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MEASUREMENT AND PREDICTION OF FLOWERING IN ANNUAL CROPS

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Environmental control of development and behaviour

In most regions where crops are grown the year is divided into at least two seasons—one during which conditions are relatively benign for growth and survival, and the other when they are inimical. Many species of plants have evolved strategies which allow them to minimize or avoid the problems of inclement seasons by adopting dormant and hardy forms—e.g. spores, seeds, underground organs of perennation, and a deciduous habit. Reproduction is often also timed so that vulnerable offspring are not subject to the worst elements of climate.

In cool temperate climates winter is the rigorous season with cold or freezing weather exacerbated by dull and short days. In Mediterranean, sub-tropical and seasonally arid tropical climates it is typically the season of drought and extreme heat which it is more important to avoid. Plants rely on environmental signals to trigger their seasonal responses—either to minimize or to avoid potentially lethal stress or, when conditions are favourable, to become fruitful and multiply. But often it would not be an effective survival strategy to respond directly and immediately to the adverse (cold or dry) or favourable (warm or wet) characteristics of the environment. Although such characteristics may be statistically associated with particular seasons, they are also subject to unseasonal fluctuations. It would not do, for instance, for hardy buds to lose dormancy in response to an unseasonably warm day in mid-winter; the new growth would result in non-hardy tissues susceptible to frost and so likely to be damaged or killed when more seasonably cold conditions returned.

The only completely reliable environmental signal with respect to calendar date at any given latitude (except at the equator) is day-length; and it is therefore not surprising that plants have evolved mechanisms which enable them to respond to photoperiod. But plants make use of temperature signals too—either as a precondition for a subsequent photoperiodic response, as in vernalization, or as a modifier of their photoperiodic response. Thus, although day-lengths have identical durations in autumn and spring, cold-temperature vernalization ensures that winter annuals, biennials and some perennials respond only to long days in the spring. Warm temperature modification of the photoperiodic response enables timing to be finely tuned so that, for example, flowering can occur earlier or later if the season is warmer or cooler than usual.

Types of flowering response to photoperiod

Although it is the duration of the dark period in each diurnal cycle which is of paramount importance, it is conventional to describe photoperiodic responses in terms of day-length. Three main categories of response are recognized: photoperiod-insensitive or day-neutral plants (DNPs), and then two types of photoperiod-sensitivity, short-day plants (SDPs) and long-day plants (LDPs). In addition, within both SDPs and LDPs there are species with obligate (or absolute or qualitative) responses to photoperiod and others with quantitative (or facultative) responses (Vince-Prue, 1975). Several variants additional to these five basic patterns have been reported but it is only necessary to add one of them here, i.e. short-long-day plants (SLDPs), in order to include the photoperiod responses of the major world crops. SLDPs flower soonest if short days are followed by long.

There is not complete unanimity in the definitions of response types and some of the associated terms, and so it is necessary to specify those adopted here. Since, as we have discussed, the ecological essence of photoperiodic responses is in the timing of biological events, we shall define flowering responses in terms of time taken to flower.

For this purpose it is simplest to begin with the responses of plants grown in artificial environments in which the photoperiod in any one environment does not vary with date. Examples of the two major types of photoperiod sensitivity are shown in *Figures 2.1*(*a*) and *2.1*(*b*) in which the times taken for a soyabean (*Glycine max*; an SDP) and a chickpea (*Cicer arietinum*; an LDP) genotype to come into flower (f) are shown as functions of photoperiod. Later, we shall show that these typical forms of the photoperiodic response curves both of SDPs and LDPs are a consequence of a linear relationship between photoperiod and rate of progress towards flowering (the reciprocal of the time taken to flower, $1/f$). These linear relationships are of negative slope in the case of SDPs (*Figure 2.1*(*c*)) and positive for LDPs (*Figure 2.1*(*d*)). Accordingly, when data are plotted as days to flower (f) in relation to day-length, there is a typical L-shaped curve for obligate LDPs (*Figure 2.1*(*b*)) while that for an obligate SDP is an L-shape in mirror image (*Figure 2.1*(*a*)). An obligate SDP is capable of flowering only when the day-length is shorter than a particular value and conversely, an obligate LDP is only capable of flowering when the day-length is longer than a particular value. What these respective values are can be most clearly seen in *Figures 2.1*(*c*) and *2.1*(*d*). The abscissa intercepts are those photoperiods in which rates of progress towards flowering are zero, i.e. when plants would take an infinite time to flower (or, in other words, they would be permanently vegetative).

Interestingly, in these two examples the photoperiod that it is necessary to exceed for flowering to occur in the LDP is just under 8 h (*Figures 2.1*(*d*)) and in the SDP the photoperiod that must not be exceeded for flowering to occur is just under 14 h (*Figure 2.1*(*c*)). These examples make it clear that, despite some misleading statements to the contrary, SDPs can often flower in relatively long days and LDPs can often flower in relatively short days. The essential difference between an obligate LDP and an obligate SDP is whether it is necessary for flowering for a particular night length to be exceeded or for it not to be exceeded, respectively: the fact that a species is categorized as either LDP or SDP tells us nothing about the duration of this critical night period.

In contrast to the obligate responses to photoperiod shown in *Figures 2.1*(*a*) and *2.1*(*b*), a quantitative response is one in which flowering is delayed but not prevented in less inductive photoperiods. Such a quantitative response can be conceived as a secondary limitation placed upon a standard obligate response curve in which there is

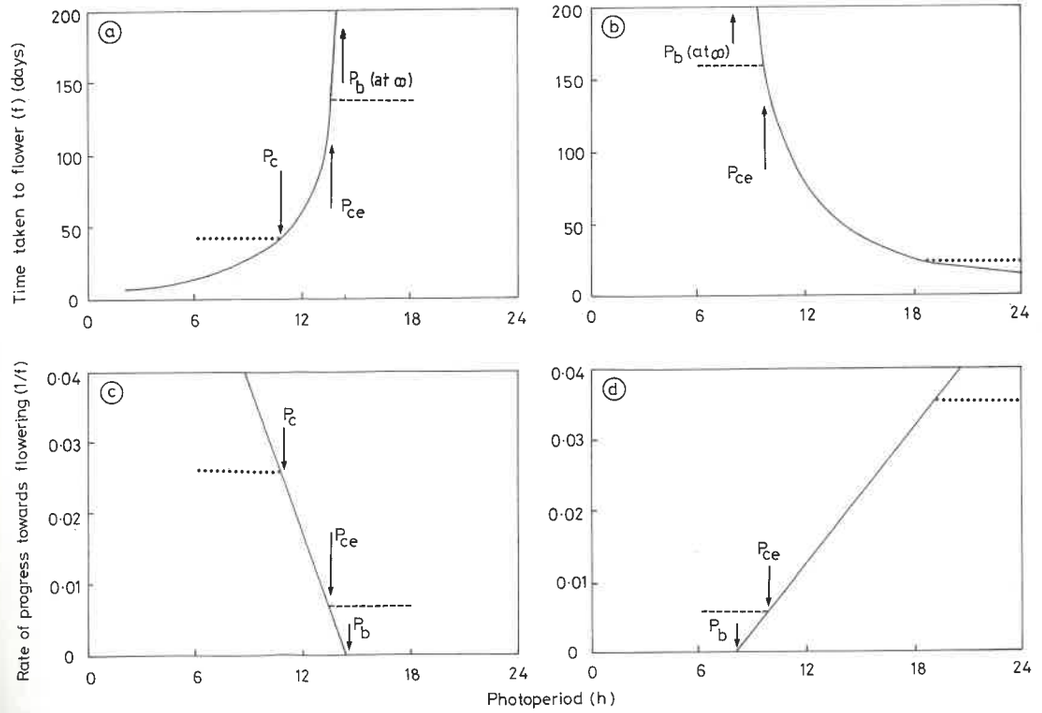

Figure 2.1 Typical photoperiodic responses of SDPs (*a, c*) and LDPs (*b, d*) when grown continuously in constant photoperiods. The upper graphs (*a, b*) show the time taken to flower (f) as a function of photoperiod, whereas the lower graphs show the same data (*c, d* respectively) when rate of progress towards flowering ($1/f$) is shown as a function of photoperiod. The SDP example (*a, c*) was calculated for a soyabean accession TGx 46-3C in photoperiods from 8 h:20 min to 15 h at a mean temperature of 22.5°C (Hadley *et al.*, 1984). The LDP example was calculated for chickpea cultivar JG62 in photoperiods from 12 to 15 h at a mean temperature of 15°C (from Roberts *et al.*, 1985). The solid curves in each case show the underlying response; the dotted line shows the minimum time taken to flower the height of which is dependent on temperature; the broken line shows the maximum time taken to flower in plants with quantitative responses only, the height of which is independent of temperature and photoperiod (plants with obligate responses do not have this limitation). Whereas the dotted and broken lines in (*a*) and (*c*) represent the actual response of TGx 46-3C, the corresponding lines in (*b*) and (*d*) are arbitrary and hypothetical since the experimental photoperiods did not cover these extremes. The base (P_b), critical (P_c) and ceiling (P_{ce}) photoperiods are defined in the text.

an overall maximum delay in flowering which is never exceeded (broken line in *Figures 2.1*(*a*) and *2.1*(*b*), which can, alternatively, be thought of as a minimum rate of progress towards flowering (broken line in *Figures 2.1*(*c*) and *2.1*(*d*)).

One further complication to the basic patterns needs to be mentioned. In the description so far it has been implied that the whole time from sowing to flowering is subject to photoperiodic control. In fact, during the vegetative period there is typically a pre-inductive phase (sometimes known as a juvenile or basic vegetative phase; Vergara and Chang, 1976) and a post-inductive phase, neither of which is sensitive to photoperiod. Between these two is an inductive phase which is sensitive to photoperiod and varies in duration (number of diurnal cycles required to complete it)

depending on the photoperiod experienced (Roberts *et al.*, 1986). The analyses of these three phases will be discussed later but their relevance here is that, strictly speaking, the responses described so far probably refer to the inductive phase rather than the whole period from sowing to flowering. This would not significantly affect the form of the response curves illustrated in *Figure 2.1* except in the most strongly inductive photoperiods where the actual duration of the inductive phase is very short and so the respective durations of the pre- and post-inductive phases are relatively long. The main effect of this is that in the response curves shown in *Figure 2.1* there will be minimum times to flower (dotted lines) which override the basic response curves (solid lines). The period represented by the values of these horizontal dotted lines on the ordinate is determined largely by mean temperature (which may affect all phases of development) and is known to occur in the SDP cowpea (Hadley *et al.*, 1983a) as well as in the specific example of soyabean illustrated in *Figures 2.1*(*a*) and *2.1*(*c*) (Hadley *et al.*, 1984). The corresponding dotted line (i.e. the minimum time to flowering) in LDPs typically intercepts the basic response curve at photoperiods between 17 and 20 h, as shown by investigations on wheat, barley, oats, rye, rape and flax (Major, 1980). Thus in most LDPs this limitation is often well outside the range of photoperiods which the crops normally experience during the pre-flowering period.

A concept commonly used in photoperiodism is that of critical day-length. Different definitions have been proposed by various authors; others have assumed that it is generally understood what is meant without definition. Hence there is some confusion. If obligate photoperiodic response curves of the type shown in *Figures 2.1*(*a*) and *2.1*(*b*) were truly L-shaped, or the mirror image (i.e. if they were exact right-angles) there would be no problem: the definition of critical day-length for an SDP would be that day-length which, if exceeded, prevents flowering; and the converse would apply to an LDP. But the curves in reality are not of this form (with a horizontal line at some point changing abruptly to a vertical line) and so other definitions must be sought.

