Photo-thermal effects on time to flowering in dolichos bean (*Lablab purpureus* (L). sweet) var. lignosus

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Prediction of time to flowering of crop plants (especially photoperiod sensitive (PS) ones) help make appropriate crop management decisions such as choosing optimum sowing and harvesting dates which in turn determine plant size and thus affect dry matter production and crop yield. Modelling time to flowering of dolichos bean, a highly PS short-day food legume crop species, indicated greater role of temperature than photoperiod in regulating time to flowering of PS genotypes. The PS and photoperiod insensitive (PIS) genotypes of dolichos bean differed for base (T_b) and optimum temperature requirement for time to flowering. However, they were comparable for critical minimum, maximum and optimum photoperiod requirement for time to flowering. Dolichos bean requires critical minimum, maximum and optimum photoperiods of 11.11, 12.28 and 12.21 h respectively, and critical minimum growing degree days of 372.05°C day^{-1} and optimum temperature of 23.13°C for time to flowering. Using average daily air temperature, and working backwards in time, it is possible to predict the combination of dolichos bean cultivar and sowing date that will produce ready for harvest crop on a predetermined day when fresh pod quality is optimal.

Keywords: Base temperature, critical photoperiod, Dolichos bean, regression models.

ONE way to improve the adaptation of crops and maximizing crop productivity is by matching the phenology to the resources and constraints of target production environment[1]. Of all the phenological events, onset of flowering is the most significant as it marks the transition of the crop from vegetative to reproductive phase[2]. Productivity potential of crops is related to the duration from sowing to flowering[2]. Flowering plasticity, especially in response to temperature and photoperiod, is a common adaptive feature of annuals, including legumes, in arid or semiarid environments[3,4]. Several studies have indicated genetic differences for time to flowering in response to both temperature and photoperiod in annual legumes[5,6]. Accordingly, prediction of time to flowering help select appropriate crop management practices such as optimum sowing and harvesting dates[2,7] which determines plant size and thus affects dry matter production and product yield[8,9].

Simple linear regression models have been proposed to predict the effects of temperature and photoperiod on flowering behaviour of a range of both long- and short-day plants[7]. The developmental rate is defined as the inverse of flowering duration (1/*f*) for developing and testing models to predict time to flowering[5]. Empirical models have been developed by linearly relating the developmental rate to mean photoperiod and/or mean temperature in crops such as soybean[7], sulla and persion clover[5,6] and pigeonpea[10]. The effects of temperature and photoperiod have proved to be additive[11]. Attempts to model time to flowering have not been reported in dolichos bean, a highly photoperiod sensitive short-day food legume crop species[12–15]. Dolichos bean (*Lablab purpureus* L.), known as lablab bean, hyacinth bean, sem, bonavist bean, etc. is cultivated in India[14] in semi-arid tropics. Based on angle of attachment of seeds to the suture of pods, two botanical types of dolichos bean (*Lablab purpureus* var. typicus and *Lablab purpureus* var. lignosus) are recognized. *Lablab purpureus* var. lignosus is an annual bushy herb cultivated as a rainfed crop for immature fresh seeds used as a vegetable in southern India, especially in southern parts of Karnataka. Most farmers' cultivars are highly photoperiod sensitive to time to flowering. Day-neutral (photoperiod insensitive) genotypes have also been reported in Australia[16] and India[13,17].

The present study was carried out to assess the relative contributions of photoperiod and temperature on time to flowering variation among a set of PS and PIS genotypes. Our objective was to determine base temperature, optimum temperature, critical minimum growing degree days (GDD), critical minimum, maximum and optimum photoperiod for floral initiation and to explore the nature of response (qualitative/quantitative) to photoperiod for time to flowering in dolichos bean.

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Materials and methods

Experimental location

A field experiment was carried out at the Zonal Agricultural Research Station (ZARS) in the University of Agricultural Sciences (UAS), Bengaluru, India. Geographically, ZARS, Bengaluru is located at 12°58′N lat, 77°35′E long and an altitude of 930 m amsl. The annual rainfall received during experimental period ranged from 578.90 to 994.50 mm. The data on average monthly minimum and maximum temperature, bright sunshine hours, photoperiod and relative humidity are furnished in Table 1.

