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Use Of Field Observations To Characterise Genotypic Flowering Responses To Photoperiod And Temperature: a Soyabean Exemplar

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Abstract Thirty-nine accessions of soyabean [*Glycine max* (L.) Merrill] and 1 of wild annual soyabean (*Glycine soja* L.) were sown at two sites in Taiwan in 1989 and 1990 and on six occasions during 1990 at one site in Queensland, Australia. On two of the occasions in Australia additional treatments extended natural daylengths by 0.5 h and 2 h. The number of days from sowing for the first flower to appear on 50% of the plants in each treatment was recorded (f), and from these values the rate of progress towards flowering ($1/f$) was related to temperature and photoperiod. In photoperiod-insensitive accessions it was confirmed that the rate is linearly related to temperature at least up to about 29°C. In photoperiod-sensitive genotypes this is also the case in shorter daylengths but when the critical photoperiod (P_c) is exceeded flowering is delayed. This delay increases with photoperiod until a ceiling photoperiod (P_{ce}) is reached. Between P_c and P_{ce}, $1/f$ is linearly related to both temperature (positive) and photoperiod (negative), but in photoperiods longer than P_{ce} there is no further response to either factor. The resulting triple-intersecting-plane response surface can be defined by six genetically-determined coefficients, the values of which are environment-independent but predict time to flower in any environment, and thus quantify the genotype×environment interaction. By this means the field data were used to characterise the photothermal responses of all 40 accessions. The outcome of this characterisation in conjunction with an analysis of the world-wide range of photothermal environments in which soyabean crops are grown lead to the following conclusions: (1) photoperiod-insensitivity is essential in soyabean crops in temperate latitudes, but such genotypes flower too rapidly for satisfactory yields in the tropics; (2) photoperiod-sensitivity appears to be essential to delay flowering sufficiently to allow adequate biomass accumulation in the warm climates of the tropics; (3) contrary to a widely held view, some degree of photoperiod-sensitivity is also needed in the tropics if crop-duration homeostasis is required where there is variation in sowing dates (this is achieved through a photoperiod-controlled delay in flowering which counteracts the seasonal increase in temperature that is correlated with increase in daylength); and (4) a greater degree of photoperiod-sensitivity is necessary to provide maturity-date homeostasis for variable sowing dates – a valuable attribute in regions of uncertain rainfall. Since the triple-intersecting-plane response model used here also applies to other species, the use of field data to characterise the photothermal responses of other crops is discussed briefly.

Key words Soyabean · *Glycine max* · Flowering · Photoperiod · Temperature

Introduction

Four main types of information are used in describing accessions in germplasm collections: passport (e.g. systematics information and provenance), management (e.g. storage locations, quantity, date and percentage seed viability when last monitored), characterisation (e.g. highly heritable characters independent of the environment such as taxonomic descriptors) and evaluation (e.g. inherited agronomic qualities, the expression of which is largely environment-dependent, such as disease resistance and crop duration).

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The latter category, evaluation information, is typically the most important to breeders and agronomists and is vital to farmers, and one of the most important items in this category is the time taken to flower. Indeed, this information is crucial in harsh environments, not only because flowering is a vulnerable stage of development but because it is also a major factor affecting variation in crop duration (time to maturity). The duration has to be sufficiently long to allow the crops to accumulate enough photosynthate for adequate yields but at the same time short enough to fit the growing season available. For example, in their review of strategies for improving yields in water-limited environments, Ludlow and Muchow (1990) listed up to 11 traits in order of priority in sorghum (*Sorghum vulgare*) and maize (*Zea mays*) for both modern ('opportunistic') and subsistence ('conservative') agriculture – each agricultural type being further split for conditions of intermittent or terminal stress. In all four cases the top priority was 'matching phenology to water supply'. Lawn and Imrie (1993) in a more general review expressed a similar view: 'The key aim is to optimise productivity by matching the ontogeny to the weather resources of the environment (e.g. duration of favourable temperature or water supply) and, where unfavourable extremes are unavoidable, to minimise their coincidence with more vulnerable stages. Not surprisingly therefore phenology is the most important single factor influencing genotypic adaptation.' Richards et al. (1993) also reached a similar conclusion: 'The development of an appropriate phenology by genetic modification so that the duration of the vegetative and reproductive periods are matched as well as possible with the expected water supply, or with crop hazards, is usually responsible for the most significant improvements in crop yield'. Descriptors relating to time of flowering or crop duration are therefore important but, despite this, the descriptor states are typically vague (e.g. early, late, very late and so on) or more accurate (e.g. 150 days crop duration) but then only valid over a limited geographical range and for a given sowing date. This is because of the common occurrence of strong genotype × environment interactions.

Dr. C. Chapman (personal communication 1987) made the perceptive suggestion that the type of photothermal model for predicting flowering which had been developed at Reading (Hadley et al. 1983; Roberts and Summerfield 1987; Summerfield et al. 1991) provided the basis for transforming location-specific evaluation information on the time taken to flower into accurate characterisation descriptors of wide application. This was because all the coefficients of the model are genotype-specific and independent of the environment. At the same time they account for the genotype × environment interaction so that the resulting phenotypic response – in this case the number of days from sowing to flower – could be predicted in any environment. The model had been developed in artificial controlled environments, but it has now been shown that the genotype-specific coefficients can be determined from observations in a number of different field environments and that the coefficients thus determined can predict phenotypic behaviour in other natural environments (Summerfield et al. 1993). This paper reports an investigation in which the genotype-specific constants of the photothermal model were estimated from observations in different field environments and compared among 40 different accessions of soyabean (*Glycine max*). The significance of these responses is then deduced by analysing the consequences in the context of the world-wide range of photothermal environments in which soyabeans are grown.

Materials and methods

Field experiments

Soyabean was chosen for investigation because of its use in a wide range of climates following its spread from early domestication in N.E. China between about 1700 and 1100 B.C. Thirty-nine genotypes of this species and 1 accession of the closely related wild species *Glycine soja* (Hymowitz and Bernard 1991) were selected to represent a broad range of adaptation and responses to photoperiod and temperature (Table 1). All 40 accessions were sown at Kaohsiung and Shanhua in Taiwan in 1989 and 1990, and six sowings were also made at the Cooper Laboratory, Lawes, Queensland, Australia in 1990. In two of the sowings at Lawes additional treatments were included in which the natural daylength was extended by either 0.5 h or 2 h by tungsten incandescent lights. The lamps (150 w) were suspended 1.5 m above the ground 1.5 m apart on a square grid giving an illuminance at ground level well above 100 lux, and so well above the value that saturates the photoperiod response of soyabean (Summerfield and Roberts 1987). In addition, for 12 of the accessions supplementary data from a previous investigation (Summerfield et al. 1993) have been included in the analyses. These accesssions are noted in Table 1 and can be identified in Table 2 since they are the only ones where $n \geq 21$. The additional information was obtained from field experiments in Australia in the following Australian locations: Katherine Research Station, Northern Territory; Kimberley Research Station, Kununurra, Western Australia; Lansdown Pasture Research Station, Townsville, Queensland; Hermitage Research Station, Warwick, Queensland; the Victorian Crops Research Institute, Horsham, Victoria.

Daily photoperiods (hd^{-1}) inclusive of civil twilight were calculated throughout the pre-flowering periods (from sowing) of all genotypes for all locations and sowing dates. Daily maximum and minimum temperatures were recorded in Stevenson screens close to the experimental plots. Two replicate rows 1.5 m long and 1.0 m apart were sown and thinned to give a spacing of approximately 10 cm between plants within the rows. Treating each row of each genotype separately, we recorded the dates by which 50% of plants had an open flower (corolla colour visible). Further details of sites, environments, culture and husbandry are given by Summerfield et al. (1993).

The photothermal model and its application

The triple-plane model was first developed from experiments in controlled environments on cowpea [*Vigna unguiculata* (L.) Walp.] (Hadley et al. 1983) and soyabean (Hadley et al. 1984a). It has subsequently been refined and applied to several species and to results from field environments (Lawn et al. 1995) including soyabean (Summerfield et al. 1993). The model is described in detail by Summerfield et al. (1991), and so only the essentials will be outlined here.