In previous papers (Hadley *et al.*, 1983a; 1984) we have defined the critical photoperiod, P_c, in SDPs as the interface between a temperature response surface and a photoperiodic response surface, which will be explained with respect to *Figures 2.4*(*b*) and *2.4*(*c*); the corresponding point has been marked in *Figures 2.1*(*a*) and *2.1*(*c*). It can be seen that, according to this definition, the critical photoperiod is that photoperiod at or below which the time to flower is minimal and is not affected by variations in day-length; photoperiods longer than P_c delay flowering. This seems a logical definition and we advocate it since there are objections to some of the more obvious alternatives. For example, in a quantitative SDP one could have chosen the ceiling photoperiod, P_{ce}, i.e. that photoperiod at and above which the greatest delay in flowing occurs or, put another way, below which flowering is hastened; but this definition can only apply to quantitative SDPs and not to those with an obligate response, and it is therefore of limited application (*Figures 2.1*(*a*) and *2.1*(*c*)). An alternative would be the base photoperiod, P_b, i.e, that photoperiod at which, if exceeded, progress towards flowering is zero so that the plant remains permanently vegetative; but this only applies to obligate responses and therefore is also of limited application (*Figures 2.1*(*a*) and *2.1*(*c*)).

It might be considered that analogous arguments should apply to LDPs, i.e. that the critical photoperiod should be considered as that photoperiod above which time to flowering is minimal and not affected by further increases in photoperiod, and below which flowering is delayed. However, as we have already mentioned, where there is evidence of such a point, its value is typically greater than the maximum day-

lengths experienced by crop species (especially between sowing and flowering) in the regions where crops are commonly grown (*see Table 2.2*). And so, it may not be of great practical significance in LDPs. Furthermore, since the angle enclosed by the two lines which define the critical photoperiod is often very obtuse (e.g. *Figure 2.1*(*b*)) then its determination experimentally may be somewhat imprecise.

An alternative definition of critical photoperiod in LDPs could be the ceiling photoperiod, i.e. that photoperiod in which there is maximum delay in flowering (*Figure 2.1*(*d*)). But this would also often lie outside the normal range of photoperiods experienced by crops and, in any case, is only applicable to quantitative LDPs.

The base photoperiod, P_b, in LDPs is that photoperiod below which progress towards flowering is zero, so that the time taken to flower would be infinite, i.e. the plants remain vegetative. This point can only be a reality in plants with an obligate response to photoperiod; but a 'nominal' base photoperiod can be calculated by extrapolation in LDPs with quantitative responses and, as we shall show later, this proves to be a useful concept in predicting times to flower in natural environments.

Recently (Roberts *et al.*, 1986), we have used the term critical photoperiod in LDPs to describe the equivalent of the base photoperiod but specifically when its value is calculated in relation to the inductive phase since this, it is argued, could be considered to be a physiological definition. But, since the examples shown in *Figure 2.1* are based on total times from sowing to flowering (rather than on the inductive phase), we have not indicated a critical photoperiod for the LDP, but the analogy would be P_b which, when based on the total period from sowing to flowering, we have called 'nominal base photoperiod' (Roberts *et al.*, 1986).

Types of flowering response to temperature

Temperature may affect times from sowing to flowering in three distinct ways:

1. There may be a specific cold-temperature hastening of flowering known as vernalization.
2. Over a wide range of temperatures the rate of progress towards flowering increases with increasing temperature to an optimum temperature at which flowering is most rapid (responses over this sub-optimal range of temperatures may be modified by photoperiod or vernalization).
3. At supra-optimal ('stressful') temperatures flowering is progressively delayed as temperatures get warmer.

GEOGRAPHICAL ORIGINS AND ADAPTATIONS OF VERNALIZATION AND PHOTOPERIODIC RESPONSES

Vernalization typically occurs at temperatures between −5 and 16 °C but with maximum effect between 0 and 8 °C (Whyte, 1946). The duration of the cold treatment needed to saturate the vernalization response can vary from a few to about 60 days, or much longer, depending on species and genotype and presumably also on temperature; but comprehensive quantitative data are lacking. Nevertheless, the literature suggests that, as with photoperiodism, there are obligate and quantitative responses to vernalization (Thomas and Vince-Prue, 1984).

The term vernalization was originally applied to treatments given to imbibed seeds

or to seedlings, but eventually it was extended to include cold treatments which have similar effects when applied to plants during later stages of development—or even to earlier stages of development when the seed is still attached to the mother plant. It is often applied, for example, to cold treatments given to some biennials and perennials which may be unresponsive to similar treatments imposed on seeds or seedlings.

In temperate climates the growing season is centred around the spring and summer months when days are warm and long. It is usually during this period when it is ecologically most appropriate for flowering to occur. Accordingly, the vast majority of crop species that originate from the temperate latitudes are LDPs. Some are also sensitive to vernalization and only respond to long days after they have experienced a cold period. This dual response presumably evolved to combat premature flowering in plants derived from seeds shed in the summer and which would experience relatively long days in early autumn. Such a dual response is common to many winter cultivars (i.e. autumn-sown cultivars) of all the temperate cereal species. But, in some of these winter forms, a period of short days may substitute for, or may be required instead of, or may enhance, the effect of cold temperatures. Because short photoperiods applied during the early stages of crop development can have similar effects on flowering to cold-temperature vernalization, this response is sometimes referred to as 'short-day vernalization', and gives rise to the photoperiodic category of short-long-day plants (SLDPs), i.e. plants in which earlier flowering is dependent on exposure to short followed by long days.

As mentioned earlier, in more tropical climates the growing season is generally delimited by lack of rain. The rainy seasons are a consequence of the adiabatic cooling of the warm rising air in the Inter-Tropical Convergence Zone, which tends to coincide with those latitudes where heat from the sun is more intense, i.e. regions where the sun is overhead at midday (Dennett, 1984). And so, within those regions approaching the Tropics of Cancer and Capricorn, say typically between latitudes 10–30 °N and 10–30 °S, the annual distribution of rainfall tends to be monomodal, with the wettest period coinciding roughly with the longer day-lengths—except, of course, in the desert areas which encroach into these regions. Rainy seasons, and so growing seasons, start in advance of the longest day and crops become reproductive towards the end of the wet season when day-lengths are shortening (e.g. Wien and Summerfield, 1980). So far as we are aware, and not surprisingly, all tropical and sub-tropical annual crops are SDPs. Of course, DNPs also occur, as they do in temperate crops, but these tend to be the products of selection for special agricultural purposes.

The known responses of some of the major field crops of temperate and tropical origin are shown in *Table 2.1* (the thirteen major grain legume crops have been excluded since these have been classified in the same way in *Table 15.1* of Chapter 15).

We conclude, therefore, that most crops of temperate origin are LDPs or DNPs, with or without a vernalization response; and that all crops of tropical or sub-tropical origin are SDPs or DNPs and, as expected since they do not normally experience cold temperatures, are insensitive to vernalization. The only exceptions to these generalizations of which we are aware are *Chrysanthemum morifolium* a native of China (Purseglove, 1968) but a complex hybrid derived from several wild species (Cathey, 1969), and *Allium cepa* which is only known in cultivation but thought to have a primary gene pool in Afghanistan (McCollum, 1974). Both of these species have been classified as quantitative SDPs in which flowering is nevertheless accelerated by vernalization (Vince-Prue, 1975). However, in *Allium cepa* the response is somewhat equivocal: flower initiation is apparently unaffected by day-length or, in one genotype at least, may even show a quantitative long-day response; but further floral development can be indirectly inhibited by long days because they stimulate bulbing

Table 2.1 PHOTOTHERMAL RESPONSES OF MAJOR FIELD CROPS (RESPONSES OF THE GRAIN LEGUMES ARE SHOWN IN CHAPTER 15)

Species	*Common name*	*Centre of origin*	*Latitude*	*Photoperiodic response*				*Vernalization response*	
				Short day DN		*Long day*			
				O	*Q*	*O*	*Q*	*O*	*Q*
Dactylis glomerata	Cocksfoot	West Europe	40–55°N			*			*
Lolium perenne	Ryegrass	West Europe	40–55°N			*	*	*	*
Trifolium repens	White clover	West Europe	40–55°N				*		*
Avena sativa	Oats spring	Central Europe	45–50°N				*		
	Oats winter						*		*
Secale cereale	Rye spring	Turkey, NW Iran, Armenia	35—45°N			*	*		
	Rye winter					*		*	*
Triticum aestivum	Bread wheat spring	Fertile crescent	30–37°N				*		
	Bread wheat winter						*	*	*
Hordeum vulgare	Barley spring	Fertile crescent	30–37°N				*		
	Barley winter					*	*	*	*
Papaver somniferum	Poppy	Turkey	37–42°N				*		*
Brassica oleracea	Cauliflower	Mediterranean/ Asia Minor	30–45°N				*		*
Brassica napus	Rape	East Mediterranean	30–45°N				*		*
Beta maritima	Beet	Mediterranean?	30–45°N			*	*		*
Spinacia oleracea	Spinach	SW Asia	30–45°N			*	*	*	*
Lactuca sativa	Lettuce	Mediterranean	30–45°N		*		*	*	*
Allium cepa	Onion	Afghanistan	30–35°N	*	*		*	*	*
Daucus carota	Carrot	Afghanistan	30–35°N			*			*
Raphanus sativus	Radish	East Mediterranean	30–45°N		*		*		*
Linum usitatissimum	Flax	India/ Afghanistan	25–35°N				*		*
Helianthus annuus	Sunflower	SW USA	30–45°N		*	*			
Stylosanthes guianensis	Stylo	S America	5°N–30°S		*		*		
Chrysanthemum morifolium	Chrysanthemum	China	20–35°N		*	*			*
Nicotiana tabacum	Tobacco	South Bolivia, North Argentina	15–30°S		*	*			
Capsicum annuum	Chilli pepper	Central America	10–30°N		*	*			
Desmodium spp.	Desmodium	Tropics			*	*			
Amaranthus caudatus	Grain amaranth	Central Andes	10–30°S		*				
Solanum tuberosum	Potatoes	Central Andes	10–30°S	*	*	*			
Gossypium hirsutum	Cotton	Central America	10–25°N		*	*			
Sesamum indicum	Sesame	Ethiopia or India	5–24°N		*	*			
Ricinis communis	Castor	Ethiopia or India	5–24°N		*	*			
Coffea arabica	Arabica coffee	Ethiopia	5–15°N	*	*				
Pennisetum americanum	Bulrush millet	West Africa	10–15°N		*				
Sorghum bicolor	Sorghum	Ethiopia or W Africa	5–15°N	*	*	*			
Zea mays	Maize	Central America	10–30°N	*	*	*			
Oryza sativa	Rice	SE Asia	15–25°N	*	*	*			
Saccharum spp.	Sugar cane	New Guinea	0–10°S		*				

O = obligate response; Q = qualitative response.

which, through the ensuing mechanical compression, can physically restrict the enlargement of floral parts (Rabinowitch, 1985).

There are two other apparent exceptions in which SDPs appear to have originated at higher latitudes than is typical. *Table 2.1* suggests that it is rare for SDPs to originate outside the 30° parallels. But the reputed centres of origin of soyabean and sunflower, north China and south-west USA respectively, are north of this area. However, we suspect that these apparent exceptions are more the result of regional perturbations in climate than biological anomalies. Because of the special continental land configurations, the summer monsoon areas in China are pushed further north than is typical so that there is a marked monomodal rainfall distribution in north China with a peak in July and August preceded by a dry winter and spring. Consequently the growing season is severely limited by water and crops tend to flower during shortening days. The climatic constraints are therefore not dissimilar from the tropics. In the south-west of the USA where sunflower is said to have originated, the pattern is less clear. There is less rainfall and more variation in it so that conditions vary more from site to site and season to season. The arguments are therefore less clear but again there tends to be more rain during the summer months; consequently similar arguments could apply to the selection of the short-day reponse in sunflower.

Finally the case of *Stylosanthes guianensis* is interesting. It has a very wide latitudinal distribution in South America, at least 5 °N to 30 °S, and types from about 25 °S are LDPs whereas those from nearer the equator are SDPs (Cameron and Mannetje, 1977). Thus unusually, within a single species, both responses are found, possibly selected during the early spread and adaptation of the species.