Plant material and experimental design

Five photoperiod sensitive (PS) genotypes (of different provincial origin) such as GL 388 (Dharwad, Karnataka), GL 365 (Ananthapuram, Andhra Pradesh), GL 161 (unknown), GL 369 (Mandya, Karnataka) and GL 371 (Bidar, Karnataka) and five photoperiod insensitive (PIS) genotypes such as HA 4 (a released variety from UAS, Bengaluru, India), FPB 5, FPB 20, FPB 14 and HA 10-8 (advanced breeding lines developed at UAS, Bengaluru) were collected and maintained at All India Coordinated Research Project (AICRP) on Pigeonpea, ZARS, UAS, Bengaluru. The 10 genotypes were evaluated in 12 monthly intervals from June 2012 to May 2013 and June 2013 to May 2014 in 24 separate experiments, each laidout in randomized block design with two replications. The seed of each genotype was planted in a single row of 3 m length following a spacing of 0.6 m between rows. After 15 days of planting, the seedlings were thinned and a total of 12 plants were maintained within a row with a spacing of 0.25 m between plants. The recommended agronomic practices were followed to raise a healthy crop.

Table 1. Weather variables prevailed in the experimental location during 2012, 2013 and 2014

Year/months	Temperature (°C) Maximum	Minimum	Mean	Photoperiod (h)
2012				
June	30.95	20.25	25.60	12.52
July	28.71	19.59	24.15	12.48
August	28.41	19.33	23.87	12.32
September	29.19	19.41	24.30	12.11
October	28.34	18.68	23.51	11.51
November	27.21	16.29	21.75	11.31
December	27.38	15.74	21.56	11.22
2013				
January	28.77	14.81	21.79	11.27
February	30.49	16.36	23.43	11.43
March	32.74	19.23	25.98	11.90
April	34.55	21.83	28.19	12.25
May	33.47	21.11	27.29	12.41
June	28.41	19.67	24.04	12.52
July	27.53	19.34	23.43	12.48
August	27.93	19.05	23.49	12.32
September	27.43	18.87	23.15	12.11
October	27.76	19.06	23.41	11.51
November	27.67	16.95	22.31	11.31
December	26.56	14.06	20.31	11.22
2014				
January	27.58	14.65	21.11	11.27
February	29.85	16.27	23.06	11.43
March	32.17	18.21	25.19	11.88
April	34.70	21.13	27.91	12.25
May	33.21	21.15	27.18	12.43
June	30.85	20.61	25.73	12.52
July	28.26	19.70	23.98	12.48
August	28.20	19.54	23.87	12.32
September	28.51	19.40	23.96	12.11

Collection of data

Replication-wise flowering time from date of planting (FTDAP) was recorded as number of days from planting to flower initiation in at least 50% of plants in each of PS and PIS genotypes. Daily maximum and minimum temperatures were recorded from the meteorological observatory located close to the experimental field. The data on daily photoperiod (P) (also called as day length), defined as the time in hours from sunrise to sunset was collected from the India Meteorological Department (IMD) located in Bengaluru. The mean daily temperature (T) and photoperiod (P) were computed for the period from planting to time at which 50% of plants flowered in each of the genotype. Replication-wise, time to flowering from first day of the year (FTDOY) was recorded by counting the number of days from 1 January until 50% of plants flowered in each of the genotype irrespective of their planting dates.