A fundamental feature of the model is that it is based on the finding that flowering responses to photoperiod and temperature are independent of each other and linear over wide defined ranges of conditions – providing the response is considered as the rate of progress towards flowering, i.e. the reciprocal of the time taken from sowing to flower. Providing temperatures are not supra-optimal, the combined response to photoperiod and temperature may be defined by a triple-intersecting-plane response surface (Fig. 1). In the case of pho-

Table 1 The 40 accessions of soyabean investigated ranked in order of increasing delay to flowering in tropical environments (see text)

Rank	Accession name (synonyms in brackets)[a]	Provenance	Ancestry	Reported adaptation	Maturity group
1	Fiskeby V[b] (CPI 68630)	Sweden	Japanese	Cool temperate summers, long days	00
2	Shinsei (CPI 120597, G2502)	Japan via AVRDC Taiwan	Tokachi Nagaha × Kamishunbetsu Zairai	Suited to spring sowing in Taiwan	000
3	AGS 292 (CPI 120603, Kaohsiung #1 G10499)	Japan via AVRDC Taiwan	Selection from Chiu Tzu Tao	Vegetable soyabean. Selected in all seasons in Taiwan for wide adaptability	II
4	PI 194647 (CPI 120595, G215)	Sweden via AVRDC Taiwan	Pagoda (2) × Fiskeby III	Cool temperate summers, long days	00
5	Farrer (CQ 3183)	New South Wales, Australia	Williams (MG III) × Calland (MG III)	Northern New South Wales around 30°S. Early maturity to avoid drought. Adapted to wide range of sowing dates	V
6	PI 248407 (CPI 120598, G1322)	Yugoslavia via AVRDC, Taiwan	From population Sremska Mitrovica	Long days in Yugoslavia	I
7	Talien Tou (CPI 121098, G9951)	AVRDC, Taiwan		Suitable for all seasons in Taiwan	
8	Clark 63 (CPI 69617)	Illinois, USA	(Clark(7) × CNS) × (Clark(6) × Blackhawk)	About 37°–41°N in USA	IV
9	Valder (CQ 3182)	New South Wales, Australia	Williams (MG III) × Calland (MG III) (cf Farrer)	Same as for Farrer	IV
10	Tidar (CPI 120599, AGS 314)	AVRDC, Taiwan	Irradiation mutant derived from G2120	Suitable for all seasons in Taiwan	IV
11	AGS 129 (CPS120600, Kaohsiung #1)	AVRDC, Taiwan	Shih Shih × SRF 400	Selected in Taiwan for wide adaptability	V
12	AGS 73 (CPI 120601)	AVRDC, Taiwan	PI 189876 × CH-2	Selected for wide adaptability	
13	Hill[b] (CQ 3301)	USA	(Dunfield × Haberlandt) × Lee sib	Warm-temperate to sub-tropical summer about 36°N in USA (reputed not to detect cool-white fluorescent lights for flowering)	V
14	Davis[b] (CPI 93922, G3898)	USA	(Roanoke × [Ogden × CNS]) × (Ralsoy × Ogden)	Warm-temperate to sub-tropical summer about 34° N in USA	VI
15	CPI 26671[b]	USA via Morocco		Warm temperate. About 40°N in USA	III
16	SJ 2 (CPI 69090, G2573)	Thailand		Monsoon dry season (Nov-April)	VIII
17	Bossier (CPI 110303)	Southern USA via Chile and Nigeria	A late mutant selected from Lee (MG VI)	Southern USA c. 30°N	VII
18	66-G-3 (CPI 69614, G20)	Taiwan		Selected in spring, summer and autumn sowings in Taiwan for wide adaptability	
19	SJ 4 (CPI 93917)	Thailand	Acadian (MG VIII) × Tainung 4	Monsoon dry season (Nov-April) selected for reduced photoperiod-sensitivity	
20	Buchanan[b] (CQ 2479)	Tropical Australia	Ogden (MG VI) × Wills (MG VIII)	Summer wet season. December sowing in Ord Irrigation Area about 15°S. 'Early tropical'	VIII
21	Chiangmai 60 (CPI 89169, Line7508)	Thailand	Williams × SJ4 Selected in Thailand	Mainly monsoon dry season (Nov-April)	VIII
22	Nakhon Sawan #1 (OCB,CPI 104272)	Thailand	Doteung × Santamaria	Selected as short-duration relay crop about latitude 15° N	VI
23	BM (CPI 93901B)	Mexico			

Table 1 Continued

Rank	Accession name (synonyms in brackets)[a]	Provenance	Ancestry	Reported adaptation	Maturity group
24	Fitzroy (CQ 2448, P25)	University of Queensland, Australia	Wills × Semstar	South-east Queensland. Best adapted to about 22° S, summer crop	VIII
25	UFV-1[b] (CPI 104461, UFV-72-1)	Minas Gerais, Brazil	Later maturing mutant from Viçoja	15°–20°S in Brazil	VIII–X
26	G8[b] (CPI 32899)	East Asia via Stoneville Miss., USA	Line rescued by R. J. Lawn from aged seed in Cunningham Laboratory	*Glycine soja* (wild annual soyabean). Produces viable hybrids with *G. max*	
27	Biloxi[b] (PI 23211)	Southern USA	Selection from Tsze Pi Tou from Tangxi, Zhejiang (30°N) China in 1908	Released 1918 in USA. Used in early experiments on photoperiodism	VIII
28	Jupiter[b] (CPI 80168)	Selected in southern USA and Puerto Rico (18°N)	Lee sib × Bilomani #3. (Bilomani has 'long juvenile' trait, but Jupiter may not)	Southern USA and Guyana	IX
29	Co 1 (CPI 120602)	AVRDC Taiwan	Originated in India	Autumn in AVRDC	
30	P44 (CQ 2632)	Queensland, Australia	Wills × Semstar	Selected in tropical and sub-tropical Queensland -not released.	VI
31	Canapolis (CQ 2632)	Brazil	D49-722 × Improved Pelican (MG VIII)	Released in North Queensland, 18°–20°S	VII
32	Ross (CQ 2370)	Queensland, Australia	Avoyelles (MG VIII) × Mamloxi (MG VIII)	Grown in tropical Australia. (A cultivar of the same name listed in the USA and Canada has a different pedigree)	
33	Indo 243 (CPI 110301, TGM 737)	Indonesia via Nigeria		Seeds have good storability	VII
34	CPI 104521[b]	Florida, USA	Foster (2) × (Forrest × D77-12480). D77-12480 is a source of 'long juvenile' gene	Selected in S. E. Queensland from F_3 population from Florida	X
35	Durack (CQ 2516)	Queensland, Australia	K8 × Daintree	Released in Ord Irrigation Area about 15°S for summer wet season	IX
36	K8 (CQ 2373)	Queensland, Australia	Sib of Ross	Very late: adapted to low latitudes (<14°S). Not released	X
37	Bossier Late (CQ 2660)		Rogue in Bossier	Adapted to about 15°S. Later than Bossier	
38	G2120[b] AGS #2, (CPI 104462)	Taiwan	Selection from small green-seeded landrace from Indonesia	'Relatively late to flower and sensitive to photoperiod'	VIII
39	Tropical (G12357, CPI 120596)	Brazil	Hampton × (Hill × Bilomani #3). Bilomani is the source of 'long juvenile' trait.	Selected in equatorial environment latitude (0°–15°S)	X
40	CPI 70242[b]	Indonesia	Small-seeded landrace collected by R. J. Lawn in East Java for long duration	Traditionally sown at end of wet season after rice and grown into the dry season on residual soil water	IX

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[a] AGS, AVRDC *Glycine* selection number; CPI, Commonwealth Plant Introduction number; CQ, CSIRO Cunningham Laboratory number; G, AVRDC *Glycine* accession number; PI, USDA Plant Introduction number

[b] These genotypes were also included in previous years' sowings (1986–1988) at six sites in Australia (Summerfield et al. 1993), and results for those sowings are also included in the models presented here

Table 2 Parameters of Eqs. 1–3 for 40 genotypes of soyabean estimated by analysing results from field trials in Australia and Taiwan