THE GENERAL EFFECT OF TEMPERATURE IN THE SUB-OPTIMAL RANGE

The second and more general effect of temperature appears to be fundamental to the majority of plant species and affects almost all developmental processes. Most simply stated it is that, in the absence of other complicating factors such as photoperiodism or vernalization, the rate of development increases linearly with temperature. Furthermore, as we seek to show later, such responses are also evident in photoperiod-sensitive species when the separate effects of photoperiod and vernalization are disentangled from those of post-vernalization temperatures.

Before discussing this fundamental response further, it has to be pointed out that rates of development cannot be observed or measured directly. And so, the end-point of a developmental process has to be timed and, as with determining the rate of movement (speed) of a vehicle or the rate of an enzyme reaction, it is the reciprocal of the time taken to reach the destination or end-point which is a measure of the rate of progress. The relation between the time taken to reach an end-point and rate of progress towards it is not linear. Therefore, if the effect of temperature on rate of progress towards flowering is linear, then the relation between temperature and the time taken to flower cannot be (*Figure 2.1*).

It is not clear why the relationship between temperature and the rate of development processes should be linear (Monteith, 1981). Most chemical reactions on which developmental processes must depend conform to the Arrhenius relationship in which the logarithm of the rate of reaction is a linear function of the reciprocal of absolute temperature. We suggest that a possible (albeit, perhaps, only partial) explanation for a linear relationship between temperature and rate of developmental processes is the consequence of two underlying principles. First, over the range of temperatures

within which plant development typically occurs, the relation between temperature (°C) and the reciprocal absolute temperature (°C + 273) would not be detectably different from linear in biological experiments; and so it would not matter whether temperature or the reciprocal of absolute temperature is taken as the independent variable. Secondly, relative growth rates and rates of plant development often relate linearly to the logarithm of the concentrations of limiting substances (e.g. of growth substances or of minor elements at sub-optimal concentrations). Thus, if a linear change in temperature affects the logarithm of the concentration of some limited factor, as implied by the Arrhenius relation, and if a logarithmic change in concentration of the limiting factor causes a linear change in rate of development, then it would be expected that the effect of temperature on rate of development would also be linear.

Whether or not this speculation is correct, it is a fortunate circumstance that the rate of developmental processes is usually a linear function of temperature, because upon this depends the concept of temperature-sum or thermal time, which enables developmental progess to be monitored and forecast in fluctuating temperatures such as occur in natural environments.

The concept of thermal time was, and still is, often referred to as the summation of 'heat units' but this terminology is misleading since it is temperature and not heat which is measured. The idea probably originated more than 250 years ago, with Réaumur in 1735 (Abbe, 1905; Aitken, 1974), but it was not exploited significantly until it was applied to the climatic zoning of crops on a continental scale in North America at the end of the nineteenth century. The notion is that the fulfilment of a developmental process in a plant requires that it experience a certain number of units (day-degrees) of thermal time above a base temperature characteristic of that process. Thermal time is calculated as the sum of daily mean temperatures above a given base temperature (Monteith, 1981). When temperature summations were first used, base temperatures were either not subtracted from mean daily values or it was assumed for no special reason—which amounts to the same thing—that the base temperature was 0 °C (Abbe, 1905). Also, it was and still is, apparently, not always realized that the validity of the concept depends on there being a linear relationship between temperature and rate of development (reciprocal of the time taken for the developmental process to be completed). It is also this relationship that enables the base temperature and thermal time (temperature-sum) to be defined accurately.

For example, there are many circumstances in which the time taken to flower (f) can be considered as a rate ($1/f$) and then related linearly to mean temperature $\bar{T}$ (°C) as follows:

$$1/f = a + b\bar{T} \tag{2.1}$$

where a and b are constants. The base temperature, T_b, is the maximum temperature at or below which the rate of progress towards flowering ($1/f$) is zero (or the time to flower, f, is infinity); its value is given by the relation:

$$T_b = -a/b \tag{2.2}$$

And the thermal time (°C d) required for flowering, θ_f, is given by:

$$\theta_f = 1/b \tag{2.3}$$

In practice, the main interest is usually in predicting times taken to flower, rather than

rates of progress towards it. Although the one value may be readily transformed to the other, analysing responses in terms of rate has at least three advantages. First, a consideration of rate rather than time is probaby one step closer to the basic cause of developmental processes: the reason why an event happens in a short time is because the rate of progress was rapid, and not vice versa. Secondly, because the relation between temperature and rate is typically linear, data from only a few environments (theoretically only two) are required to define and quantify it. Thirdly, the two constants that define the rate relation (Equation 2.1) can be applied, via thermal time (Equations 2.2 and 2.3), to predict times of flowering in natural environments in which temperatures fluctuate.

In spite of these advantages, the concept of thermal time has been little used until recently, except by growers contracted to the vegetable processing industry who have used various systems of 'heat units' to predict dates of harvest and the timing of successive plantings of crops such as peas, beans (*Phaseolus* spp.) and maize destined for canning or freezing. A preoccupation with 'dates' in the traditional 'heat unit' approach to the management of what are often relatively minor crops (or minor uses of otherwise major crops), coupled with a neglect of photoperiodic effects on development in these crops, probably contributed to the proliferation of rather vague or arbitrary temperature summation methods (e.g. *see* Arnold, 1959; Wang, 1960; Cross and Zuber, 1972). Furthermore, in the case of major world crops, it seems that the discovery of photoperiodism by Tournois (1914) and its rediscovery by Garner and Allard (1920) probably drew attention away from temperature as a factor modulating development. Also, because of the influence of photoperiodism and vernalization on flowering there are many circumstances in which the concept of thermal time will not apply without some modification.

The concept of thermal time, which depends on the application of Equation 2.1, is most clearly seen in developmental processes unaffected by photoperiod. One process in which the most detailed analyses have been made concerns rates of seed germination (e.g. Garcia-Huidobro *et al.*, 1982a, b; 1985; Covell *et al.*, 1986; Ellis *et al.*, 1986). These studies have shown clearly that the concept can be used not only to analyse the times taken for seeds to germinate from a base to an optimum temperature, but that there is also a linear decrease in rate of germination with increase in temperature above the optimum temperature to a ceiling temperature at which the rate of germination is again zero. We shall return to the latter concept later when dealing with supra-optimal temperatures for flowering, after concluding our discussion of the effects of sub-optimal temperatures in circumstances when photoperiodism does not interfere.

In those species classified as SDPs (*Tables 2.1* and *15.1*) there are two circumstances in which photoperiodism does not obscure the effects of temperature on flowering: first, in photoperiod-insensitive genotypes (*see Figure 2.4*(*a*)), and secondly in photoperiods shorter than the critical value in SDPs (*see Figures 2.4*(*b*) and *2.4*(*c*)) (Hadley *et al.*, 1983a, b; 1984). In each of these cases the flowering response is modulated solely by mean temperature according to Equation 2.1. Analogous examples occur in LDPs. For example, some barley and non-vernalized faba bean genotypes are insensitive to photoperiod and respond to temperature as indicated by Equation 2.1 (Cooper *et al.*, 1987; Ellis *et al.*, 1987e). And similar responses are found in LDPs in photoperiods longer than the ceiling value (*see Figure 2.5*(*a*); recalculated from data in Berry and Aitken, 1979). The concept of thermal time can also be applied, with some modification, as we discuss later, in circumstances where photoperiod also affects flowering. But before dealing with such situations, the special effects of very warm temperatures, which may be stressful, need to be considered.

THE EFFECT OF TEMPERATURE IN THE SUPRA-OPTIMAL RANGE

There is obviously an upper temperature limit above which Equation 2.1 is no longer valid. Beyond some point on the response curve, which may be defined as the optimum temperature, T_O, it would be expected that further increases in temperature would be detrimental and would decrease the rate of progress towards flowering. Although there is much less quantitative information on the effects of supra-optimal temperatures on rates of progress towards flowering than there is for effects on rates of germination mentioned earlier, that evidence which is available suggests that the

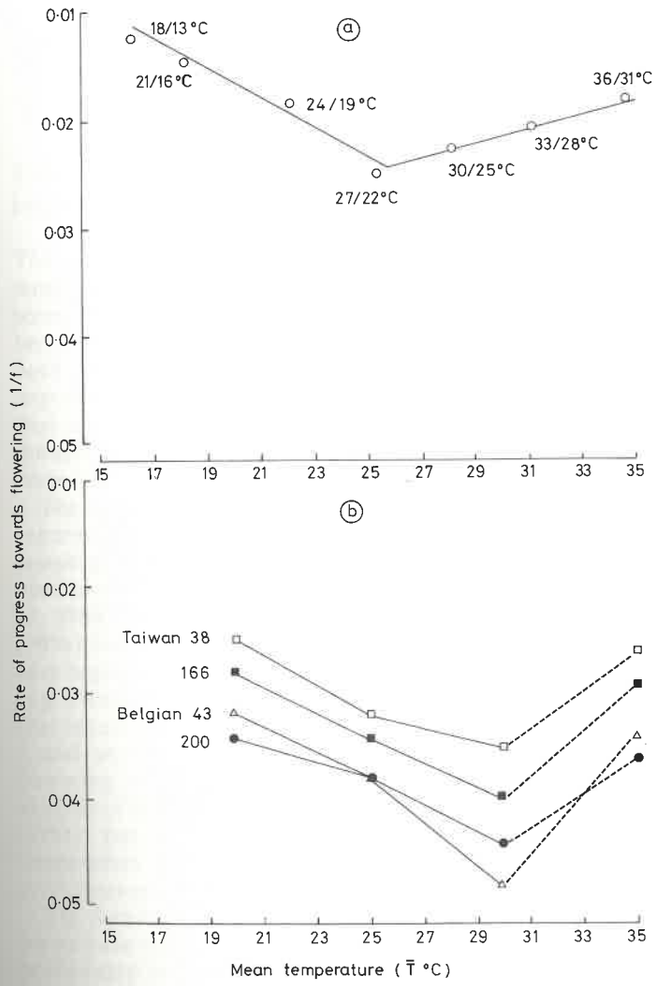

Figure 2.2 Relations between mean temperature ($\overline{T}$°C) and rates of progress towards flowering ($1/f$) of: (*a*) the photoperiod-sensitive soyabean cultivar Wayne grown in long (16 h) days in the various day and night temperatures indicated (calculated from data presented in Shibles *et al.*, 1975); and (*b*) four photoperiod-insentitive soyabean genotypes grown in natural days which varied in duration from 13 h 30 min to 14 h 20 min (calculated from data presented in Inouye *et al.*, 1979).

effect is similar: i.e. at supra-optimal temperatures the rate of progress towards flowering is linearly related to mean temperatures but, instead of the relation being positive as it is at sub-optimal temperatures, it is now negative. An example is shown for the soyabean cultivar Wayne in *Figure 2.2(a)* (calculated from the data of Shibles *et al.*, 1975), which has an optimum mean temperature close to 26 °C, and for diverse genotypes of soyabean in *Figure 2.2(b)* (calculated from data presented in Inouy *et al.*, 1979) where the optimum mean temperature, in each case, is close to 30 °C. Wayne is a cultivar recognized to be well adapted to the 'Corn Belt' states in the USA (and