Statistical analysis

Estimation of growing degree days: Heat units or thermal time (T_t) expressed as growing degree days (GDD), is an accumulated air temperature above a base temperature (T_b) below which development ceases[18]. Estimate of base temperature (T_b) is a prerequisite for estimation of GDD. There are two methods for estimating T_b (1) using thermal model (equation (1)) by extrapolation of regression line; $T_b = -(a/b)$ and (2) using least standard deviation (in days) method. In statistics, estimating T_b by extrapolation of regression line is not acceptable[19]. Hence, T_b was calculated based on the method of least standard deviation (in days)[20].

$$T_b = \sum_{i=1}^{p} T_i - \frac{\sum_{i=1}^{n} T_i D_i^2 - n\sum_{i=1}^{n} T_i^2 D_i^2}{n\sum_{i=1}^{n} T_i D_i^2 - n\sum_{i=1}^{n} T_i D_i \sum_{i=1}^{n} D_i}, \quad (1)$$

where T_i is mean diurnal temperature prevailing from planting date to time to flowering, D_i the days to flowering of ith genotype and n is the number of planting dates. Replication-wise GDD between planting dates to time to flowering (n) were estimated as the sum of the differences between the mean daily T and T_b for all the genotypes using the following equation[21].

$$\mathrm{GDD}(T_t) = \sum_{i=1}^{n}[T - T_b]. \quad (2)$$

Mean FTDAP, FTDOY and GDD of PS and PIS genotypes were computed. Mean of time to flowering (FTDAP) averaged over replications and over two years were considered for predicting time to flowering using regression models.

Combined analysis of variance

Combined analysis of variance of PS and PIS genotypes for FTDAP, FTDOY and GDD was performed using PROC GLM of SAS 9.3 version to partition total variability into different sources. Mean squares due to PS/PIS genotypes and those due to their first-order interactions (PS/PIS genotypes × planting dates/years) and their second-order interactions (PS/PIS genotypes × planting dates × years) for FTDAP, FTDOY and GDD were estimated and tested for their statistical significance using F test.

Photoperiod-thermal models to predict time to flowering

The rate of progress or development ($1/f$) in days, defined as the inverse of duration from sowing to flowering initiation for each genotype, averaged over two replications, was related to mean diurnal temperature (T, °C) averaged over replication, to mean photoperiod (P, h day^{-1}) averaged over replication, or to both. Using three linear models, such as (a) thermal model based on temperature alone: $1/f = \alpha + bT$(3), in which time to flowering was predicted assuming the absence of photoperiod sensitivity to time to flowering or assuming that photoperiod is less than the critical photoperiod, (b) photoperiodic model based on photoperiod alone: $1/f = a + cP$(4) in which time to flowering was predicted assuming the absence of effect of temperature and (c) the photoperiod-thermal additive model based on temperature and photoperiod: $1/f = a' + b'T + c'P$(5), in which time to flowering was predicted when prevailing photoperiod is more than critical photoperiod, where α, b, a, c, a', b' and c' were genotype specific constants[11]. The constants of all the three models were estimated through linear regression of T and P on $1/f$ of each genotype using PROC REG of SAS 9.3 version.

Optimum photoperiod and temperature requirement

In order to estimate optimum photoperiod requirement for time to flowering and minimum days to flowering, second-degree polynomials of the form $y = a + bx + cx^2$ were constructed using PROC REG of SAS 9.3 version. Here y is days to flowering and x is the photoperiod in hours[22]. The days to flowering reaches a minimum value when the first differential coefficient is zero. As $dy/dx = b + 2cx = 0$, the optimum photoperiod has the value $-b/2c$. The days to flowering corresponding to this optimum photoperiod was designated as minimum days to flowering, and was shown by $a - b^2/4c$ after substituting the $x = -b/2c$ in equation $y = a + bx + cx^2$. Similarly, optimum temperature requirement for time to flowering and minimum days to flowering were estimated using $y' = a' + b'z + c'z^2$, where y' is days to flowering and z is the temperature in °C.

Critical minimum and maximum photoperiod and GDD

GDD versus FTDOY graph (Figure 1) was drawn to estimate the critical minimum GDD and photoperiod for time to flowering. The critical maximum photoperiod (P_c) (photoperiod beyond which flowering ceases) was estimated when the photoperiod–thermal model intersects with the thermal model given by equation: $P_c = [\alpha - a' + (b - b')T]/c'(6)$[11].