Rank	Genotype	Thermal response plane			Photothermal response plane				Maximum flowering delay plane	Overall model		
		a (SE) × 1000	*b* (SE) × 1000	R^2 (*n*)	*a′* (SE) × 1000	*b′* (SE) × 1000	*c′* (SE) × 1000	R^2 (*n*)	(1/*d′*), days (*n*; SE)	R^2	SE	*n*
1	Fiskeby V	–9.93 (2.23)	1.804 (0.103)	0.91 (30)	–	–	–	–	–	0.88	1.30	30
2	Shinsei	–7.34 (5.69)	1.622 (0.241)	0.83 (10)	–	–	–	–	–	0.81	0.94	10
3	AGS 292	–8.93 (4.70)	1.688 (0.196)	0.91 (8)	–	–	–	–	–	0.92	0.68	8
4	PI 194647	–11.12 (6.0)	1.759 (0.256)	0.84 (10)	–	–	–	–	–	0.85	0.81	10
5	Farrer	–11.90 (5.06)	1.740 (0.214)	0.88 (10)	–	–	–	–	–	0.82	1.04	10
6	PI 248407	–16.24 (8.38)	1.875 (0.354)	0.75 (10)	–	–	–	–	–	0.78	1.33	10
7	TalienTou	–	–	–	32.34 (12.80)	1.090 (0.269)	–2.026 (0.751)	0.74 (10)	–	0.84	0.77	10
8	Clark 63	–	–	–	13.80 (14.29)	1.507 (0.310)	–1.423 (0.831)	0.76 (10)	–	0.82	1.07	10
9	Valder	–	–	–	16.56 (13.07)	1.580 (0.298)	–1.882 (0.745)	0.81 (10)	–	0.87	1.06	10
10	Tidar	–	–	–	14.29 (8.14)	1.237 (0.207)	–1.660 (0.439)	0.86 (10)	–	0.92	0.94	10
11	AGS 129	–25.03 (9.113)	2.298 (0.391)	0.94 (3)	52.74 (17.06)	1.378 (0.377)	–4.537 (0.905)	0.89 (7)	–	0.96	0.99	10
12	AGS 73	–20.44 (9.978)	1.854 (0.430)	0.90 (3)	38.23 (9.37)	1.350 (0.227)	–3.692 (0.502)	0.94 (7)	–	0.98	0.78	10
13	Hill	–13.87 (2.54)	1.714 (0.123)	0.94 (14)	65.53 (18.70)	1.112 (0.254)	–5.151 (1.090)	0.82 (16)	–	0.77	2.60	30
14	Davis	–14.92 (2.57)	1.766 (0.134)	0.94 (12)	50.29 (7.03)	1.429 (0.126)	–4.633 (0.392)	0.96 (19)	–	0.70	4.20	31
15	CPI 26671	–11.84 (3.67)	1.652 (0.174)	0.88 (13)	76.52 (12.80)	1.354 (0.176)	–6.298 (0.809)	0.92 (13)	160 (3;3.0)	0.98	0.90	29
16	SJ 2	–22.09 (9.11)	2.164 (0.391)	0.94 (3)	93.81 (28.87)	0.803 (0.784)	–6.644 (1.518)	0.84 (7)	–	0.85	3.47	10
17	Bossier	–16.44 (3.03)	1.766 (0.130)	0.99 (3)	73.10 (16.50)	0.598 (0.399)	–4.961 (0.839)	0.87 (7)	–	0.95	1.60	10
18	66-G-3	–21.98 (2.70)	1.963 (0.116)	0.99 (3)	56.36 (11.80)	1.051 (0.298)	–4.541 (0.633)	0.92 (7)	–	0.95	1.55	10
19	SJ 4	–	–	–	72.29 (13.34)	1.969 (0.403)	–7.334 (0.994)	0.83 (9)	153 (1)	0.99	1.24	10
20	Buchanan	–22.31 (3.06)	2.130 (0.145)	0.95 (13)	143.70 (22.80)	1.176 (0.360)	–11.060 (1.570)	0.84 (11)	156 (5;9.8)	0.95	1.90	29
21	Chiangmai 60	–20.80 (10.15)	1.933 (0.438)	0.90 (3)	73.99 (17.09)	1.252 (0.504)	– 6.168 (0.949)	0.88 (7)	–	0.95	3.00	10
22	Nakhon Sawan #1	–23.23 (10.03)	2.024 (0.430)	0.92 (3)	66.19 (6.89)	1.053 (0.191)	– 5.284 (0.356)	0.98 (7)	–	0.94	2.33	10
23	BM	–	–	–	71.13 (6.79)	2.102 (0.446)	–7.629 (1.145)	0.94 (5)	212 (1)	0.99	0.89	6
24	Fitzroy	–	–	–	119.40 (19.45)	0.843 (0.582)	–8.724 (1.447)	0.81 (9)	216 (1)	0.99	1.40	10
25	UFV-1	–18.12 (2.54)	1.860 (0.111)	0.96 (13)	123.40 (17.8)	0.799 (0.225)	–9.137 (1.180)	0.87 (12)	178 (4;11.1)	0.91	2.80	29

Table 2 Continued

Rank	Genotype	Thermal response plane			Photothermal response plane				Maximum flowering delay plane	Overall model		
		a (SE) × 1000	b (SE) × 1000	R^2 (n)	a' (SE) × 1000	b' (SE) × 1000	c' (SE) × 1000	R^2 (n)	($1/d'$), days (n; SE)	R^2	SE	n
26	G8	–16.56 (8.27)	1.893 (0.421)	0.73 (8)	126.90 (21.8)	0.006 (0.043)	–7.859 (1.130)	0.81 (13)	–	0.87	4.40	21
27	Biloxi	–15.94 (0.31)	1.622 (0.143)	0.90 (15)	143.70 (44.2)	1.021 (0.189)	–10.890 (3.030)	0.86 (9)	200 (4;17.3)	0.92	2.80	28
28	Jupiter	–18.62 (5.52)	1.751 (0.258)	0.76 (15)	163.00 (29.10)	1.024 (0.226)	–12.480 (2.11)	0.83 (10)	221 (4;7.3)	0.96	2.20	29
29	Co 1	–	–	–	68.31 (6.41)	1.498 (0.206)	–6.440 (4.809)	0.96 (9)	227 (1)	0.99	0.95	10
30	P44	–	–	–	109.30 (14.93)	0.608 (0.480)	–7.818 (1.108)	0.86 (9)	234 (1)	0.98	2.73	10
31	Canapolis	–	–	–	106.20 (14.93)	1.331 (0.468)	–8.854 (1.122)	0.88 (9)	231 (1)	0.98	2.41	10
32	Ross	–	–	–	108.90 (13.45)	1.29 (0.423)	–9.057 (1.031)	0.90 (9)	–	0.88	3.19	9
33	Indo 243	–	–	–	84.00 (8.237)	1.716 (0.292)	–8.134 (0.795)	0.94 (8)	242 (1)	0.97	3.43	9
34	CPI 104521	–	–	–	36.89 (3.87)	1.617 (0.120)	–4.517 (0.120)	0.92 (19)	137 (3;6.0)	0.96	1.40	22
35	Durack	–	–	–	91.68 (7.367)	1.263 (0.247)	–7.899 (0.579)	0.96 (9)	227 (1)	0.98	2.83	10
36	K8	–	–	–	109.80 (10.89)	1.081 (0.351)	–8.919 (0.850)	0.93 (9)	234 (1)	0.97	3.57	10
37	Bossier Late	–	–	–	64.17 (8.29)	1.427 (0.282)	–6.145 (0.667)	0.91 (9)	160 (1)	0.98	1.53	10
38	G 2120	–	–	–	33.19 (4.91)	1.206 (0.125)	–3.565 (0.419)	0.84 (23)	215 (5;16.9)	0.89	3.80	28
39	Tropical	–	–	–	49.32 (12.98)	1.535 (0.525)	–5.401 (0.674)	0.91 (7)	236 (1)	0.99	2.27	8
40	CPI 70242	–22.84 (6.99)	1.822 (0.356)	0.78 (7)	47.33 (5.13)	0.826 (0.100)	–3.874 (0.330)	0.94 (17)	212 (3;12.7)	0.96	2.00	27

toperiod-insensitive cultivars (i.e. day-neutral plants), only temperature affects the rate and so one plane is sufficient to describe this response. This plane also describes the response of photoperiod-sensitive genotypes when their photoperiod-sensitivity genes are not expressed, i.e. when the daylength is shorter than the critical photoperiod. In short-day plants (SDP) such as soyabean, when the critical photoperiod is exceeded, flowering is delayed and the rate of progress towards flowering is then a negative linear function of photoperiod but there is often still also a positive linear response to temperature. Both responses are independent and so no interaction term is needed within this plane. Finally, if the photoperiod is further increased to the ceiling photoperiod, P_{ce}, and beyond, another plane of maximum photoperiodic delay is exposed where, in soyabean at least, neither further increase in photoperiod nor variation in temperature have any further effect on the time of flowering.

Accordingly, the entire response surface (Fig. 1) may be described at sub-optimal temperatures by three equations that define each of the three planes, i.e. the thermal plane

$$1/f = a + bT \tag{1}$$

the photothermal plane

$$1/f = a' + b'T + c'P \tag{2}$$

and the plane of maximum photoperiod delay

$$1/f = d' \tag{3}$$

where f is the number of days from sowing to first flower, T is the mean pre-flowering temperature (°C), P is the mean pre-flowering photoperiod (hd^{-1}) and a, b, a', b', c' and d' are genotype-specific coefficients.