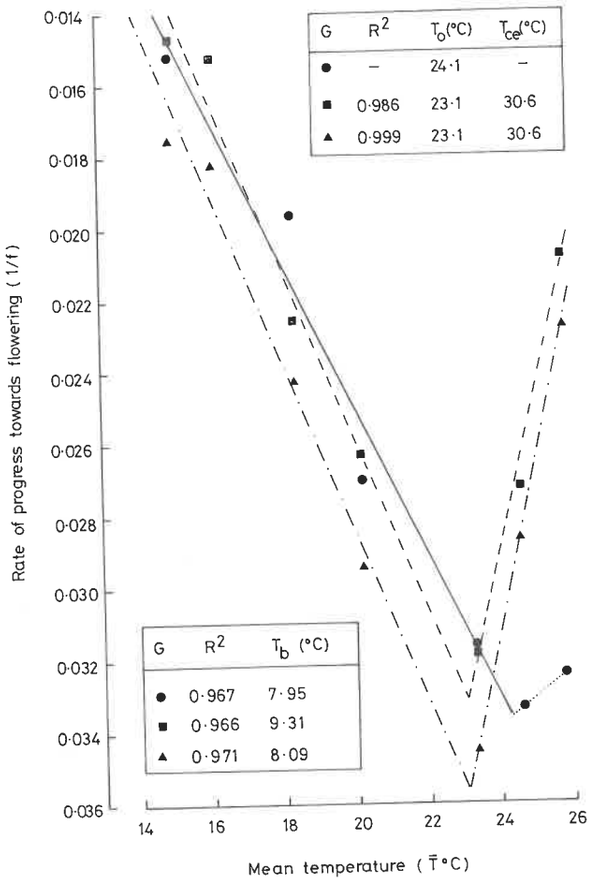

Figure 2.3 Relations between mean temperature ($\overline{T}$°C) and rates of progress towards flowering ($1/f$) of three cultivars of *Phaseolus vulgaris* said to be (Wallace, 1985) either lowland adapted (JU-80-13; ●–●) or highland adapted (San Martin; ■– – –■ and Negro Patzicia; ▲—·—▲) when grown at elevations from 50 to 1800 m in Guatemala. The fitted lines are based on Equation 2.1 for $\overline{T} < T_o$ and for $\overline{T} > T_o$. Tabulated information within the body of the figure are, bottom left, genotype symbol (G), coefficient of multiple determination (R^2) for each fitted line when $\overline{T} < T_o$, and the base temperature for flowering (T_b) calculated from Equation 2.2; top right, the r^2 values are for the fitted lines when $\overline{T} > T_o$, the optimum mean temperature for flowering (T_o), and the ceiling temperature for flowering (T_{ce}), as described in the text. All data (recalculated from Wallace, 1985) are mean values of experiments conducted in 1982 and 1983.

especially within the approximate range of latitudes from 40 ° to 42 °N; Scott and Aldrich, 1970) whereas the genotypes investigated by Inouye *et al.* are of tropical or sub-tropical origin.

The fact that optimum mean temperatures for flowering vary, not only within species for genotypes of different origin, but also between species is illustrated by comparisons of *Figures 2.2(a)* and *2.2(b)* with *Figure 2.3*. Here, we have replotted the data on *Phaseolus vulgaris* reported by Wallace (1985) for three cultivars, two said to be highland adapted and the other said to be lowland adapted when grown at various elevations in Guatemala. It is clear from *Figures 2.3* that the optimum mean temperature (T_o) for flowering in all three cultivars is within 0.9 °C of 24 °C. Furthermore, the base (T_b) and ceiling (T_{ce}) temperatures (i.e., the cooler and warmer values at which extrapolations indicate that rates of progress towards flowering would be zero) are also apparently very similar, and close to 8.5 °C and 30.6 °C, respectively.

Effects of photoperiod on rates of progress towards flowering and interactions with temperature

The previous section has shown several advantages in considering the effects of temperature in terms of the rate of progress towards flowering. It is therefore somewhat surprising that, until recently, an analogous approach has seldom, if ever, been used to quantify the effects of photoperiod on flowering. Furthermore, since both temperature and photoperiod can modulate flowering of a given genotype, it is important to quantify the response to each factor in the same way for it is only then that the possibility of interactions can be explored. Moreover, there is a school of thought which maintains that the concept of biological interactions is only valid with respect to rate processes (Drury, 1980).

These were the arguments that led us to the approach which we are using in experiments designed to quantify flowering responses to the combined effects of temperature and photoperiod in controlled environments. So far, seven species have been investigated—two SDPs, cowpea (Hadley *et al.*, 1983a) and soyabean (Hadley *et al.*, 1984) and four LDPs, chickpea (Roberts *et al.*, 1985), lentil (Summerfield *et al.*, 1985a), barley (Cooper *et al.*, 1987) and faba bean (Ellis *et al.*, 1967). Furthermore, we have begun to reanalyse published data for several other species, including both SDPs (e.g. *Phaseolus vulgaris; Figure 2.3*) and LDPs (e.g. *Pisum sativum; see Figure 2.5(a)*). Our reanalyses, in terms of $1/f$, usually simplify the traditional approach, which uses f, and we believe offer a more plausible explanation of photo-thermal effects on flowering. A similar approach, i.e. one based on rate processes, has been used for the analysis of field data by Gallagher *et al.* (1983) and advocated by France and Thornley (1984); but it is difficult, if not impossible, to discern the separate effects of temperature and photoperiod from field data without supporting evidence from investigations in controlled environments.

The details of the experimental design of our investigations in controlled environments have varied according to species, but several principles underlie them all. First, preliminary investigations are undertaken to identify cultural techniques, especially light quality (combination of lamp types), which ensure that pot-grown plants closely resemble those grown in the field in terms of morphology, phenology and, in the case of grain legumes, in their relative reliance on symbiotically fixed and inorganic nitrogen (e.g. Summerfield *et al.*, 1985b). Secondly, different day and night temperatures are used and, in order not to depart too far from the typical phase-shift in the

natural diurnal temperature cycle, which lags asymmetrically behind the natural photoperiod, the switch from 'night' to 'day' temperature in the controlled environments is programmed to occur 2 h after lights-on, while the switch to 'night' temperature coincides with lights-off. Thus, although thermoperiod does not coincide precisely with photoperiod it is deliberately partially confounded with it.

Of course, when photoperiods differ as well as day and night temperatures within the same experiment, then confounding of some sort between photoperiod and temperature is inevitable; but deliberate confounding can be exploited.

A typical orthogonal design may consist of 3 photoperiods × 2 day temperatures × 2 night temperatures. Such a design will reveal whether there are separate specific effects of day temperature or night temperature and thermoperiod and, if not (as has been found in each of the seven species investigated so far), the flowering response can be analysed as a function of mean temperature. And, because of the variation in thermoperiod as well as in both day and night temperatures implicit in the design, there are twelve different mean temperatures which are sufficient to quantify accurately the response surface for the effects of mean temperature on flowering. Such designs are therefore powerful and economical. In each species, several genotypes, selected to represent a wide geographical range of origin, are simultaneously investigated; and when LDPs are investigated, two additional treatments, vernalized and non-vernalized seeds, are normally included.

Figures 2.4 and *2.5* show typical examples to illustrate the range of responses encountered in these investigations; each column of graphs shows the response of a single genotype of each species. The results for any one genotype are presented in four different ways, since different presentations emphasize different features. The upper graphs in each example (*Figures 2.4*(*a–c*) and *2.5*(*a–c*) are isometric three-dimensional displays and gives the most comprehensive view of rates of progress towards flowering as functions of both photoperiod and mean temperature. (Note that the ordinate scales are drawn so that $1/f$ increases downwards, and accordingly times taken to flower (f) increase upwards.) The second series of graphs in each example (*Figures 2.4*(*d–f*) and *2.5*(*d–f*)) are the relations between photoperiod and $1/f$ at three different mean temperatures (this convention corresponds to that used in *Figures 2.1*(*c*) and *2.1*(*d*) but where the results for only one mean temperature were shown). Below (*Figures 2.4*(*g–i*) and *2.5*(*g–i*) the same data are replotted so that f is the ordinate scale instead of $1/f$ (corresponding to the convention used in *Figures 2.1*(*a*) and *2.1*(*b*)). Finally, the bottom series (*Figures 2.4*(*j–l*) and *2.5*(*j–l*) show the relations between $1/f$ and mean temperature at three different photoperiods.

The first example is for a photoperiod-insensitive genotype of cowpea (*Figure 2.4*(*a,d,g,j*)) but similar examples could have been illustrated for other photoperiod-insensitive genotypes of different species, e.g. the soyabean cultivar Fiskeby V (Hadley *et al.*, 1984). In these photoperiod-insensitive genotypes it is clear that rate of progress towards flowering is a linear function of mean temperature and that this

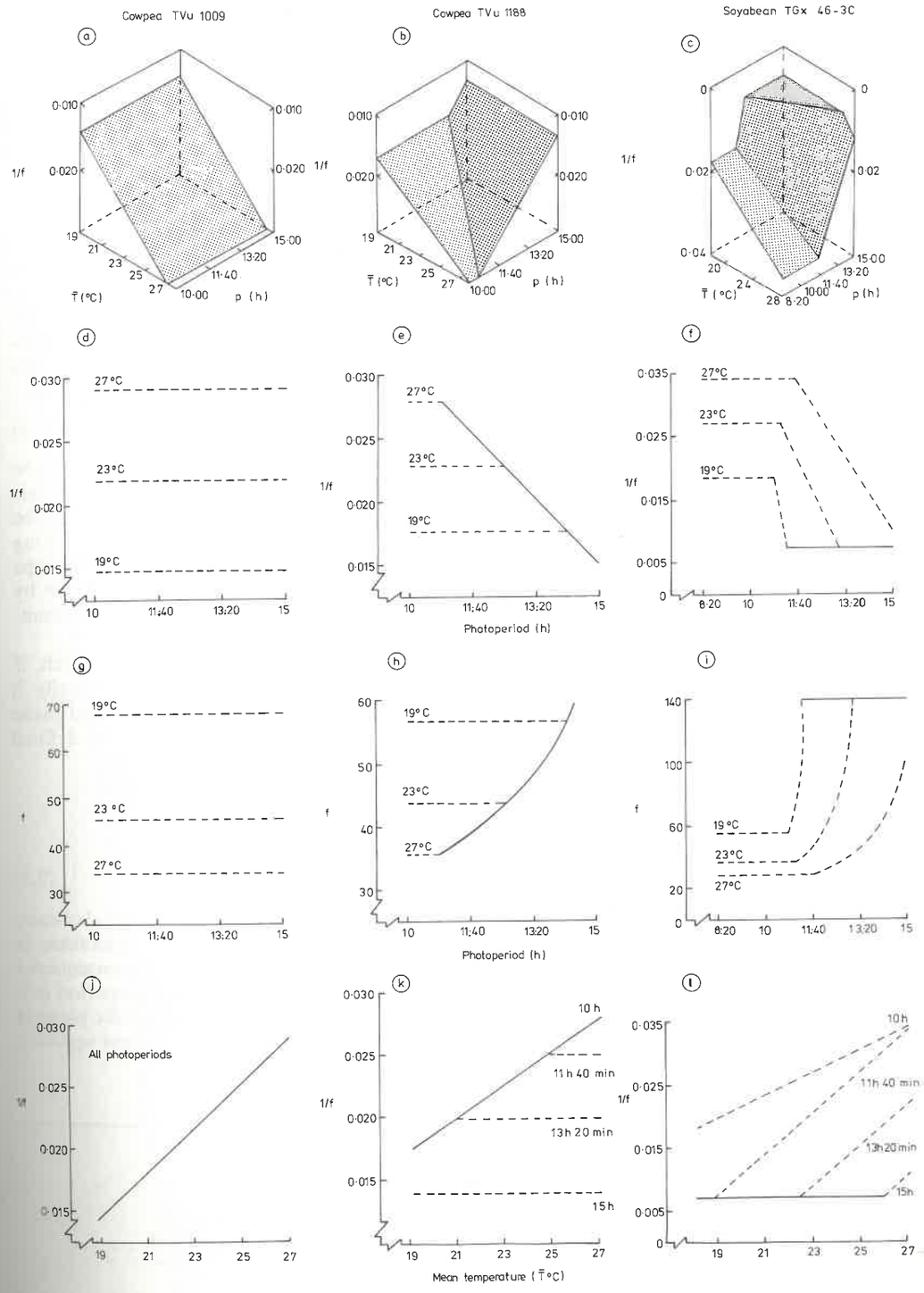

Figure 2.4 Photo-thermal effects on flowering in three SDPs: (*a*), (*d*), (*g*) and (*j*), a photoperiod-insensitive genotype of cowpea (TVu 1009); (*b*), (*e*), (*h*) and (*k*), a photoperiod-sensitive genotype of cowpea (TVu 1188); and (*c*), (*f*), (*i*) and (*l*), a photoperiod-sensitive genotype of soyabean (TVx 46-3C). Data for cowpea (*Vigna unguiculata*) are from Hadley *et al.* (1983a); those for soyabean are from Hadley *et al.* (1984). In figures other than the isometric projections (*a*, *b* and *c*), broken lines indicate individual responses to photoperiod at different values of mean temperature or vice versa; solid lines indicate where the responses overlap.

response is unaffected by day-length. Is is also unaffected by total radiation receipts because, in the experimental design used, photoperiod is confounded with total radiation.