Results and discussion

Combined analysis of variance

Combined analysis of variance indicated significant differences among PS genotypes for FTDAP, FTDOY and GDD for time to flowering (Table 2). These could be attributed to relatively lower temperature that prevailed during 2013–14 compared to 2012–13. Significant interaction of PS genotypes with planting dates for FTDAP and GDD indicated their differential response to different photoperiods. The PS genotypes displayed significant interaction with years of planting for FTDAP and GDD requirement for time to flowering. On the other hand, PIS genotypes interacted significantly with years of planting only for GDD for time to flowering. There was minimal difference in time to flowering when PS and PIS genotypes were planted during 2012–13 December and 2013–14 January, indicating that December and January are ideal for planting both PS and PIS genotypes to ensure flowering synchrony between them (Figure 2). Flowering synchrony is necessary to effect pre-planned crosses among PS genotypes and between PS and PIS genotypes throughout the year to augment the genetic variability and reduce the time required to develop improved pureline varieties in dolichos bean.

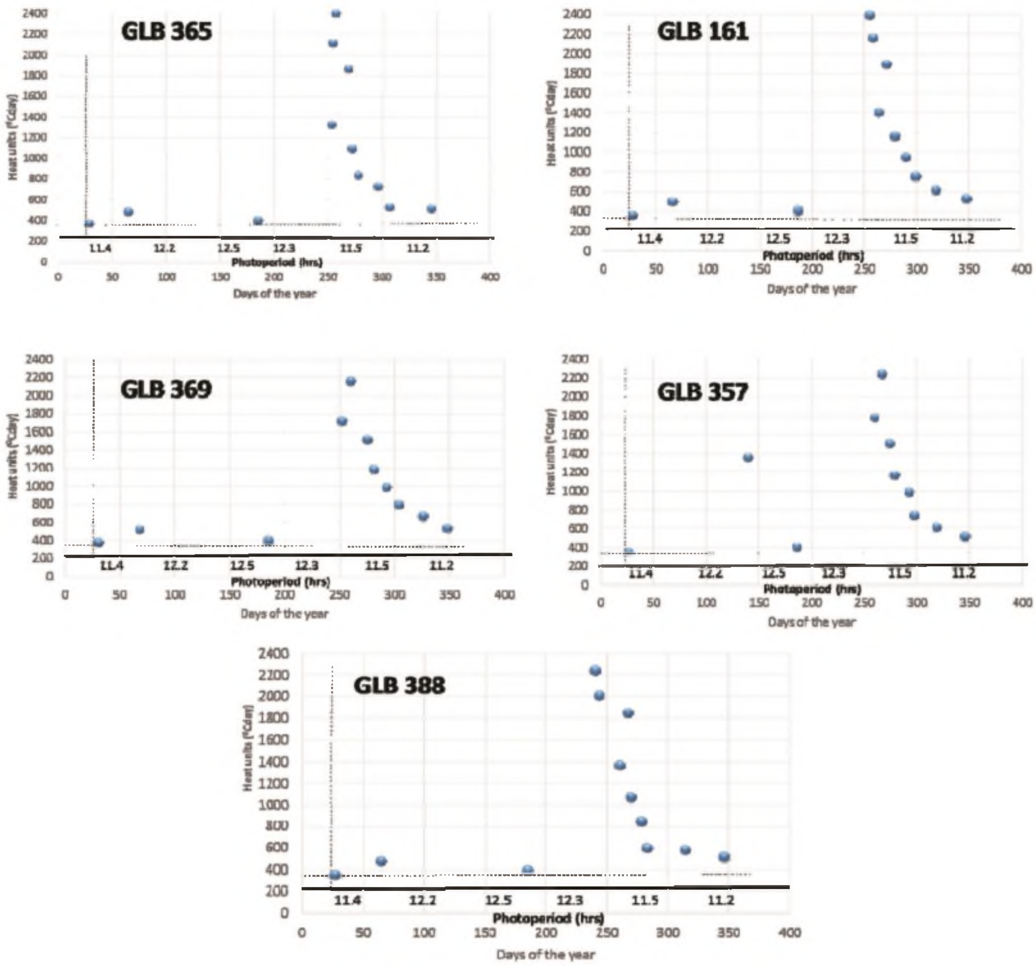

Figure 1. Heat units and calendar date of flowering initiation for photoperiod sensitive genotypes growing at various planting dates. The two dotted lines indicate the derived critical minima for heat unit and photoperiod.