These coefficients also indirectly determine where the planes intersect with each other, i.e. the boundaries between them. One of the important boundaries is the critical photoperiod, P_c, which is defined by

$$P_c = [a - a' + T(b - b')]/c' \tag{4}$$

which gives, for any temperature, the critical photoperiod above which in SDP photoperiod-sensitivity genes are expressed and thereby delay flowering. The second significant boundary, the ceiling photoperiod, P_{ce}, is given by

$$P_{ce} = [d' - (a' + b'T)]/c' \tag{5}$$

which defines, for any temperature, the photoperiod above which further increases cause no additional delay.

Two other boundaries need mentioning, although these are not frequently reached under natural conditions. The base temperature,

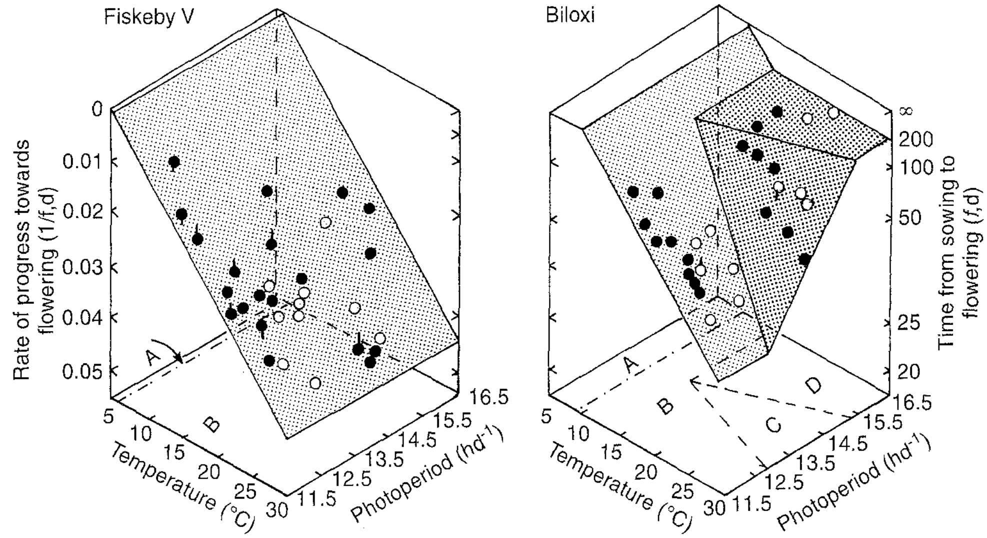


Fig. 1 Effects of photoperiod and temperature on the rate of progress from sowing towards first flowering (*left vertical scale*; transformed to days to flower on *right vertical scale*) in soyabean cultivars, 'Fiskeby V' (photoperiod-insensitive) and 'Biloxi' (photoperiod-sensitive). Results from six contrasting sites in Australia from 1986 to 1988 (●) and one in Australia and two in Taiwan in 1989–1990 (○). *Vertical lines* indicate deviations from fitted planes. Projection of the boundaries between response planes to the base (*broken lines*) show four environmental domains where progress towards flowering is *A* impossible (too cool), *B* solely temperature-dependent, *C* dependent on both photoperiod and temperature, and *D* maximally delayed by photoperiod and unresponsive to variation in either photoperiod or temperature. The fitted planes are quantified in Table 2. The boundaries between the domains are defined by T_b (between A and B), P_c (between B and C), T_p (between B and D) and P_{ce} (between C and D): see text for further explanation. (From Summerfield et al. 1993.)

T_b, is that temperature at and below which flowering is impossible since the rate of progress towards flowering is zero. It is given by

$$T_b = -a/b \tag{6}$$

Finally T_p is the lower temperature limit for the expression of photoperiodic delays. At this boundary, the delay due to temperature equals that due to photoperiod. It is given by

$$T_p = (d' - a)/b \tag{7}$$

The model comprising these three planes and four boundaries is illustrated for the photoperiod-sensitive cultivar 'Biloxi' (a classic subject for photoperiodic studies) in Fig. 1. The boundaries have been vertically projected to the base area in Fig. 1 to illustrate four domains of photothermal environments in which (A) it is too cool for any development towards flowering, (B) where the rate is dependent solely on temperature, (C) where it is dependent on both photoperiod and temperature acting independently and (D) where there is maximum delay due to photoperiod and within which variation in neither photoperiod nor temperature has any effect. Figure 1 also shows an example of a photoperiod-insensitive cultivar, 'Fiskeby 5'. In this case no flowering delay is caused by photoperiod, and so the responses are confined to the two domains (A and B).

Estimation of genotypic coefficients

If a genotype is photoperiod-insensitive, and providing maximum daily mean temperatures do not exceed the optimal value for a significant number of days by a large margin, then Eq. 1 is sufficient to describe the response. If a genotype is photoperiod-sensitive then, depending on how wide a range of photoperiods is considered, up to three planes may be required – Eqs. 1, 2 and 3, but in some cases the range of environments under investigation may not expose more than one or two planes.

Analysis of data

The approach to analysing the field data was to use an iterative least-squares minimisation routine in conjunction within GENSTAT (Genstat V Committee 1987) in which the effects of T and P on $1/f$ were tested by an increasingly complex set of sub-models, starting with Eq. 1. At any given stage, a more complex sub-model comprising Eq. 2, Eqs. 1+2, Eqs. 2+3 or Eqs. 1+2+3 was only accepted if it significantly ($P<0.05$) reduced the residual deviance for the dependent variable $1/f$. The method is described in detail by Summerfield et al. (1993). A computer programme for undertaking the task has now been developed (Watkinson et al. 1994).

Results and discussion

The coefficients applicable in Eqs. 1, 2 and 3 to each of the 40 accessions were estimated from the observations made in all field trials and are shown in Table 2. In the photoperiod-insensitive lines Eq. 1, the thermal plane, was sufficient to describe the overall response (accessions 1–6 in Table 2). All other genotypes were photoperiod-sensitive, and so flowering was delayed in daylengths longer than the critical photoperiod. Accordingly Eq. 2 or some combination of equations always including Eq. 2 were required in these cases to describe the responses adequately (accessions 7–40 in Table 2).

Before relating these responses to problems of crop adaptation it is necessary to consider the photothermal environments where soyabeans are cultivated. Fergusson (1952) devised a graphical system of photothermographs for describing climates with respect to the main factors that affect plant development, photoperiod and temperature. This system employs a grid formed by one axis for photoperiod and another for temperature. On this grid a continuous line is formed by joining points representing the

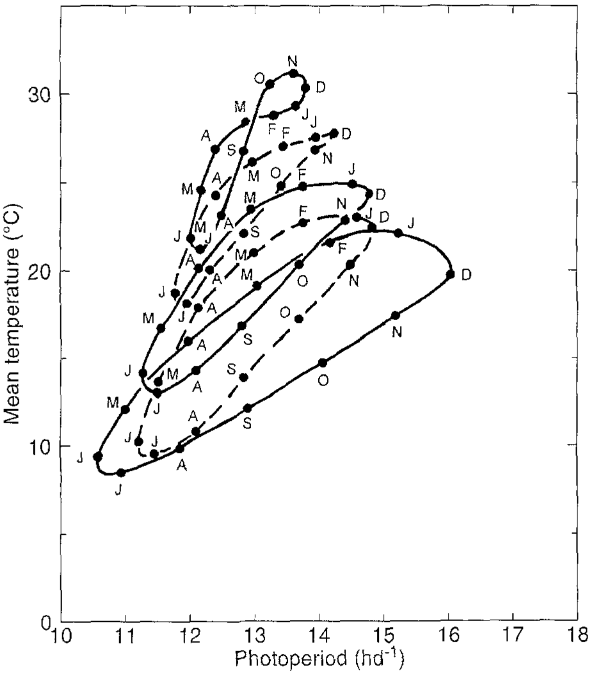


Fig. 2 Complete photothermographs describing the photothermal climates of five of the sites in Australia used to generate some of the data on times taken from sowing to flowering. Each point represents the mean temperature for the month indicated and the photoperiod (sunrise to sunset plus civil twilight) for the 21st day of that month. From *top* to *bottom*: Katherine, NT (14°28′), Lansdown, Qld (19°40′S), Lawes, Qld (27°33′S), Hermitage, Qld (28°13′S), Horsham, Vic. (36°43′S)

monthly mean values of photoperiod and mean diurnal temperature. In our version the photoperiod for each month is represented by the daylength (sunrise to sunset) plus civil twilight (sun 6° below the horizon); thus the beginning and end of the photoperiod is marked by an illuminance of approximately 4 lux [see Summerfield and Roberts (1987) for a justification of this value]. The photoperiod on the 21st day of each month is chosen as representative since the complete photothermograph then includes in the display the longest and shortest days in the year. Various climates described in this way are illustrated by Roberts et al. (1993, 1996) where they are discussed in relation to soyabean development. Figure 2 shows some examples of photothermographs for five of the seven experimental sites referred to under the Materials and methods. A modified version of this type of photothermograph has also been used by Lawn et al. (1995).