Accordingly, in this and similar examples the concept of base temperature and thermal time (Equations 2.1–2.3) may be applied without complications in natural environments where both temperature and photoperiod vary—a proposition confirmed by comparisons made between data from controlled environments and the field (Summerfield and Roberts, 1985).

Figures 2.4(b,e,h,k) show a typical example of a photoperiod-sensitive cowpea genotype. This probably represents the simplest type of a SDP response. Clearly, there is an underlying (or basic) temperature response similar to that shown by photoperiod-insensitive genotypes (*Figure 2.4(a)*). But this basic temperature response is overlaid with a photoperiodic response in which rate of progress towards flowering is a linear negative function of photoperiod and so can be described as:

$$1/f = a' + c'P \tag{2.4}$$

where P is photoperiod (h) and a′ and c′ are constants. Once the values of the constants in Equations 2.1 and 2.4 have been determined for genotypes of this response category, the time taken to flower in any given constant environment can be predicted by solving both Equations 2.1 and 2.4 for that environment and taking whichever is the larger value of f given by either equation. In other words, in this type of response the time taken to flower is determined *either* by temperature *or* by photoperiod (whichever calls for the greater delay in flowering) but in no circumstances by both factors.

If the critical photoperiod (P_c) is defined in SDPs as that photoperiod which, if exceeded, causes a delay in flowering, then it will be seen that geometrically it corresponds with the line of intersection of the basic temperature-determined plane and the photoperiod-determined plane in *Figure 2.4(b)*. This line can be defined algebraically as:

$$P = P_c \text{ when } a + b\overline{T} = a' + c'P$$

and so:

$$P_c = (a + a' + b\overline{T})/c' \tag{2.5}$$

Note that, since c′ has a negative value in SDPs, the critical photoperiod *decreases* with increase in temperature (in this genotype by about 27 min per °C increase in mean temperature). The extent to which P_c varies is a simple geometric consequence of the relative sensitivity of the genotype to temperature (b) and to photoperiod (c′). In genotypes that are very sensitive to photoperiod (where the photoperiodic plane in a three-dimensional projection of the type shown in *Figure 2.4(b)* is almost vertical), there is very little variation in P_c with temperature.

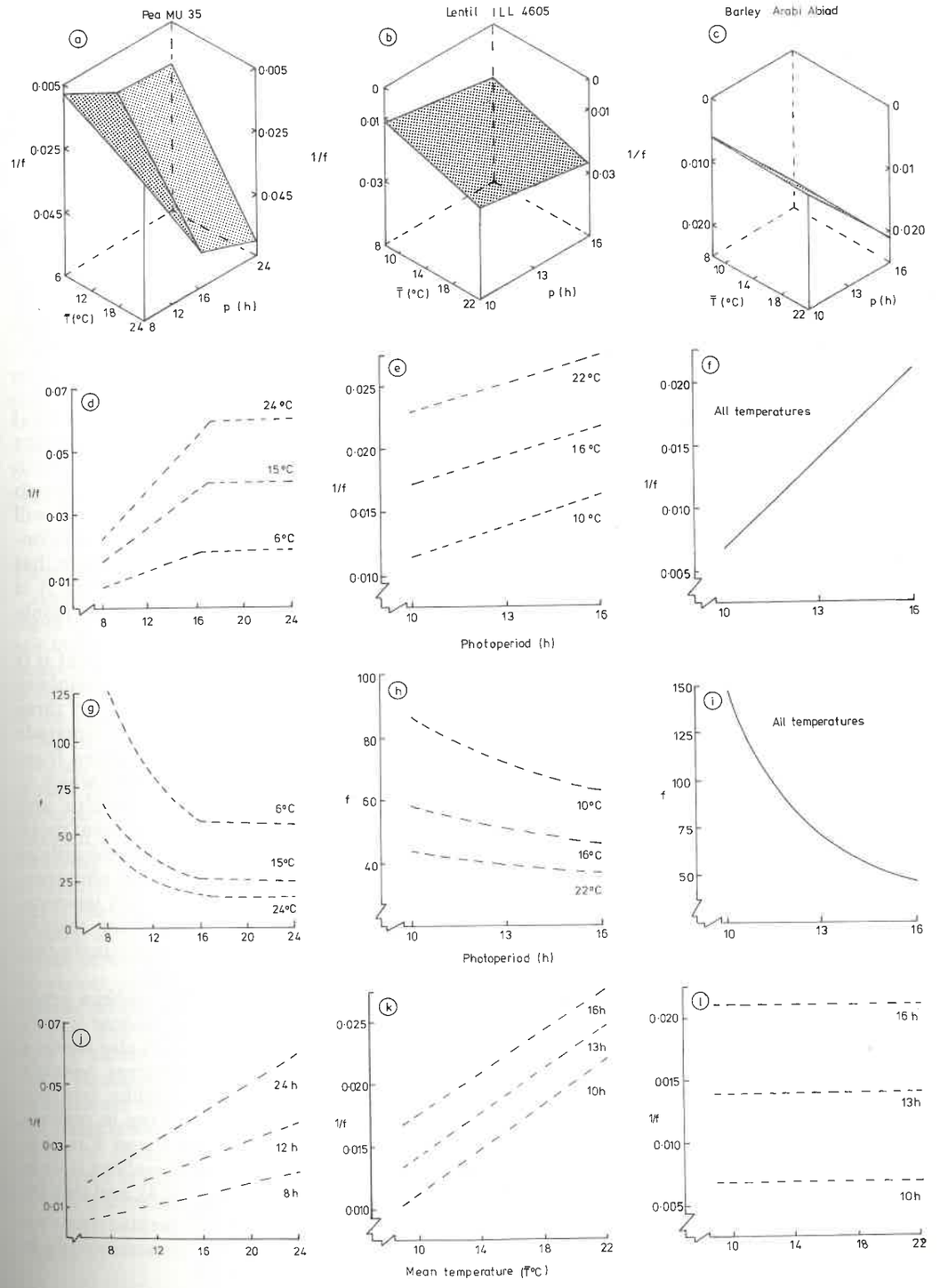

Figure 2.5 Photo-thermal effects on flowering in three LDPs: (*a*), (*d*), (*g*) and (*j*), a photoperiod-sensitive genotype of pea (MU 35); (*b*), (*e*), (*h*) and (*k*), a photoperiod-sensitive genotype a lentil (ILL 4605); and (*c*), (*f*), (*i*) and (*l*), a photoperiod-sensitive, vernalized land race of barley (Arabi Abiad). Data for pea are from Berry and Aitken (1979); those for lentil (*Lens culinaris*) are from Summerfield *et. al.* (1985a); and those for barley (*Hordeum vulgare*) are from Cooper *et al.* (1987). Otherwise, explanation as for *Figure 2.4*.

If a natural environment were such that the day-length experienced was always shorter than the critical photoperiod (which is improbable) then time to flower in a fluctuating environment could be determined entirely on the basis of thermal time. On the other hand, if the environment were such that the photoperiod experienced was always longer than the critical photoperiod (which is more probable) then time to flower could be determined by an approach analogous to the thermal time concept, namely by calculating a base photoperiod, P_b, as follows:

$$P_b = -a'/c' \tag{2.6}$$

and so the photoperiodic time (*h d*) for flowering, φ_f, which is the number of hours of light in excess of the base photoperiod which has to be accumulated before flowering occurs, is given by:

$$\varphi_f = 1/c' \tag{2.7}$$

Equations 2.6 and 2.7 offer a practical approach to predicting flowering in natural environments in which photoperiod varies, providing the day-length is always longer than the critical photoperiod. Although this approach involves an assumption which is almost certainly incorrect (Roberts *et al.*, 1986), i.e. that plants are sensitive to photoperiod throughout the period from emergence to flowering, in practice this will not necessarily lead to serious problems in applying the concept to natural environments. However, we shall discuss this difficulty later. Here, we simply recognize that P_b and φ_f probably have less fundamental significance than T_b and θ_f since it is probable that temperature affects rates of development throughout the life of plants and so no similarly questionable assumption is involved.

A final implication of the type of response illustrated in *Figure 2.4*(*b*) is that it is possible to estimate the values of the four constants that define the entire response surface from experiments in only four different environments. (Indeed, just three environments could be used provided that they included two different photoperiods *and* two different mean temperatures.) *Figure 2.4*(*b*) shows that data obtained from two environments with different photoperiods and a temperature regime which is warm, but not necessarily controlled, will define the photoperiodic constants (a′ and c′) without interference from temperature. While two environments of different mean temperature in photoperiods, again not necessarily constant, shorter than the critical value, will define the thermal constants (a and b) without interference from photoperiod. By these means the separate genetically controlled photoperiodic and temperature responses can be isolated and so germplasm can be screened for relative sensitivity of both responses using very simple schemes involving field experiments (Hadley *et al.*, 1983a, b; 1984).

Figure 2.4(*c*) shows a typical example of a photoperiod-sensitive soyabean genotype. In photoperiods shorter than the critical value the type of response is very similar to cowpea, i.e. it conforms to Equation 2.1. And, like cowpea, it also shows a negative linear relationship between photoperiod and rate of progress towards flowering in photoperiods longer than the critical value. But, unlike cowpea, temperature also has some effect on rate of progress towards flowering in regimes where $P > P_c$, although there is no evidence of interaction between P and $\overline{T}$ in this response plane. Accordingly, this photoperiodic response plane for soyabean is only slightly more complicated than that described for cowpea (Equation 2.4), and may be written as:

$$1/f = a' + b'\overline{T} + c'P \tag{2.8}$$

where a′, b′ and c′ are the constants which apply when day-lengths are longer than the critical photoperiod. (Equation 2.4 for cowpea can be considered as a special case of Equation 2.8 in which the value of b′ is zero.)

Finally, in some soyabean genotypes there appears to be a minimum rate of progress towards flowering (or a maximum time to flower) irrespective of photothermal conditions; in other words they have a quantitative rather than an obligate response to photoperiod. This limitation is represented by a horizontal plane in *Figure 2.4*(*c*) (and *see* Major, 1980).

The fact that temperature also has a positive effect on rates of progress towards flowering in photoperiods longer than P_c results in a slight rotation of the photoperiodic-response plane with respect to the ordinate compared with the response in cowpea. In turn, this alters the angle of intersection with the basic temperature-response plane (which is exposed in photoperiods shorter than P_c) such that variations in temperature in soyabean have smaller effects on the value of the critical photoperiod as compared with cowpea. Furthermore, in contrast to cowpea, the value of the critical photoperiod *increases* in warmer environments (often by about 11 min $°C^{-1}$). Algebraically, the photoperiod becomes critical when the value of f given by Equation 2.1 is equal to that given by Equation 2.8. Hence, the critical photoperiod, P_c, in soyabean is given by:

$$P_c = [a - a' + \overline{T}(b - b')]/c' \tag{2.9}$$

These arguments are considered in greater detail elsewhere (Hadley *et al.*, 1984).

Another consequence of temperature having an effect on progress towards flowering in day-lengths longer than the critical photoperiod is that the base photoperiod is not independent of temperature and neither is the base temperature for this plane independent of photoperiod. The implications of this complication are discussed later in relation to LDPs, where temperature can have relatively greater effects on the form of the photoperiodic response plane.