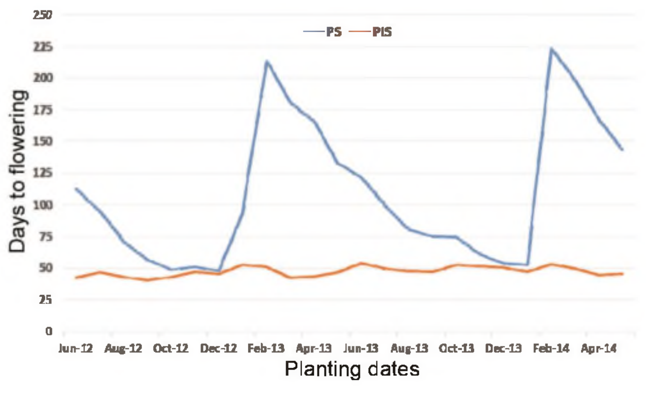

Figure 2. Difference in mean time to flowering of photoperiod sensitive and photoperiod insensitive genotypes of dolichos bean under different photo–thermal regimes.

Genetic differences for FTDAP, DOY, GDD and T_b

While the PS genotypes differed in terms of FTDAP, FTDOY and GDD for time to flowering, the parameters in PIS genotypes were comparable (Table 3). On an average, PS genotypes required higher T_b and GDD than PIS genotypes for flowering initiation.

Photoperiod–thermal models to predict time to flowering

The time to flower and the degree to which it is responsive to photoperiod is a key factor in the adaptation of a species to different eco-geographic locations[23,24] and dolichos bean is not exception to this. Genetic variation that affects the timing of flowering and its regulation by photoperiod is significant for the performance of crop species[22]. Hence, accurate prediction of time to flowering allows the selection of appropriate sowing and harvesting time to optimise productivity. However, a plant will not always need the same amount of calendar time to switch over from vegetative into reproductive phase as temperature also affects such switch over[25]. Linear regression models are considered useful for predicting the rate of progress towards flowering[11]. In the present study, linear models accounted for 61–93% of variation (adjusted R^2) observed

Table 2. Combined analysis of variance of selected dolichos bean photoperiod sensitive and photoperiod insensitive genotypes for flowering time in days after planting flowering time from date of planting (FTDAP), growing degree days (GDD) and flowering time in days of the year flowering from first day of the year (FTDOY)

		FTDAP		GDD (°C day)		FTDOY	
Source of variation	*df*	Mean squares	Pr > F	Mean squares	Pr > F	Mean squares	Pr > F
Replication	1	3.85	0.86	793.15	0.83	346.80	0.73
Year	1	3450.77	<0.0001	311,633.65	<0.0001	33,969.68	0.0006
Planting dates (PD)	11	32,546.95	<0.0001	6,118,425.77	<0.0001	329,193.31	<0.0001
Genotypes (G)	9	51,576.26	<0.0001	3,349,549.64	<0.0001	40,669.94	<0.0001
Photoperiod sensitive (PS) genotypes	4	1616.49	<0.0001	185,888.78	<0.0001	1,613.69	>0.05
Photoperiod insensitive (PIS) genotypes	4	115.39	>0.05	45,931.73	<0.05	2,143.45	>0.05
PS versus PIS	1	457,258.80	<0.0001	29,218,664.72	<0.0001	351,000.83	<0.0001
Year × G	9	464.99	0.0001	117,915.91	<0.0001	2,096.25	0.669
Year × PS genotypes	4	963.42	<0.0001	109,223.99	<0.0001	965.64	>0.05
Year × PIS genotypes	4	16.43	>0.05	147,205.15	<0.0001	2,622.39	>0.05
PD × G	99	3757.82	<0.0001	451,317.87	<0.0001	6,767.17	<0.0001
PD × PS genotypes	44	455.30	<0.01	55,986.72	<0.01	455.66	>0.05
PD × PIS genotypes	44	4.60	>0.05	3,782.67	>0.05	2,728.17	>0.05
Year × PD × G	99	4182.67	<0.0001	512,824.47	<0.0001	16,187.46	<0.0001
Year × PD × PS genotypes	44	1373.41	<0.0001	170,817.55	<0.0001	15,061.95	<0.0001
Year × PD × PIS genotypes	44	36.38	>0.05	26,534.26	<0.05	9,214.93	<0.01
Pooled error	349	123.22	–	16,536.00	–	2,820.73	–