Three-dimensional topography can be represented by contour maps. Likewise the three-dimensional graph for cv ‘Biloxi’ shown in Fig. 1 can be translated to an isochrone chart in which the isochrones are analogous to contour lines (Fig. 3). Each isochrone represents the number of days taken to flower if a plant were maintained continuously in that combination of photoperiod and temperature. Figure 3 also shows another example for cv ‘Hill’. Both isochrone charts have been superimposed with photothermographs for Chicago, Illinois; Nashville, Tennessee; and Mobile, Alabama.

These combined photothermograph and isochrone charts enable the developmental process of flowering to be analysed and related to natural photothermal environments. So, for example, cv ‘Biloxi’ is classified as Maturity Group VIII and is suitable for climates in the USA represented by the photothermograph for Mobile (30°N), whereas cv ‘Hill’ is classified as Maturity Group V and is adapted to climates represented by Nashville (36°N). Chicago (42°N) is suitable for cultivars of Maturity Group II and therefore suitable for neither ‘Biloxi’ nor ‘Hill’.

Notice that if ‘Biloxi’ were sown in mid-May in Chicago the conditions at that time would be in the domain D where maximum photoperiodic delay is observed – and if a crop were maintained in such conditions it would not flower for 200 days. These conditions would continue until almost mid-August. Thus after the first 3 months the crop would have progressed by about 3x30/200 days towards flowering, i.e. about 45% of the way. Conditions would then become less inhibitory until early September, but then more inhibitory again. However, from mid-August to mid-September the average conditions would suggest about 70 days would be required to flower of which 30 days would be experienced, i.e. the crop would have progressed another 30/70=43% of the way towards flowering and the accumulated progress by mid-September would be 88% of the way towards flowering. Continuing with similar arguments it would be seen that the crop might flower towards the end of September (if not frosted) but now too late in the season to ripen.

In contrast if ‘Biloxi’ were sown near Mobile in mid-May it will be seen that by mid-July it will have progressed about 70% of the way towards flowering and should flower soon afterwards. On the other hand ‘Hill’, which is adapted to about 36°N in North America, would flower prematurely near Mobile but too late near Chicago.

In the present investigation we used photothermographs to examine a large number of climates in which soyabeans are cultivated. When this was done it was found that all of them fall within a range of environments described by a roughly triangular area marked in Fig. 4. Natural growing seasons are normally limited by cool temperatures in temperate latitudes and often by water shortage in the dry season in sub-tropical and tropical latitudes. Lack of water, however, can be overcome in certain circumstances by irrigation, e.g. in Thailand where about one-half of the soyabean production area is sown in the dry season in December and harvested in April. The triangular area encompasses the whole of the thermographs in the tropics and sub-tropics, and thus includes conditions experienced during off-season production in warm climates. Little can be done about overcoming cool temperatures and so winter production is not feasible in latitudes greater than about 25°; and so the triangle only includes those warmer months for the thermographs in higher latitudes during which soyabean growth is feasible.

There is one limitation not fully accounted for in the triangle that describes the range of photothermal climates for soyabean. Although the optimum mean temperature for rate of development in soyabean must be at least 29°C

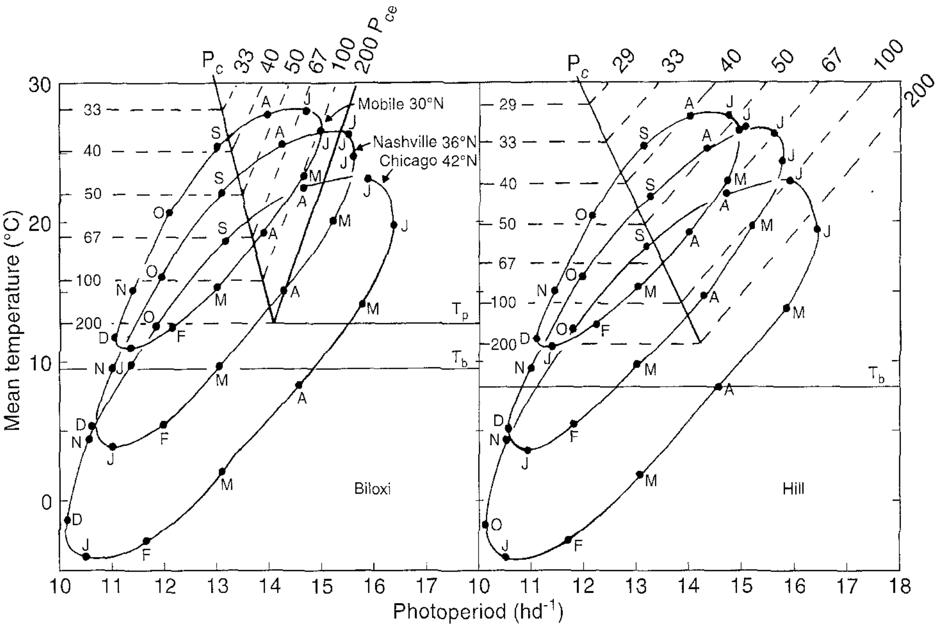


Fig. 3 Isochrone charts of flowering responses of cvs 'Biloxi' and 'Hill'. The isochrones (*broken lines*) indicate the time taken to first flower (days) in any of the combinations of photoperiod and temperature indicated assuming that the plants remain in that environment. The boundaries (*solid lines*) between the photothermal domains are indicated as follows: critical photoperiod (P_c), ceiling photoperiod (P_{ce}), base temperature (T_b) and the minimum temperature for the expression of photoperiodic delay (T_p). The photothermographs for Mobile, Nashville and Chicago, USA, have been superimposed on each isochrone chart

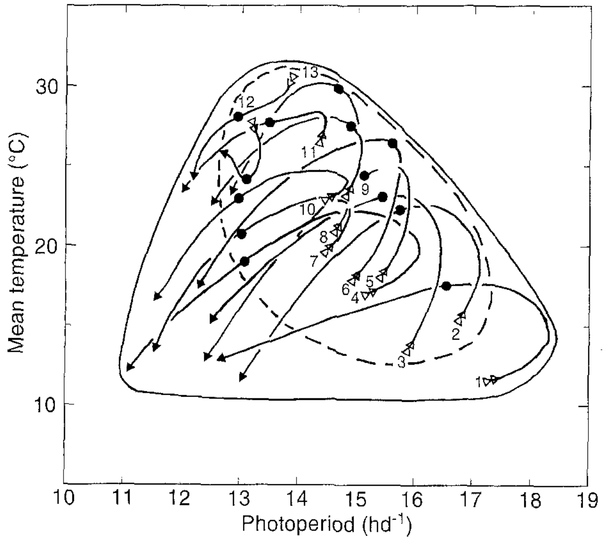


Fig. 4 Partial photothermographs showing the change in photoperiod and mean temperature during the natural growing seasons in representative environments where soyabean crops are cultivated. Typical conditions at sowing, first flowering and harvest are shown by *fletching*, *solid circles* and *arrowheads*, respectively. The *triangular area* enclosed by a *solid line* shows the photothermal limits to soyabean production, including irrigated areas. The *oval area* bounded by a *broken line* shows the range of environments that determine when flowering occurs (excluding environment (*1*) and irrigated areas in the tropics – see text). Key to environments: *1* Reading, UK (51°29′N), *2* Harbin, China (45°43′N), *3* Chicago, Ill., USA (41°53′N), *4* Horsham, Vic., Australia (36°43′S), *5* Tai Yuan, China, (37°54′N), *6* Nashville, Tenn., USA (36°10′N), *7* Hermitage, Qld., Australia (28°13′S), *8* Hankow, China (30°35′N), *9* Mobile, USA (30°42′N), *10* Lawes, Qld, Australia (27°33′S), *11* Shanhua, Taiwan (23°07′N), *12* Ibadan, Nigeria (7°26′N), *13* Katherine, NT, Australia (14°28′ S)

(Summerfield et al. 1993), little is known about the effect of maximal daily temperatures if they rise substantially well above this value for several hours each day and for a substantial number of days, but in such circumstances flowering is likely to take longer than is implied by the model. Or, conversely, if the photothermal coefficients were determined from data which included such environments with extreme daily maxima, the values determined are likely to over-estimate the time taken to flower under cooler conditions. Otherwise, the triple-plane model illustrated in Figs. 1 and 3, is sufficient to deal with most cropping environments described within the triangle in Fig. 4.