Whilst it is clear that mean temperature can strongly modulate rates of progress towards flowering in soyabean in photoperiods both shorter and longer than the critical photoperiod, many accessions and cultivars are so extremely sensitive to photoperiod (their relative sensitivity is given by the value of the photoperiod slope constant, c′, in Equation 2.8) that this factor is the major determinant of the timing of flowering. Cregan and Hartwig (1984) emphasized the importance of these differences in relative sensitivity to photoperiod for soyabean adaptation and cultivar development. They quantified the effect of photoperiod on the time from sowing to flowering, f, using linear and quadratic models. Their approach was statistically successful (R^2 values between 0.87 and 0.97) but not easy to relate to the biology of photoperiodism. Moreover, when the original responses (*Figure 2.6*(*a*)) are replotted in the form of rates of progress towards flowering in relation to photoperiod (*Figure 2.6*(*b*)), a much simpler, and biologically more plausible, model emerges, i.e. Equation 2.4 applies; with R^2 values for different genotypes of between 0.87 and 1.00. (Equation 2.4 rather than Equation 2.8 was applied since the cultivars were grown under similar temperature conditions.) We have also found that a re-analysis (not shown here) of the times to flowering of diverse genotypes of mung bean (*Vigna radiata*) in a wide range of photoperiods (Bashandi and Poehlman, 1974) is as successful as that illustrated in *Figure 2.6*.

It is interesting to note the relative sensitivity to photoperiod of flowering in the soyabean cultivar Biloxi (*Figure 2.6*(*b*))—one of the classical genotypes used in studies of photoperiodism (Garner and Allard, 1923; Hamner, 1969). This cultivar has the

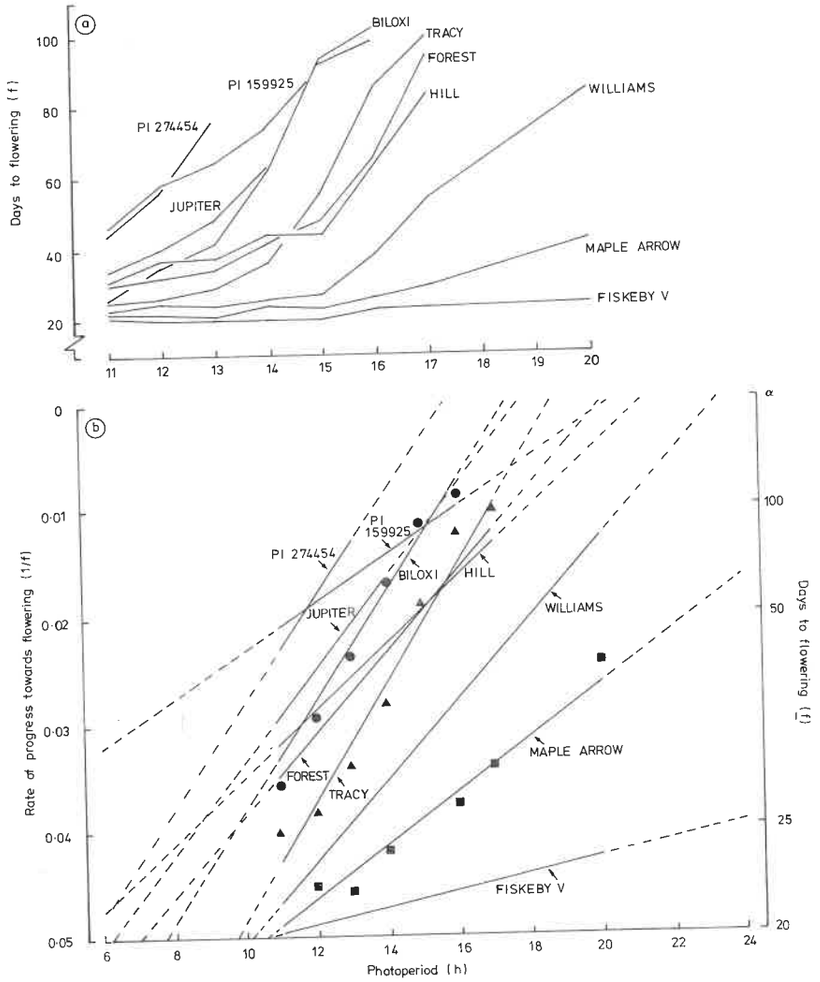

Figure 2.6 (*a*) Relations between photoperiod and days from emergence to flowering (f) in each of ten diverse genotypes of soyabean, i.e. cultivars adapted to various regions in the USA and Canada, plant introductions and experimental lines (data replotted from Cregan and Hartwig, 1984); and (*b*) the same data as in (*a*) replotted in the form of $1/f$ in relation to photoperiod. The lines for each genotype are linear regressions based on Equation 2.4; original data points are shown for three genotypes (● Biloxi; ▲ Tracy; ■ Maple Arrow) to indicate the typical goodness of fit of the model (R^2 values of between 0.87 and 1.00). Extrapolations to the abscissa for PI 274454, Hill and PI 159925 are 5.6, 5.2 and −2.0 h, respectively.

largest photoperiod constant, c′, of the ten genotypes tested—supporting our earlier suggestion that such dramatic responses to photoperiod, being assumed (incorrectly) to be typical of the species, have probably led to the neglect of temperature as a factor that also controls development in the major world crops. Whether this speculation is correct or not, the observations of Garner and Allard more than 60 years ago (1923) and, more recently, of Salisbury (1982), have not been sufficiently heeded: 'tempera-

ture is undoubtedly the most important environmental factor in relation to the action of the light period on plant growth'; and 'In virtually every case where studies have been extensive enough, photoperiodic response has been readily modified in one way or another by changing temperature'.

Among the nine soyabean genotypes evaluated by Hadley *et al.*, 1984, critical photoperiods decreased from 10–12 h at a mean temperature of 24 °C to 9–10.5 h at a mean temperature of 20 °C. And so, with the prevailing monthly mean temperature experienced during the investigation by Cregan and Hartwig (1984), i.e. 18.6–24.9 °C, the conditions were probably always on that part of the photo-thermal response surface which is modulated mainly by photoperiod and never on that part modulated solely by temperature (except for Fiskeby V and, perhaps, Maple Arrow).

The fact that critical photoperiod varies with mean temperature—as described by Equations 2.5 and 2.9—does not support the traditional viewpoint that P_c 'remains relatively resistant to changing temperatures' (Schwabe, 1971; Vince-Prue, 1975; Salisbury, 1982). A reappraisal of earlier data on species such as *Xanthium* and *Pharbitis* (where changes in f have often been related to the temperature experienced during darkness) in terms of $1/f$ and $\overline{T}$ would seem to be justified.

We now turn to photo-thermal responses of LDPs (*Figure 2.5*). Data published by Berry and Aitken (1979) for a photoperiod-sensitive genotype of pea are reanalysed in *Figure 2.5*(*a*). This response is essentially a mirror-image of the example shown of a photoperiod-sensitive genotype of soyabean (*Figure 2.4*(*c*)) except that, within the range of photoperiods studied (which more than covers the range of photoperiods experienced by the pea crop in natural environments), a plateau of maximum delay in flowering is not evident. Indeed it is possible that this cultivar would have been shown to be an obligate LDP if sufficiently short photoperiods had been included in the experiment. That part of the response surface which responds to photoperiod is described by Equation 2.8, except that in the case of pea the value of the photoperiodic constant, c′, is positive, since it is an LDP, rather than negative as it is in SDPs. The fastest rate of progress towards flowering in this example is achieved with a ceiling photoperiod of just over 16 h. In photoperiods longer than P_{ce}, i.e. in the most inductive conditions, the rate of development is now limited by temperature and accordingly the underlying temperature response is revealed which, again, is described by Equation 2.1.

In passing, it is worth noting that flowering data for the pea cultivar, Alaska, obtained over the same range of photoperiods and temperatures, showed complete insensitivity to photoperiod (Berry and Aitken, 1979) so that the form of the three-dimensional isometric projection is identical with that in *Figure 2.4*(*a*) except that, of course, the numerical values are different.

Figure 2.5(*b*) shows the response typical of the lentil crop. In this species we are not yet aware of a genotype that is either completely insensitive to photoperiod or to temperature (Summerfield *et al.*, 1985a)—but 400 genotypes will be evaluated in 1986. The wide ranges of each of photoperiod and mean temperature which have been comprehensively investigated to date (10–16 h and 9–20 °C) cover most, and perhaps all, agricultural situations but are not as great as the ranges investigated for pea (8–24 h and 6–24 °C). And so, it may be for this reason that a ceiling photoperiod has not been reached exposing a response plane for lentil where only temperature has an effect. Certainly, had this narrower range of conditions been applied to the pea example, a ceiling photoperiod would not have been revealed. Nevertheless, we have chosen to illustrate lentil as an example, since later we use experiments on this species to analyse the photoperiod-sensitive and insensitive phases of development. Further-

more, over a similar range of conditions, the type of response shown for lentil appears to be common in other LDPs, e.g. in chickpeas (Roberts *et al.*, 1985) and in some, but not all, cultivars of barley (Cooper *et al.*, 1987) and of faba bean (Ellis *et al.*, 1987).

Barley has proved to be an extremely variable species within which a wide range of response types has been identified from the diverse range of genotypes examined in factorial experiments including day-lengths from 10 to 16 h and mean temperatures from 9 ° to 22 °C (Cooper *et al.*, 1987). For example, we have identified cultivars that are apparently completely insensitive to photoperiod, to temperature and to vernalization; others that are sensitive to photoperiod and not to mean temperature, but in which the photoperiod response only becomes marked after vernalization; and yet others that are insensitive to vernalization but their response to both photoperiod and temperature is reminiscent of that in the pea example shown in *Figure 2.5*(*a*) (Berry and Aitken, 1979). It is not possible to give examples of all these response types here, and so we have chosen to illustrate that of a land-race which, after imbibed seeds have been vernalized for 30 h at 1 ± 0.5 °C, is sensitive to photoperiod but not to mean temperature (*Figure 2.5*(*c*)). This response provides a contrast to that of cowpea TVu 1009 shown in *Figure 2.4*(*a*), which is sensitive to mean temperature but not to photoperiod.

Taken altogether, the first impression of *Figures 2.4* and *2.5* might be that the effects of photoperiod and temperature on flowering are dauntingly complex. However, we believe that, once the responses to both temperature and photoperiod are conceived as rates of progress towards flowering, several simplifying principles emerge which may be summarized as follows:

1. Rates of progress towards flowering, almost without exception, tend to be linear functions of either temperature, or photoperiod, or both.
2. The responses to both environmental determinants can be expressed simultaneously as response surfaces. It then becomes apparent that one plane is sufficient to describe the response of photoperiod-insensitive plants (DNPs); whereas in photoperiod-sensitive species (both SDPs and LDPs), a second plane is also required to describe obligate responses; and to these a third plane has to be added to describe quantitative responses.
3. The first of these planes, the basic temperature response, is probably common to almost all annual crops; it is not affected by photoperiod (at least over the range of day-lengths which cover all agricultural situations) and describes the underlying response of flowering to mean temperature when photoperiod does not interfere. Accordingly, Equation 2.1 describes the typical response of DNPs, and also of photoperiod-sensitive species when photoperiods are sufficiently inductive for the limiting factor to become temperature. This occurs in photoperiods shorter than the critical day-length in SDPs and in the photoperiods longer than the analogous ceiling photoperiod in LDPs.
4. The second plane, the photoperiod-temperature sensitive response, is common to all photoperiod-sensitive species, whether SDPs, LDPs obligate or quantitative. This plane emerges in photoperiods longer than the critical photoperiod in SDPs or in day-lengths shorter than the ceiling photoperiod in LDPs. Within this plane there is a positive response to photoperiod in LDPs and a negative response to photoperiod in SDPs; at the same time there is normally a positive response to mean temperature—although this may vary in magnitude, even to zero (as in the case of cowpea; *Figure 2.4*(*b*)). The magnitude of the c′ constant which describes the slope of the plane with respect to day-length, i.e. the photoperiod sensitivity, varies among species and cultivars; but the highest values are found amongst tropical (short-day) plants, presumably since it is these that need to respond to relatively small differences in day-length (*Table 2.2*).
5. The third plane, which may be considered as an environment-insensitive plane, describes the minimum rate of progress towards flowering (or, if preferred, the maximum delay in flowering) in quantitative photoperiod-sensitive plants. There is generally no response to either mean temperature or to photoperiod, and so the plane is horizontal in the case of the three-dimensional projections shown in *Figure 2.4*.
6. The generalizations above refer to 'non-stress' temperatures; at supra-optimal temperatures there is a negative linear relation between mean temperature and rate of progress towards flowering. It is not yet known how this response is affected by photoperiod.
7. Since the three possible components of the overall response surface for rates of progress towards flowering are normally planes, the implication is that there are no interactions between mean temperature (up to the optimum) and photoperiod when photo-thermal responses are expressed as rates within the range of combinations of mean temperature and photoperiod described by any one of the planes. (Interactions would, however, occur if data were analysed in the traditional manner, i.e. in terms of days to flowering.) When dealing with rates, interactions only emerge when intersections between planes are transgressed.
8. Because responses to mean temperature and to photoperiod with respect to rates of progress towards flowering can be described as planes, it follows that variable daily contributions of the environment towards the induction of flowering can be treated as additive increments. This has already been discussed in terms of thermal time for the contribution of temperature; we later discuss how photoperiod can be similarly treated (i.e. in terms of photoperiodic time) and combined with mean temperature to predict durations to flower under natural and therefore variable conditions.