Table 3. Days after planting (DAP), day of year (DOY), base temperature (T_b) and growing degree days (GDD) required by dolichos bean photoperiod sensitive and photoperiod insensitive genotypes for flowering

Genotypes	Parameters	FTDAP (day)	FTDOY (day)	GDD (°C day)	T_b (°C)
Photoperiod sensitive genotypes					
GLB 365	Mean	105.11	233.80	1052.47	14.26
	CV	6.48	2.90	5.81	
	SD	6.78	6.78	60.79	
GLB 161	Mean	109.32	237.98	1096.46	14.18
	CV	5.13	2.27	4.92	
	SD	5.50	5.50	53.39	
GLB 369	Mean	111.01	239.61	1111.43	14.19
	CV	4.46	1.99	4.13	
	SD	4.85	4.85	45.21	
GLB 357	Mean	117.59	246.25	1187.68	14.19
	CV	4.94	2.34	4.58	
	SD	5.87	5.87	55.12	
GLB 388	Mean	102.52	231.19	1025.56	14.25
	CV	6.77	2.93	5.95	
	SD	6.84	6.84	60.25	
Photoperiod insensitive genotypes					
HA 4	Mean	47.63	191.50	632.94	10.90
	CV	2.29	0.57	3.78	
	SD	1.09	1.09	22.30	
FPB 14	Mean	47.52	176.30	556.74	12.56
	CV	2.87	1.31	6.07	
	SD	3.19	2.16	33.89	
FPB 5	Mean	48.13	184.42	628.47	11.53
	CV	1.57	0.62	3.57	
	SD	0.75	1.03	19.70	
FPB 20	Mean	44.77	188.65	593.80	11.01
	CV	4.04	0.96	6.59	
	SD	1.82	1.82	23.99	
HA 10-8	Mean	48.85	177.54	594.43	11.66
	CV	2.63	0.73	4.50	
	SD	1.29	1.29	21.96	

CV, Coefficient of variation (%); SD, Standard deviation.

Table 4. Estimates of parameters (× 10^{-3}) of linear regression of the rate of progress to flowering ($1/f$) on mean air temperature, photoperiod and both in dolichos bean

Genotypes	Thermal model			Photoperiod model			Photo–thermal model			
	α	b	Adjusted R^2	a	c	Adjusted R^2	a'	b'	c'	Adjusted R^2
Photoperiod sensitive genotypes										
GLB 365	107.39**	–3.98**	79.23**	123.84**	–9.35**	64.56**	117.86**	–3.15*	–2.55	78.71**
GLB 161	109.31**	–4.10**	83.08**	128.95**	–9.84**	77.36**	128.14**	–2.57**	–4.63*	88.35**
GLB 369	107.71**	–4.05**	85.63**	116.56**	–8.82**	75.36**	124.11**	–2.70**	–4.05*	92.38**
GLB 357	113.59**	–4.29**	82.46**	119.04**	–9.05**	61.46**	126.40**	–3.37**	–2.92	84.02**
GLB 388	108.75**	–4.04**	81.71**	117.54**	–8.82**	68.00**	119.62**	–3.01*	–2.98	82.90**
Photoperiod insensitive genotypes										
HA 4	14.21	0.28	14.73	13.44	0.64	–1.49	14.72**	0.29	–0.06	5.32
FPB 14	15.45	0.23	7.92	6.47	1.23	22.93	6.75**	0.05	1.11	14.81
FPB 5	14.22	0.27	10.68	7.30	1.14	16.03	7.78**	0.13	0.83	9.98
FPB 20	17.64	0.19	2.18	10.19	1.02	10.30	10.58**	0.06	0.87	1.00
HA 10-8	15.45	0.21	8.11	6.90	1.15	25.06	7.13**	0.04	1.05	17.19