Figure 4 also shows 13 representative partial photothermographs covering the range of soyabean cultivation but including only that section of each that extends over the natural growing seasons (i.e. excluding dry seasons in the tropics). Let us now consider that part of the growth cycle from sowing to flowering (excluding the photothermographs from Reading where soyabean would be marginally beyond the region for commercial cultivation). This has been done for many climates, the range of which is illustrated by the examples in Fig. 4. They all indicate that the normal period from sowing to flowering could be fitted within the ovoid area indicated by a broken line. Thus, under most natural conditions it is evident that photoperiods shorter than 12.8 hd^{-1} seldom influence the time soyabean crops take to flower; although under irrigation in the tropics photoperiods as short as 11.5 hd^{-1} may be experienced.

In most crops, conversion of intercepted photosynthetically active radiation to biomass is more-or-less a constant, irrespective of genotype, across a wide range of environments, except when severe water stress is encountered. In soyabean, the conversion rate has been estimated at between 0.98 and 1.15 g above-ground dry matter per Mega Joule photosynthetically active radiation (Mayers et al. 1991c, e) which is close to the value, 1.20 g, reported by Sinclair et al.(1988). Consequently, providing that plant population density is optimised for maximum light interception, biomass production is largely a function of crop duration (Egli 1993). Too short a duration in soyabean severely limits biomass yield, and extending crop duration by increasing photoperiod increases biomass yield as a linear function of PAR interception, irrespective of genotype or specific photoperiodic treatment (Mayers et al. 1991 a–e).

However, in practice there are other considerations. Lawn (1989) has listed some advantages and disadvantages of a relatively short crop duration in tropical grain legumes. Advantages include: increased harvest index (HI), less tendency to lodge, less susceptibility to disease, greater synchrony of flowering and pod set and less likelihood of suffering end-of-season constraints (e.g. shortage of water or cold nights affecting pod development). To this list one could add that relay cropping systems also sometimes demand short-duration crops. Disadvantages include: insufficient light interception, decreased yield homeostasis (because low HI and excess leaf area provide some insurance against physical damage and environmental stress) and less nitrogen-fixation (which may not occur significantly until flowering, particularly in early-flowering types).

In line with these considerations, a survey of the soyabean literature suggests that although 30 days may be satisfactory in some warm, moist and fertile conditions, times to flower of less than 40 days often lead to restricted yield. In some cases, for example in relay cropping systems, farmers may be prepared to tolerate considerable yield reduction and use cultivars with shorter vegetative periods in order to accommodate the demands of other crops in the rotation. In many other circumstances, however and assuming the satisfactory plant population density, a time of 40–50 days to first flower or sometimes a little longer is a satisfactory target.

Figure 5 shows graphically the calculated flowering responses to photoperiod and temperature (Table 2) of all 40 accessions investigated here. The zone in which flowering may be expected to occur within 40–50 days after sowing is identified by hatching. For each accession, the extent of soyabean cultivation with (triangle) or without (ovoid) irrigation has been transposed from Fig. 4. The position of the hatched band was in fact used to establish the rank order of accessions in this diagram and in Tables 1 and 2. Specifically, those accessions in which this band appears nearest the bottom of the ovoid (i.e. in the climates representing cooler conditions) are placed first, and the remainder are ranked in order as the band moves towards the top left of the ovoid (accession 38) and beyond (accessions 39 and 40) in Fig. 5, i.e. towards the shorter daylengths and warmer temperatures found in the tropics. In other words the 40 accessions are ranked in order of increasing delay in flowering under tropical conditions.

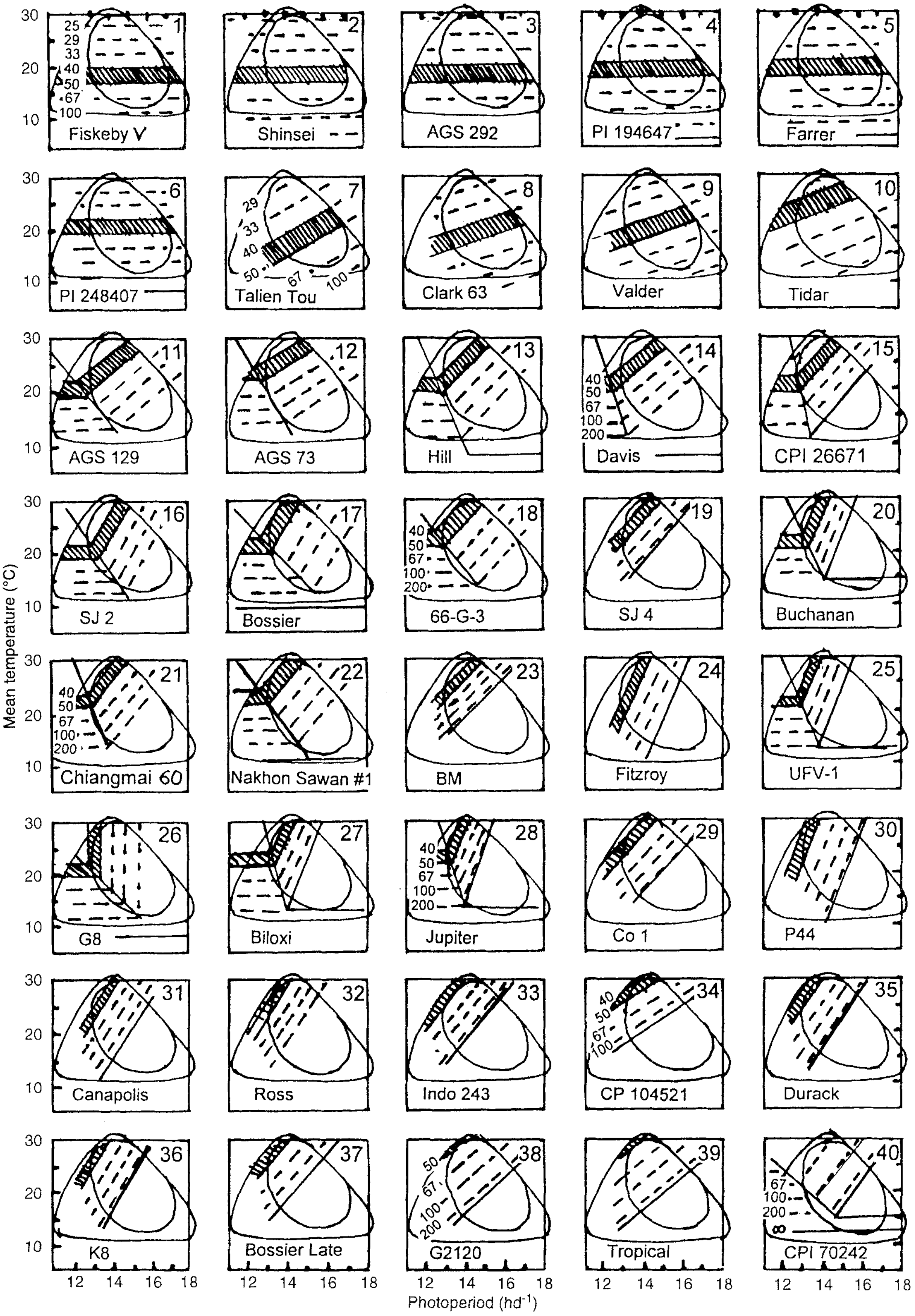
Reference to the examples of photothermal climates shown in Fig. 4 and the genotype response characteristics shown in Fig. 5 reveals that in cool temperate climates it is necessary to have photoperiod-insensitive cultivars, otherwise flowering would be excessively delayed. Such cultivars are, however, generally less suited to the tropics (represented at the top left of the triangle) since in these warm regions they tend to flower too soon to allow sufficient biomass to accumulate before the onset of reproductive development.

In order to delay flowering sufficiently in tropical climates it appears to be desirable to have a considerable degree of photoperiod sensitivity, as in the middle order or higher-ranking accessions shown in Fig. 5. However, such genotypes are completely ill-adapted to cooler conditions with longer days because flowering would not occur within the season available.

