) in which the phases – pre-emergence, pre-inductive, inductive and post-inductive – are not separately identified. This involves an assumption of linearity between photoperiod and $1/f$ which may not be strictly correct but not sufficiently incorrect to have serious practical consequences.

If this suggestion is adopted, and following the demonstration here that the underlying concept can accommodate changes in photoperiod during the course of development, then the accumulation of hours of light above a 'nominal base photoperiod' in the field could be calculated using the constants derived from eqn (1), i.e. on the basis of differences in f. But, the 'nominal base photoperiod' and 'nominal light sum' in this case will have different values from the 'critical photoperiod' and 'photoperiodic sum', which are calculated using the constants in eqn (2) and which reflect the change in i with photoperiod. For this reason, and to avoid confusion, we have made these deliberate distinctions in terminology.

Calculations show that when eqn (1) is used, nominal base photoperiods can often have negative values at ambient temperatures and so cannot easily be related to photoperiodic theory; they are, instead, simply arbitrary values which result from the inclusion of non-photoperiodically modulated entities (g, j and d) in their calculation. We reserve the term 'critical photoperiod' for those situations where calculations are based on the inductive phase only; this term has positive values (e.g. Table 2) and is

probably of real physiological significance. Indeed, although it is more rigorously defined here than is generally the case in the literature (e.g. Bernier *et al.*, 1981), 'critical photoperiod' could be taken to be identical with the term as it is more generally understood in long-day plants, viz. that photoperiod below which flowering does not occur (time to flower is infinite) and above which flowering is induced – the rate of progress towards flowering being directly proportional to the extent by which the experienced photoperiod exceeds the critical one.

Returning to the more arbitrary concept of the 'nominal base photoperiod' and the development of a model for application to the varying field environment, it is clear from eqn (1) that the nominal base photoperiod will vary with temperature since at any given temperature:

$$1/f = k' + cp, \tag{5}$$

where

$$k' = a + b\bar{t}. \tag{6}$$

The number of hours of light accumulated daily in excess of the nominal base photoperiod, the nominal light sum, is given by $1/c$, and so is unaffected by temperature. But, since k' is a function of temperature (eqn 6), then the nominal base photoperiod, $-k'/c$, will vary with temperature.

One approach to dealing with field conditions would therefore be to calculate daily nominal base photoperiods using standard meteorological data for mean temperature and the values of the constants calculated for individual genotypes using eqn (1); the daily contribution to the nominal light sum being the difference between the nominal base photoperiod and the actual photoperiods experienced each day. Threshold and saturation irradiance values for photoperiodic detection in lentils are relatively large and so the time from sunrise to sunset is the most convenient and appropriate basis for the calculation of daylength in relation to this species (Summerfield and Roberts, 1987). In short, the contribution each day to the nominal light sum would be given by:

$$l_d = p_d - (a + b\bar{t}_d)/c, \tag{7}$$

where, for the day in question, l_d is the daily contribution to the nominal light sum, p_d is the experienced photoperiod (sunrise to sunset) that day, $\bar{t}_d$ is the mean temperature that day, and, a, b and c are constant values applicable in eqn (1) for the genotype being considered.

Calculations involving the diverse range of genotypes studied so far (Summerfield *et al.*, 1985) suggest that the nominal base photoperiods will always be shorter than the experienced photoperiods and indeed will often have negative values. However, the validity of this approach for interpreting and predicting field behaviour depends on the assumption that the photoperiod experienced, p_d, is not only greater than the nominal base photoperiod but is also greater than the critical photoperiod, p_c, (eqn 3). Where values of p_c are known (Table 2) it is clear that this constraint is not a problem in cvs Precoz and Laird. But since p_c increases at cooler temperatures, then it is possible that during the early stages of growth of the Syrian Local landrace in its country of origin, the photoperiods experienced may be completely non-inductive. In Syria, farmers traditionally sow this landrace during December and January when the daylength is about 10 h and the mean temperature is about 6 °C. The value of p_c at 21 °C is about 9 h 14 min (Table 2) but it will be longer in cooler situations, and therefore almost certainly longer than the actual photoperiods experienced by vegetative crops during the early stages of growth.

It is interesting to note that fewer hours of daylight, and indeed none in some cases, may be photoperiodically active in winter because cool temperatures increase the value of the critical photoperiod. On the other hand, flowering in most lentil genotypes is

hastened by vernalization (e.g. Summerfield *et al.*, 1985). And so, although no photoperiodic induction may occur during the early stages of growth of Syrian Local in its traditional region of cultivation, vernalization may well be affecting the subsequent progress towards flowering. Changes in the values of the constants a, b and c as a result of vernalization reported previously (Summerfield *et al.*, 1985) show that in the two genotypes for which data are most reliable, the effect of a seed vernalization treatment was to reduce the value of the nominal base photoperiod while having little or no effect on the nominal light sum. In reality, we believe this must be a reflection of a reduction in the value of the critical photoperiod by vernalization.