*Significant at $P = 0.05$; **Significant at $P = 0.01$.

in time to flowering of PS dolichos bean genotypes (Table 4). The thermal and photoperiod-based regression models, considered separately, explained 61% variation (adjusted R^2) in time to flowering of PS genotypes suggesting utility of either of the models for reliable prediction of time to flowering in dolichos bean.

However, photoperiod–thermal additive model (when both photoperiod and temperature included in the model) suggested significant influence of both temperature and photoperiod (for GLB 161 and GLB 369) with a greater role of temperature on the variation of time to flowering of PS genotypes. Similar trend has been reported for crops such as cowpea[6], sulla and persion clover[25,26]. However, in dolichos bean, both temperature and photoperiod are of equal importance in controlling time to flowering[27,28]. The differences in the reports of the past and the present studies[27,28] for time to flowering in dolichos bean could be attributed to differences in the range of photoperiod and temperature to which genotypes were exposed. Several reports attribute equal importance to both temperature and photoperiod in controlling the time to flowering of crops such as soybean[29] and forage legumes[25,26,30]. The greater influence of temperature than photoperiod on time to flowering of dolichos bean PS genotypes in the present study could be attributed to confounding effects of photoperiod with those of temperature on time to flowering as indicated by significant high correlation between mean day temperature and photoperiod ($r = 0.75$, $P < 0.05$). The prevalence of photoperiod within the critical minimum and maximum limits could be another cause for reduced photoperiod influence on time to flowering in dolichos bean. Repetition of the experiment in locations where prevailing photoperiods are greater than that of critical photoperiod for time to flowering would provide conclusive evidence for the effect of photoperiod in dolichos bean.

In all PS genotypes, statistically negative and significant estimates of regression model parameters (b and b'; c and c') suggested accelerated progress towards flowering by cooler temperatures and shorter photoperiods. The variation in magnitude of regression coefficients b and b' among the PS genotypes shows genotype-dependent responses to time to flowering[31]. Higher sum of squares of thermal model compared to those of photoperiodic model and significant temperature and photoperiod-dependent regression coefficient in photoperiod–thermal model indicates predictability of time to flowering of PS dolichos bean genotypes based on GDD with a specific T_b and photoperiod.

Base temperature (T_b) and optimum temperature requirement

The concept of T_b can be described either physiologically or statistically. Physiologically, crop growth and development will cease below the T_b. Each developmental phase may have different T_b and it is difficult to determine physiological T_b. Statistically, T_b indicates lowest variation in GDD. In most cases, T_b is determined statistically rather than physiologically[20]. However, average T_b for time to flowering tends to be similar for different cultivars of a crop but varies with crop species. For example, cool-season species such as pea have $T_b = 4°C$, while warm-season species such as sweet corn and cowpea have $T_b = 8–10°C$ (ref. 32). The present study indicates higher T_b and average GDD requirement for PS genotypes compared to PIS dolichos bean genotypes (Table 3). The study indicates that dolichos bean require an average T_b of 11–13°C for time to flowering. However, the T_b and GDD requirements of PS genotypes need to be validated by evaluating them in environments with temperatures different from that in the present study. Further, dolichos

Table 5. Critical minimum GDD, minimum and maximum photoperiod and optimum photoperiod and temperature required for flowering initiation in photoperiod sensitive and photoperiod insensitive genotypes of dolichos bean