It has often been argued that photoperiod-insensitivity provides the basis of wide adaptability since crop duration is unaffected by daylength variation due to season or latitude. Indeed, this concept was part of the ‘green revolution’ approach to both wheat (*Triticum aestivum*) (Hanson et al. 1982) and rice (*Oryza sativa*) improvement (Chandler 1979; de Datta 1981). However, photoperiod-insensitivity in short-day plants results in relatively short-duration crops in tropical climates. This is because, providing there is sufficient water, the rate of progress towards flowering is solely a function of temperature; and the evidence suggests that the variation in response to temperature amongst photoperiod-insensitive genotypes is not great (cf. accessions 1–6 in Fig. 5 or the values of their corresponding coefficients in Table 2). On the other hand, it has now become clear that photoperiod-sensitivity genes in soyabean act by *delaying* flowering in longer photoperiods (and not by inducing earlier flowering in shorter days). This is illustrated by comparing the photothermal responses of typical photoperiod-insensitive and photoperiod-sensitive cultivars in Fig. 1 and elsewhere (Hadley et al. 1984a; Summerfield et al. 1993). Furthermore, we have now shown that three of the more important ‘maturity’ genes in soyabean (E_1, E_2, E_3) specifically delay flowering in long days to various extents without affecting temperature sensitivity (Upadhyay et al. 1994a). The main effects of these E genes are on the value of the c' coefficient of Eq. 2; i.e. they affect sensitivity to photoperiod.

An alternative approach to delaying flowering in tropical climates is to incorporate the ‘long-juvenile trait’, a character which finds expression in a relatively long pe-

Fig. 5 Isochrone charts for the time taken from sowing to first flowering in 40 accessions of soyabean, ranked and numbered according to increasing time taken to flower under tropical conditions. The number of days to flower is shown against the isochrones (*broken lines*) on representative charts (at least one chart per row and column). The range of time taken to flower of 40–50 days is identified by *hatching*. Where there were sufficient data to calculate their positions *solid lines* indicate photothermal domain boundaries, P_c (accessions 11–18, 20–22 and 25–28), P_{ce} (accessions 15,19, 20, 23–25, 27–31 and 33–40), T_b (accessions 4–6, 13–14, 17, 22, 26 and 40), and T_p (accessions 13, 15, 20, 25, 27, 28 and 40)


Mean temperature (°C)
Photoperiod (hd⁻¹)
30
20
10
12
14
16
18
25
29
33
40
50
67
100
200
∞
1 Fiskeby V
2 Shinsei
3 AGS 292
4 PI 194647
5 Farrer
6 PI 248407
7 Talien Tou
8 Clark 63
9 Valder
10 Tidar
11 AGS 129
12 AGS 73
13 Hill
14 Davis
15 CPI 26671
16 SJ 2
17 Bossier
18 66-G-3
19 SJ 4
20 Buchanan
21 Chiangmai 60
22 Nakhon Sawan #1
23 BM
24 Fitzroy
25 UFV-1
26 G8
27 Biloxi
28 Jupiter
29 Co 1
30 P44
31 Canapolis
32 Ross
33 Indo 243
34 CP 104521
35 Durack
36 K8
37 Bossier Late
38 G2120
39 Tropical
40 CPI 70242

riod after emergence during which the plant does not respond to photoperiod (Kiihl and Garcia 1989). The accessions CPI 104521 and CPI 70242, ranked 34 and 40 respectively in Tables 1 and 2 and Fig. 5, are examples of genotypes said to possess this trait. The juvenile phase is equivalent to what we have referred to more specifically as the photoperiod-insensitive pre-inductive phase, which we have estimated in four of the accessions that we have also used here (Collinson et al. 1993). At a mean temperature of 25°C the duration of this phase increased in line with the rank order established in this paper. Thus, the accessions ranked 25, 27, 34 and 38 had pre-inductive phases estimated as 11.2, 11.9, 18.6 and 32.7 days, respectively. The corresponding estimates of the coefficient of photoperiod-sensitivity (c' in Eq.. 2) shown in Table 2 are –0.00914, –0.01089, –0.00452 and –0.00357, respectively (Table 2). It would appear, then, that the relatively long durations of the accessions ranked 34 and 38 under tropical conditions (Fig. 5) are in no small measure due to their comparatively long pre-inductive ("juvenile") phases.

It is important to recognise that the responses due to the activity of the long-juvenile gene(s) are not yet fully understood. A long juvenile photoperiod-insensitive phase can, by definition, only be recognised if followed by a photoperiod-sensitive phase. It is therefore a character restricted to photoperiod-sensitive genotypes. Furthermore, it is known that genes other than those said to endow the long-juvenile trait also affect the duration of this photoperiod-insensitive phase. For example, we have shown that although the main effects of the three 'maturity' genes mentioned earlier – E_1, E_2 and E_3 – is on photoperiod-sensitivity, they also have some effect on the duration of the photoperiod-insensitive pre-inductive phase (Upadhyay et al. 1994b). By combining data previously presented separately (Upadhyay et al. 1994a, b) we show here (Fig. 6) that both effects are strongly correlated. Thus it seems that the E maturity genes may have a pleiotropic action in which they affect both photoperiod-sensitivity and the duration of the pre-inductive or juvenile period which is insensitive to photoperiod. These specific gene effects are in line with the more general and speculative conclusion reached previously by Major and Kiniry (1991) that there is a positive association in soyabean between photoperiod-sensitivity and the duration of the juvenile phase.

Since genes increasing the duration of the pre-inductive phase only occur or are only expressed in photoperiod-sensitive genotypes, and since those genes which induce photoperiod sensitivity (the E genes) have a dual effect in which they delay the rate of development in long days and also increase the duration of the juvenile phase, we conclude that photoperiod-sensitivity is generally a desirable characteristic of genotypes adapted to tropical conditions. If there is an alternative delaying gene which is effective in photoperiod-insensitive genotypes, it was not expressed in any of the photoperiod-insensitive genotypes investigated here (accessions ranked 1–6 in Fig. 5), since they all flowered relatively quickly.

The need to use photoperiod-sensitive genotypes in the tropics is not necessarily a disadvantage, however. In spite of the belief of some breeders that photoperiod-insensitivity is needed to stabilise crop duration if sowing dates are liable to vary in a particular region, in most cases in the tropics photoperiod-insensitivity would not necessarily lead to this outcome. Figure 7 shows two examples of complete photothermographs typical of the tropics, on which are superimposed the flowering isochrones of accessions adapted to those regions. Note that the isochrones tend to follow the diagonal trace of the photothermographs. This is because of the dominance of Eq. 2 in photoperiod-sensitive cultivars grown under natural conditions in the tropics. This equation determines that the isochrones are diagonal in domain C (Figs. 3, 5 and 7). Photothermographs tend to follow a similar diagonal course because of the general climatic correlation of longer days with warmer temperatures. As a consequence it can be seen that the photoperiod-sensitivity genes tend to delay flowering in longer days and compensate for the more rapid development due to warm temperatures that would otherwise occur during the warmer part of the year. Clearly, if photoperiod-insensitive genotypes with horizontal isochrones (as in accessions ranked 1–6 in Fig. 5) were grown in these tropical regions, the time taken to flower would vary with sowing date due to the seasonal march of temperature. Photoperiod-sensitivity is therefore not only necessary to achieve sufficiently long durations in the tropics but can also lead to homeostasis of crop duration when sowing dates vary.

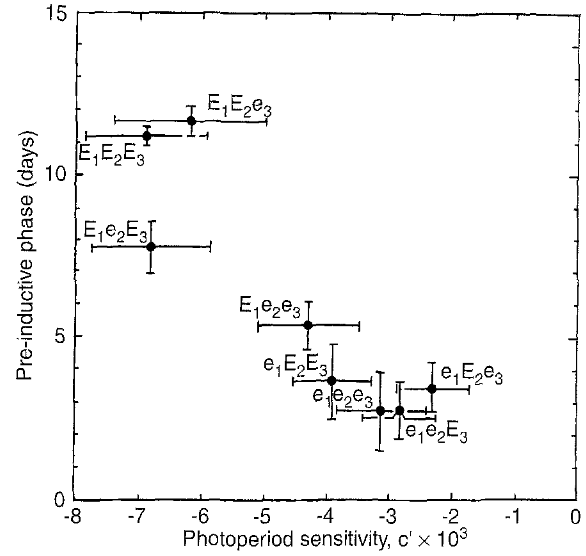


Fig. 6 The effect of maturity genes E_1, E_2, and E_3 in a cv 'Clark' background on photoperiod sensitivity ($10^3 \times c'$ in Eq. 2) and on the duration of the pre-inductive or juvenile phase (days) for plants of eight isolines grown at a mean temperature of 25°C. Standard errors for each parameter are shown by *vertical* and *horizontal* lines, respectively. Data from Upadhyay et al. (1994a, b)

In some cases, however, homeostasis of crop duration is not required: it is more important to achieve homeostasis of flowering date in circumstances where the sowing date varies (e.g. Curtis 1968; Bunting 1975). A.H. Bunt-