Table 2.2 VARIATION IN DAY-LENGTH WITH LATITUDE

Latitude	*Day-length, sunrise to sunset*			*Day-length, including civil twilight**		
(°N or S)	*Longest day (h:min)*	*Shortest day (h:min)*	*Annual variation in day-length (h:min)*	*Longest day (h:min)*	*Shortest day (h:min)*	*Annual variation in day-length (h:min)*
0	12:07	12:07	0:00	12:50	12:50	0:00
10	12:43	11:33	1:10	13:29	12:19	1:10
20	13:21	11:14	2:07	14:11	11:44	2:27
30	14:05	10:34	3:31	15:01	11:04	3:57
40	15:01	9:46	5:15	16:01	10:22	5:39
50	16:23	8:42	7:41	17:53	9:20	8:33
60	18:52	5:53	12:59	22:25	7:48	14:37
70	24:00	0:00	24:00	24:00	0:00	24:00

* Civil twilight begins before sunrise and ends after sunset when the true centre of the sun is 6 degrees below the horizon; it corresponds to an illuminance of about 3–4 lux. Day-length defined in this way is that which is probably perceived by most but not all species (*see* Chapter 15).

In these descriptions of the combined effects of mean temperature and photoperiod on flowering, we have avoided discussing how the responses are modified by vernalization in the case of LDPs. This is because, so far, insufficient data are available for a clear picture to have emerged (e.g. compare Murneek and Whyte, 1948 with Napp-Zinn, 1984). In a few species (e.g. celery) plants may be virtually insensitive to photoperiod after vernalization (Salisbury, 1982), but in general it seems that vernalization tends to allow subsequent stimulatory effects of photoperiod, or of warm temperatures, or of both, to be expressed. In lentils, at least, the resulting response surfaces for flowering of plants grown from vernalized seeds may still be described as planes (Summerfield *et al.*, 1985a). And with faba beans and barley, some genotypes become acutely sensitive to photoperiod and/or mean temperature only after vernalization; when grown from non-vernalized seeds they are either insensitive or far less sensitive to photo-thermal conditions during vegetative growth (Ellis *et al.*, 1987b and Cooper *et al.*, 1987, respectively).

Changes in photoperiod sensitivity during development

Whereas it is known that temperature may affect rates of development throughout the life of a plant, it has generally been acknowledged that there is a 'juvenile' phase in most plants during which they are unresponsive to day-length. It is often claimed that after this juvenile phase has ended plants tend to become increasingly sensitive to photoperiod. For example, the number of long days required to elicit flowering response in the LDP *Lolium temulentum* decreases as the plants get older: for example, when plants were grown in 8 h days, after they were 1 week old, then six 24 h diurnal cycles of continuous light (i.e. six 24 h photoperiods) were needed for all the replicates to respond whereas when they were 6 weeks old only a single 24 h cycle was required (Evans, 1960). However, unless it is also shown that an 8 h day is shorter than the base photoperiod, this interpretation is open to question because, as we have shown earlier, any photoperiod longer than the base photoperiod can have some inductive effect, as least up to the ceiling photoperiod. Within the range from base to ceiling photoperiod, although longer photoperiods are more inductive than shorter ones, all photoperiods are inductive to some extent. Furthermore, it follows from Equations 2.4 and 2.6–2.8 that the effects of consecutive photoperiodic cycles which are longer than the base photoperiod in LDPs, or shorter than the critical photoperiod in SDPs, are additive. And so in many experiments it could appear as though plants become more sensitive to photoperiod as they age, whereas this apparent increase in relative sensitivity may be a product of the number of cycles already received and the relative inductiveness of those cycles. We believe, however, that this is not a function of plant age but of the sum total of inductive stimulus the plants have experienced.

This argument does not preclude the existence of a photoperiod-insensitive juvenile phase. Furthermore, it also seems probable that once the flowering stimulus has been irreversibly induced there will be an inevitable delay from the completion of induction until the appearance of the first flower. This implies the existence of a post-inductive phase which is also insensitive to photoperiod.

In order to test these ideas, a series of reciprocal-transfer treatments were imposed on three genotypes of lentil of diverse origin. The experiments comprised 22 photoperiodic treatments in which plants were transferred from short days (normally 10 h) to long days (16 h) or vice versa at 4-day intervals and the consequences for

flowering were recorded. All three genotypes responded similarly to the treatments and differed only in relative sensitivity: *Figure 2.7* shows the response of the most sensitive genotype, the land-race Syrian Local Large (Roberts *et al.*, 1986).

After sowing, there was an initial pre-emergence phase, g, during which the seedlings were in the dark. This was followed by a pre-inductive phase after the seedlings had emerged, *j*, and which lasted about 8 days (i.e. from time E_m to *X* in *Figure 2.7*) during which time photoperiod had no significant effect on the time taken to flower: compare the similarity of the results of treatments **I** and **J** (which either had 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).

The pre-inductive phase was followed by a period during which the plants were very sensitive to photoperiod, and which therefore may be called the inductive phase, *i*. It began at time *X* and its duration depended on the photoperiodic regimes experienced thereafter. In a continuous succession of 16 h photoperiods the inductive phase was completed at time *Y*; and so in *Figure 2.7* the inductive phase in treatments **I** to **Q** is from *X* to *Y*. This can be deduced by noting the similarity of the results of treatment **Q** (in which 12 days of 16 h photoperiodic cycles immediately following the

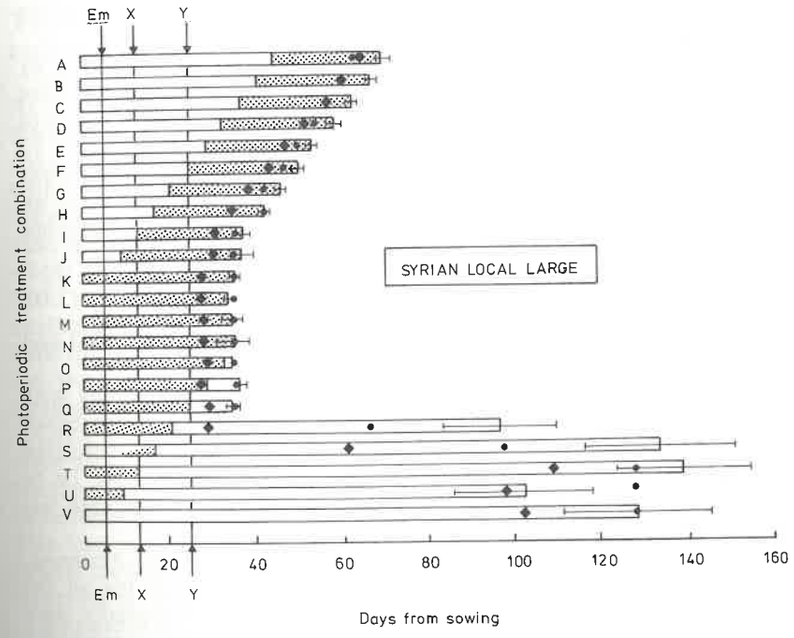

Figure 2.7 Effects of various photoperiod treatments (**A–V**) on days from sowing to the appearance of first flowers (complete histograms) and to first flower buds detectable by eye ( ) in the lentil land race Syrian Local Large grown at a mean temperature of 21.25°C. Open and stippled areas within individual histograms are 10 h and 16 h photoperiods, respectively. Horizontal lines spanning times to first flowers are standard deviations. *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 (i.e. in treatments **I–Q**; *see* text). Theoretical times from sowing to first flower (days from emergence to first flower + 5 days) calculated according to the method described in the text are shown as ● within or adjacent to individual histograms.

pre-inductive phase were sufficient to minimize the time taken to flower) with those of treatments **I** to **P** (in which the 16 h cycles after the pre-inductive phase were continued after time *Y*). It is therefore clear that 12 days of 16 h photoperiods satisfy the inductive phase in this genotype when grown at a mean temperature of 21 °C. This conclusion is confirmed by the fact that when 10 h days were substituted for 16 h cycles during any part of the period *X* to *Y*, then flowering was delayed (i.e. in treatments **F**, **G** and **H**, or even more dramatically if one compares treatments **R**, **S** and **T** with treatment **Q**).

Although 12 days 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 induction is completed until 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 all these treatments the post-inductive phase (which started at time *Y*) was of almost exactly the same duration—10 days—despite large variations amongst the treatments in the number of 10 h and 16 h cycles given during this final phase. It follows that the post-inductive phase is not affected by photoperiod.

In *Figure 2.7*, the duration of the inductive phase, *i*, can be calculated by subtracting the durations of the pre-emergence phase (5 days), the pre-inductive phase (8 days), and the post-inductive phase (10 days) from the total time taken to flower. From this calculation it can be shown that the inductive phase lasted for 12 days when 16 h photoperiods were applied throughout it; whereas its duration was 105 days in continuous 10 h photoperiods. These values can be applied in an equation, based on Equation 2.8, but in which the temperature can be ignored (since it did not vary between treatments), as follows:

$$1/i = \mathrm{k} + \mathrm{c}''P \tag{2.10}$$

where k and c″ are constants, the values of which were calculated as −0.113491 and 0.012302, respectively, by simultaneous equations.

From these results the base photoperiod, P_b, was calculated (by analogy with Equation 2.6) using the relation $-\mathrm{k}/\mathrm{c}''$, and has a value of 9.23 h. The total number of inductive hours of light, i.e. the photoperiodic time, required to be accumulated above the base photoperiod each day in order to complete the inductive phase, i.e. to induce flowering, is given (by analogy with Equation 2.7) by $1/\mathrm{c}''$ and, in this case, has a value of 81 h.

Having calculated the base photoperiod and the photoperiodic time for flowering, the expected durations of the inductive phase can then be calculated for all the treatments in *Figure 2.7*. For example, in treatment A, where the plants were transferred from 10 h photoperiods to 16 h photoperiods 45 days after sowing, the first 13 days will have occurred during the pre-emergence and pre-inductive phases and so will have no effect, leaving 32 days of 10 h photoperiods which would have been inductive. To calculate their contribution to photoperiodic time, 9.23 h has to be subtracted from the photoperiod experienced each day; thus their total contribution will have been $32 \times (10 - 9.23) = 24.6$ h. Since the photoperiodic time for flowering is 81 h, this leaves 56.4 h to be contributed after transfer of the plants to the 16 h photoperiods. The number of days required to complete induction in this regime is therefore given by $56.4/(16 - 9.23) = 8$ days.