For adequate field models, more experiments are needed to quantify the effects of vernalization in terms of time and temperature of exposure, and to check that the main effect of vernalization is indeed to shorten the critical photoperiod. And for more accurate models, the effects of temperature on the durations of the pre- and post-inductive phases need to be quantified, as we discussed earlier. Models which use critical photoperiod rather than nominal base photoperiod will be more satisfactory; not only are they likely to be more accurate but they would also relate more closely to our understanding of the physiology of photoperiodism.

One additional problem, at least, remains to be evaluated – that is the effect of the seed production environment on photo-thermal responsiveness in the subsequent generation. In other long- and short-day grain legumes (e.g. *Vicia faba* and *Glycine max*, respectively) flower initiation and responsiveness to vernalization can be altered significantly, even dramatically, by variations in field temperature during fruit maturation on the parent plants (e.g. Evans, 1959; Unander, Lambert and Orf, 1983). To our knowledge there are no comparable data yet available for lentils. Whilst it is clear from Figs 3 and 4 that the *relative* effects of the diverse photoperiod treatment combinations imposed on cultivar Precoz in Reading and Pullman, respectively, were closely similar, it is also clear that plants grown in Pullman flowered consistently later (by about 10–25 d) than those at Reading (and see Table 2). We suspect that abortion of successive flower buds in the less-precisely regulated artificial climate at Pullman (see Materials and Methods) will have contributed to the longer durations to flowering – especially in the 8 h (less-inductive) enclosure, which became hotter and more arid than intended; and, as we have emphasized earlier, the photoperiodic treatments were not identical (e.g. the short-day regime was less strongly inductive in Pullman than in Reading; 8 and 10 h, respectively). But also, different seed stocks were used for the two investigations (Table 2) and so we cannot preclude effects of maturation environment on these differences in phenology.

These collective recommendations for additional experiments might seem to represent a considerable undertaking. But, the identification of four distinct phases of development (the first two and last of which are insensitive to photoperiod), the evidence that temperature and photoperiod affect the intervening inductive phase in a simple manner, and the evidence that there is little or no change in sensitivity to photoperiod with time during the inductive phase, all make the task simpler than might have been expected. Furthermore, a major advantage we see in the approach outlined here is that it allows variations with time in both photoperiod and temperature to be accommodated rationally. All these features commend themselves to the development of a model which could be applied with confidence in the field.

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Survivorship and Spatial Development of *Spartina alterniflora* Loisel. (Gramineae) Seedlings in a New England Salt Marsh

W. SCOTT METCALFE, AARON M. ELLISON*† and MARK D. BERTNESS

Graduate Program in Ecology and Evolutionary Biology, Brown University, Box G, Providence, Rhode Island, 02912 USA

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ABSTRACT

Patterns of survival and spatial arrangement of tillers of *Spartina alterniflora* were examined in natural and in artificially produced bare areas, and in pure stands of adult *S. alterniflora* in a New England salt marsh. Seedling growth and survival were high in naturally occurring bare patches and in artificial patches, whether created by continual clipping of adult plants to ground level throughout the growing season or by providing bare substrate after removal of adult plants. Seedling growth and survivorship increased with increasing size of bare area. *S. alterniflora* seedlings were also common in areas dominated by adult plants, but no seedlings survived a whole first growing season under the mature canopy, probably because of competition from adult plants.

In large bare areas, *S. alterniflora* seedlings grew non-directionally, reaching heights of 0·5 m, and producing as many as 36 tillers in one growing season. Examination of leaf area ratios suggested that the production of tillers increased photosynthetic capacity in seedlings with several tillers in contrast to seedlings without tillers. Thus, seedlings can apparently tiller and colonize free space radially without a loss of photosynthetic capacity.

These results suggest that while seedling success is generally limited by adult plants in monocultures of *S. alterniflora*, in disturbed spaces seedling success is high and results in a rapid non-directional proliferation of sexually generated clones that ultimately preclude the successful invasion of future seedlings.

Key words: Clones, directional growth, leaf area ratio, salt marsh cordgrass, seedling survivorship, *Spartina alterniflora* Loisel.

INTRODUCTION

The rhizomatous perennial grass *Spartina alterniflora* Loisel. is a dominant species in coastal salt marsh communities of eastern North America, usually occurring in dense monospecific stands along the seaward edge of marshes. *S. alterniflora* regenerates both vegetatively and by seed. Investigators, however, have not agreed on that relative importance of vegetative growth and sexual reproduction in maintaining natural populations. Chapman (1974) reported that seeds have low viability, and the colonization is accomplished primarily by a vegetative spread of rhizomes rather than by a dissemination of seeds. In contrast, Mooring, Cooper and Seneca (1971) reported 52 per cent germination success of *S. alterniflora* seeds in the laboratory, and Broome, Woodhouse and Seneca (1974) stated that seedlings are the primary means of natural colonization of *S. alterniflora* on freshly deposited sediments in North Carolina. Broome *et al.* also reported success in establishing new stands by artificial seeding. In Great Britain, the role of seedlings of *Spartina anglica* C. E. Hubbard in marsh establishment has been investigated (Ranwell, 1964; Hubbard, 1965, 1970; Taylor and Burrows, 1968),

* For all correspondence.

† Current address: Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, New York, 14853 USA.

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