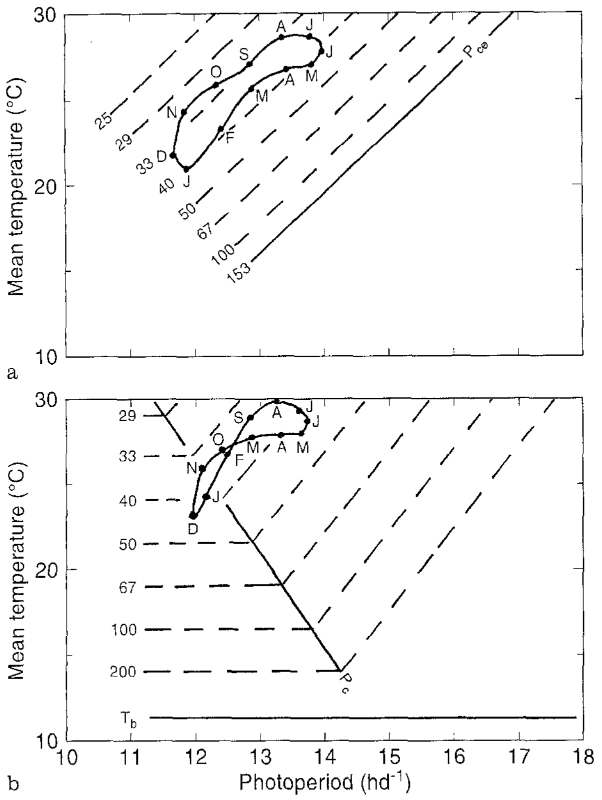


Fig. 7a, b Examples of photothermal flowering responses of 2 cultivars of soyabean adapted to tropical conditions in Thailand. In each case a photothermograph representing the local conditions to which the genotype is adapted is superimposed on its isochrone chart. The isochrones (*broken lines*) are marked in number of days from sowing to first flower and the critical photoperiod (P_c), ceiling photoperiod (P_{ce}) and base temperature (T_b) are shown (*solid lines*) where there were sufficient data to calculate their positions. **a** Chart for cv 'SJ4' with photothermograph for Chiang Mei (18°47′N); **b** Chart for cv 'Nakhon Sawan #1' with photothermograph for Nakhon Ratchasima (11°58′N)

ing has argued that this property has considerable value in the semi-arid tropics where the onset of the rains is erratic but their end is more uniform from year to year (Dennett et al. 1983). In these circumstances farmers should exploit the immediate advantages of sowing at the beginning of the season, which include the capture of nitrogen released by mineralisation and improved weed control. But sowing at the first opportunity also has the additional potential bonus, in those more favourable seasons when the rains come early, of exploiting a longer growing season with the possibility of intercepting light for a longer period and so securing a bumper yield. The response required in these circumstances is a homeostatic flowering date towards the end of the growing season achieved irrespective of sowing date. For this purpose, pronounced photoperiod-sensitivity (i.e. a large absolute value of c') is required, e.g. as in 'Buchanan', 'Biloxi' and 'Jupiter' (ranked 20, 27 and 28 in Table 2). This genetically controlled response leads to isochrones that are more vertical and are close together with respect to the photoperiod axis (Fig. 5).

Soyabean was chosen for this investigation since more was known about its photothermal responses than those of other crops and because a wide range of germplasm was available specifically adapted to precisely defined photothermal conditions. However, there is evidence that the triple-intersecting-plane rate model used here is also applicable to a wide range of other crops; cowpea (Hadley et al. 1983; Ellis et al. 1994a; Craufurd et al. 1996); pea, *Pisum sativum* L. (Hadley et al. 1984b); chickpea, *Cicer arietinum* L. (Roberts et al. 1985; Summerfield et al. 1989; Ellis et al. 1994c); pigeonpea *Cajanus cajan* L. Millsp. (Lawn and Troedson 1990); lentil, *Lens culinaris* L. (Summerfield et al. 1985; Erskine et al. 1990); common bean, *Phaseolus vulgaris* L. (Roberts and Summerfield 1987), faba bean, *Vicia faba* L. (Ellis et al. 1988a,b), barley, *Hordeum vulgare* L. (Ellis et al. 1988c, 1989); wheat, *Triticum aestivum* L. (Perry et al. 1987; Loss et al. 1990); rice, *Oryza sativa* L. (Summerfield et al. 1992); mungbean *Vigna radiata* L. Wilczek (Summerfield and Lawn 1987, 1988; Ellis et al. 1994b); other tropical *Vigna* species (Ellis et al. 1994a); and subterranean clover, *Trifolium subterraneum* L. (Evans et al. 1992). This list includes species which are tropical, temperate, short-day, long-day, and which belong to the two major families of arable crops – Gramineae and Leguminoseae. So far no species which has been thoroughly investigated fails to comply with the triple-plane rate model for describing and predicting its photothermal flowering responses. Consequently, it is reasonable to suppose that the approach tested in this paper could provide a basis for characterising the photothermal flowering responses of large germplasm collections of very many species.

The number of response planes which need to be considered for any species depends on its characteristics and the range of environments in which it is cropped. In lentil, which we believe is typical of many long-day crops, the photothermal plane, bounded by the critical and ceiling photoperiods, extends over a wide range of photoperiods, and consequently only the coefficients of Eq. 2 need to be determined (e.g. Erskine et al. 1990). In contrast, short-day plants typically originate in the tropics (Roberts 1991) where daylengths vary less. Consequently the photoperiod-sensitivity of short-day plants is often greater than long-day plants, i.e. the absolute values of c' are often greater than in long-day plants, and the range between P_c and P_{ce} can be less. Accordingly, the problems of genetic characterisation of short-day crops such as soyabean are potentially greater since the range of environments of interest may extend to include all three response planes. However, in all the photoperiod-sensitive accessions investigated here (numbers 7–40 in Fig. 5) it will be seen that the critical photoperiod, P_c, either falls outside the ovoid region relevant to the prediction of flowering in most non-irrigated regions or slices the edge of it in the area that represents those conditions just before flowering in many of these regions (Fig. 4). Furthermore, examination of Figs. 3 and 5 makes it clear that, for most genotypes in these circumstances, little error would result from assuming that the response was described entirely by the photothermal plane (Eq. 2). Conditions where photoperiods are shorter than P_c are therefore in practice mostly of interest in soyabean under circumstances in which the crop is sown in the tropics in the dry season (winter) as, for example, is the practice for about half of the crop area in Thailand. In such cases, the triple plane model still applies since it is valid whether photoperiods are decreasing (which is usual) or increasing, as it often does when the crop is sown in the tropics under irrigation (Summerfield et al. 1993).

When the triple-plane response model for soyabean was first developed using controlled environments (Hadley et al. 1984a) it was indeed suggested that in applying it to natural environments it would be possible to ignore the critical photoperiod. When controlled environments would be used it was also suggested that a minimum of four environments would then be needed to characterise the photothermal responses. It was pointed out then that three environments were the theoretical minimum needed to determine the three coefficients (a', b', c') defining the photothermal plane, and the following combinations were suggested: 21°C/12 hd^{-1}, 25°C/12 hd^{-1} and 25°C/14 hd^{-1}. One additional environment would be needed to determine the coefficient (d') of the plane of maximal delay; for this 21°C/14 $hd^{-1}$was suggested.

Given the more comprehensive experiment undertaken here, however, there is now much more information concerning the extent to which the positions of P_c and P_{ce}vary with genotype. Clearly, any set of three environments used to determine the coefficients for the photothermal plane need to be within the roughly triangular boundary set by maximum photoperiod values of P_c ,minimum photoperiod values of P_{ce} and minimum temperature boundaries of T_p (see for example, the genotypes ranked 15, 20, 25, 27, 28 and 40 in Fig. 5). Taking all the values of P_c and P_{ce} from Fig. 5 we suggest that the three suitable photothermal environments that would always be within the photothermal plane are as follows: 26°C with 13 hd^{-1}, 26°C with 14.5 hd^{-1} and 21°C with 14 hd^{-1}.A suitable environment which would nearly always be within the plane of maximum delay (where this can be detected) would be 21°C with 15 hd^{-1}. The few cases where this environment might still be within the photothermal plane would emerge from the analysis and would seldom be of any practical consequence since the delay to flowering would be considerable in these circumstances. When different planting dates and the possibility of supplementary lighting are taken into account, it may be that only two sites would be needed to undertake a comprehensive screening programme involving these four environments in order to characterise soyabean photothermal responses.

In some other species, however, the optimum temperature, T_0 , for flowering is relatively low: for example in pigeonpea (*Cajanus cajan*) the value is typically 22°–23°C (Omanga et al. 1995, 1996). Therefore, a fourth plane needs to be added to the triple plane model to include the negative response to temperature above the optimum. Indeed, the response in this domain may well play an adaptive role in this species for delaying flowering in warm climates. Much more needs to be known about supra-optimal temperature responses in all species and the nature of the photoperiodic response under such conditions.

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