Finally, the total number of days to flower, *f*, is calculated by adding the following components: a pre-emergence phase of 5 days; a pre-inductive phase of 8 days; an inductive phase comprising 32 days of 10 h photoperiods followed by 8 days of 16 h photoperiods, i.e. a total of 40 days; and a post-inductive phase of 10 days. Accordingly, the total calculated time to first flower is 63 days, whereas the observed time was 70 days. It is clear that while there are minor discrepancies between observed and calculated durations to flowering, as in the example just described, the values calculated on this basis are generally very close to those observed (*Figure 2.7*). It is also clear that these simple assumptions also account very adequately for what otherwise would be a rather perplexing distribution of *f* amongst the various treatments as indicated by the histograms.

This evidence suggests that there is no change in photoperiod-sensitivity *per se* during the inductive phase, and that its duration is a simple consequence of the number and duration of the photoperiodic cycles which are required to complete the induction stimulus. Futhermore, similar conclusions may also apply to barley (Roberts *et al.*, 1987).

The development of predictive models for flowering in natural environments

As the example for lentils illustrates, large experiments are needed to quantify the duration of the inductive phase. And so, in order to evaluate the photo-thermal characteristics of flowering in large numbers of genotypes—a common objective in crop breeding—we have suggested a cruder approach based on Equation 2.8 in which the duration of the inductive phase is not separately identified and quantified. In this case, when the analysis of flowering responses in natural environments is based on the whole of the time taken to flower, *f*, instead of on the inductive phase, *i*, we suggest that, in order to avoid confusion, a different terminology is used because the analogous values obtained will be different from the base photoperiod and photoperiodic time as calculated on the basis of the inductive phase. Thus we now recommend the terms 'nominal base photoperiod' and 'nominal photoperiodic time' when calculations are based on the entire period from sowing to flowering.

Calculations show that when Equation 2.8 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. This fact, we suggest, is a plausible explanation for the 'negative base temperatures (which are) not feasible in the physiological sense' which have been calculated for flowering in sunflowers (Goyne *et al.*, 1977) and elsewhere (Arnold, 1959).

We have shown (Roberts *et al.*, 1986a) that when Equation 2.8 applies, the nominal base photoperiod is given by $-(\mathrm{a}' + \mathrm{b}'\overline{T})/\mathrm{c}'$. This value, subtracted from the actual photoperiod experienced in any day will give the contribution of that day to nominal photoperiodic time. And so:

$$l_d = P_d + (\mathrm{a}' + \mathrm{b}'\overline{T}_d)/\mathrm{c}' \tag{2.11}$$

where l_d is the contribution each day to nominal photoperiodic time, P_d is the photoperiod experienced, which is sunrise to sunset in lentils (*see* Summerfield and Roberts, chapter 15), $\overline{T}_d$ is the mean temperature that day, and a′, b′ and c′ are the constants whose values are obtained from Equation 2.8 (Roberts *et al.*, 1986).

It follows from Equations 2.8 and 2.11 that in this case the nominal base photoperiod varies with temperature; but the nominal photoperiodic time which has to be accumulated above this nominal base photoperiod for flowering to occur is given by 1/c′ and thus is independent of temperature. This model has been shown to predict time of flowering with considerable accuracy for spring sowings of lentils at Tel Hadya in Syria and at Leonessa in Italy. It has yet to be tested for winter sowings (which can, in some years, lead to severe frost damage during the vegetative period) and further work is necessary to quantify the effects of vernalization in lentils and other LDPs more accurately.

WHEAT MODELS

Since bread wheat is the most important world crop it is not surprising that many attempts have been made to model the growth and development of this species (e.g. Robertson, 1968; Halsse and Weir, 1970; Porter, 1983; Weir *et al.*, 1984; French and Hodges, 1985; Porter, 1985). Despite these intensive efforts internationally, and the advances that have been made, 'consistent accurate prediction is not yet a reality ... remaining anomalies, which require further experimental work and a better understanding, concern the early stage of crop development' (Porter, 1985). It is not possible here to consider all of these models but, since Equations 2.8 and 2.11 appear to describe the responses common to several LDPs, it is interesting to consider briefly those wheat models which appear to include assumptions which have some similarities with those implicit in these equations.

In order to facilitate comparisons, it is necessary first to point out that Equation 2.11 states the implications of Equation 2.8 in terms of calculating the photoperiodic time in excess of a nominal base photoperiod which is contributed towards the completion of flower induction, and it indicates that the nominal base photoperiod (and not the photoperiodic time required, given by 1/c′) is modified by mean temperature. Furthermore, it is possible to state exactly the same concept in terms of the thermal time required for flowering in excess of a base temperature. Then, it is evident that the base temperature (and not the thermal time required) varies with photoperiod. The expression for calculating the daily contribution to thermal time (which can be used as an alternative to calculating nominal photoperiodic time as in Equation 2.11) is as follows:

$$t_d = \overline{T}_d + (a' + c' P_d)/b' \qquad (2.12)$$

where t_d is the daily contribution to thermal time, $\overline{T}_d$ is the mean temperature that day, and a′, b′ and c′ are the constants for the genotype being considered and which apply in Equation 2.8.

In some wheat models which have been developed on the basis of field data, it is assumed that it is the thermal time in excess of a given constant base temperature which is modified by photoperiod (e.g. Gallagher *et al.*, 1983; Weir *et al.*, 1984). This contrasts with the variation in base temperature according to photoperiod as Equations 2.8 and 2.12 imply. The response described by Equation 2.8 is shown in *Figure 2.5*(*b*) and, more clearly for the present purpose, in *Figure 2.5*(*k*). In contrast with *Figure 2.5*(*k*), the wheat models imply lines of common origin on the abscissa, with slopes that vary according to photoperiod.

While the distinction between the two models may appear fundamental, in practice in field experiments, where mean temperatures for the most part are warmer than the

base temperature and where mean temperature and photoperiod tend to be confounded, it may not be easy to distinguish between the two. To confirm that the assumptions on which the field models of wheat are based are indeed the most appropriate would require factorial experiments in controlled environments.

Epilogue

We would like to end where logically we might have begun—by quoting Bernier *et al.* (1981) who, in the first chapter of their twin-volume work on *The Physiology of Flowering*, point out that, '... despite manifold attempts to achieve a universally accepted system, the measurement of flowering remains as varied as the species under investigation.'

There is no reason, of course, why there should be a single system; the system chosen should be that most appropriate to the purpose of the investigation. However, in their discussion of the various measurement systems that have been used in studies on the environmental control of flowering, it emerges that Bernier *et al.* consider three types have been predominant:

1. Those in which the number of days taken from sowing or emergence are recorded for plants to reach a particular and defined stage in their reproductive development—days to double ridge formation in cereals or to first open flower or anthesis in many dicotyledons are traditional examples.
2. Those where an index of vegetative development prior to flowering is recorded—the number of nodes or leaves below that subtending the first flower being a common example.
3. Treatments in which plants are sampled after specified times and scored according to some arbitary system which depends on the stage of development each replicate has reached.

We believe that for most purposes the last system is the least useful; the second has a number of virtues; but it is the first that is the most useful—hence our exclusive concentration upon it. It is the time taken to flower which is usually of greatest ecological and agricultural interest and which therefore needs to be predicted. But, between measurements of the time taken to flower in experimental treatments and its reliable prediction in various other circumstances, comes analysis and synthesis, and for these intermediate steps we have argued that it is usually helpful if times of development are transformed into rates. Furthermore, when this approach is combined with the concepts of thermal time (e.g. Monteith, 1981) and of photoperiodic time it seems probable that the modelling of crop phenology will be simplified, more reliable, and more biologically plausible. Models which, on the other hand, seek to correlate dates of flowering (or days to flowering, f) with various states of environmental factors such as temperature or photoperiod using formal statistical procedures seem, inevitably, destined towards increasing complexity; these models can become so bulky and unwieldy that, ultimately, they may suffer the same fate as the dinosaurs (Monteith, 1977). Reevaluations of previous efforts to predict the flowering and/or maturity of both soyabeans (e.g. Brown, 1960; Major *et al.*, 1975; and Meyer *et al.*, 1979) and maize crops (e.g. Gilmore and Rogers, 1958; Coligado and Brown, 1975; and Rinne, 1984) in terms of rates of progress towards these events and the concepts of thermal and photoperiodic time might well be fruitful (and *see* Angus *et al.*, 1981a, b).

Finally, two practical applications of the approach advocated here also merit comment. Plant breeders recognize the importance of matching crop phenology to cropping seasons and that an understanding of the environmental and genetic control of development is central to their efforts to improve and stabilize yields (e.g. Wallace, 1985). However, unless phenology can be predicted accurately, then extensive (and expensive) testing of germplasm in different locations is seen as the only practical alternative. Furthermore, in seeking to utilize both exotic and local germplasm in their hybridization programmes, rates of progress can be limited if the flowering of diverse genotypes cannot be synchronized or manipulated (e.g. Hellmers and Burton, 1972). We have described elsewhere in this volume how artificial manipulations of photoperiod using incandescent lamps in the field can help to synchronize (or, if required, to delay) the onset of flowering in LDPs (Summerfield and Roberts, Chapter 15). What is now clear is that a knowledge of response surfaces for flowering (e.g. *Figures 2.4* and *2.5*) can be exploited—by reducing the number of field locations required for evaluating phenological responses to climate (as we have discussed earlier) and to ensure the meaningful genetic analysis of these responses in SDPs and LDPs by evaluating the outcome of hybridization in locations known to lie within particular planes of the overall response surface. When this approach is taken actual or variable rather than mean weather parameters can be converted more simply to phenological statistics. Practical utility demands both simplicity and a proven ability to anticipate biological events (Waggoner, 1974).

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3

MEASUREMENT AND PREDICTION OF FLOWERING IN CLONAL PLANTS

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Introduction

The fundamental mechanisms of the flowering process have remained extremely intractable, despite an immense amount of research effort (Bernier, Kinet and Sachs, 1981a, b; Kinet, Sachs and Bernier, 1985). The problem discloses itself in the apparently bewildering diversity of flowering responses to variations in the environment of plants. Investigators naturally have tended to seek out and concentrate on the simplest model systems available. We know most about the responses of a small and eccentric group of species that is not even representative of herbaceous plants: experimental subjects are predominantly annuals, with more or less determinate growth and rapidly satisfied inductive requirements (Schwabe, 1971). The responses in question are mainly those of isolated individuals to straightforward combinations of conditions in otherwise static, controlled environments.

Many plant species, including certain important crops, exist as clones of reiterated modules with varying degrees of physiological integration and varying longevity. Modular clonal growth is essentially indeterminate in nature and raises conceptual and practical problems for both the measurement and prediction of flowering. Measurements are confounded because flowering is at the same time a property of the genetic individuals (genets) and their component clonal modules (ramets): prediction, on the other hand, requires knowledge of the often quite distinct influences on flowering attributable to ramet and genet levels of organization. Prediction of flowering in natural communities or crops implies an understanding of the possibly overriding influences of neighbouring individuals (of both the same and different species), herbivores, mycorrhizal symbionts and parasites. It also involves responses to field environments, with their continually changing combinations of conditions. Protracted conditioning may be required in the field to induce, evoke and allow development of inflorescences. The outcome is often dramatic, unexplained variations in flowering from year to year, and from population to population (Schemske *et al.*, 1978; Wells, 1981; Inghe and Tamm, 1985).

The purpose of this chapter is to address the issues raised by clonal plants, particularly as they behave in the field. Work is described for two herbaceous species that have contrasting variations on a very common growth form: initiation of an inflorescence terminates the main axis of the semelparous (monocarpic) module, and clonal growth proceeds sympodially from axillary buds. One, *Deschampsia cespitosa*, is a grass that forms densely packed tussocks of tillers interconnected by very short