Genotypes	Critical minimum GDD (°C day)	Critical photoperiod (h day^{-1})		Optimum	
		Minimum	Maximum	(h day^{-1}) Photoperiod	Temperature (°C)
Photoperiod sensitive genotypes					
GLB 365	370.60	11.33	12.34	11.53	22.35
GLB 161	366.82	11.33	12.32	11.57	22.00
GLB 369	378.31	11.34	12.33	11.33	21.58
GLB 357	354.50	11.32	12.36	11.23	22.04
GLB 388	357.59	11.32	12.32	11.50	22.12
Mean	365.56	11.33	12.33	11.43	22.02
Photoperiod insensitive genotypes					
HA 4	496.01	11.31	12.34	12.12	23.31
FPB 14	431.42	11.31	12.30	11.54	20.63
FPB 5	465.34	11.32	12.27	12.15	18.64
FB 20	448.09	11.29	12.32	12.03	22.02
HA 10-8	441.41	11.33	12.26	12.04	18.77
Mean	456.45	11.31	12.30	11.98	20.67

bean require optimum temperature of 21.35°C for time to flowering (Table 5) which is comparable to warm season short-day legume crop such as pigeonpea (24°C)[33] and slightly higher in soybean (26–28°C)[5,7].

Critical minimum and maximum GDD and photoperiod requirement

GDD versus FTDOY graph (Figure 1) indicates the requirement of critical minimum GDD and photoperiod for time to flowering. The critical minimum GDD required for flowering initiation in PS genotypes ranged from 354.50°C day^{-1} to 378.31°C day^{-1} with an average of 365.56°C day^{-1}. The critical minimum GDD for time to flowering of PIS genotypes was higher than that of PS genotypes in dolichos bean (Table 5). On an average, dolichos bean requires critical minimum GDD of 411°C for time to flowering in Bengaluru environment. Forage legumes such as fava bean and pea required higher critical minimum GDD of 833°C and 770°C respectively, for time to flowering in Mediterranean environments[25]. GDD systems are empirical approaches used to predict the time to flowering of PS genotypes. Using average daily air temperature, and working backwards in time, it is possible to predict the combination of dolichos bean PS cultivar (based on GDD and T_b requirement) and sowing date that will produce crops ready for harvest on a predetermined day when pod quality is optimal. GDD systems have been successfully used to choose grape cultivars for different end-uses in California[32].

The PS and PIS genotypes of dolichos bean differed for base and optimum temperature besides GDD for time to flowering. However, PS and PIS genotypes were comparable for critical minimum, maximum and optimum photoperiod requirement for time to flowering. On an average, dolichos bean requires critical minimum, maximum and optimum photoperiod of 11.32, 12.32 and 12.10 h respectively (Table 5). Earlier studies reported temperature-dependent critical photoperiod requirement for flowering time in dolichos bean[27]. For instance, it was reported that critical photoperiod requirement of flowering time is 13 h at 25°C, while it is between 10 and 11 h at 30°C. Further, all PS genotypes did flower when the prevailing temperature was ≤20°C irrespective of photoperiod. Earlier reports support low temperature requirement under long days for flowering time in dolichos bean[34]. Fava bean and pea require critical minimum photoperiods of 12.00 h for time to flowering in Mediterranean environments[25] while, soybean require maximum photoperiod of 13.50 h for time to flowering[35]. A qualitative short-day plant fail to initiate flowering if the prevailing photoperiod exceeds the critical maximum photoperiod and a quantitative short-day plant requires short-days for flower initiation but continues to flower even beyond critical maximum photoperiod although time to flowering is delayed. From the present results, it is difficult to determine whether dolichos bean is a quantitative/qualitative short-day plant as photoperiod of the experimental location falls within the limits of minimum and maximum critical photoperiod.

Conclusion

The study indicates a significant role for both photoperiod and temperature with a greater role of temperature than photoperiod in controlling the time to flowering of dolichos bean. It is possible to characterize time to flowering responses of working germplasm accessions to variation in photoperiod and temperature in a way which enable prediction of time to flowering for any given data on latitude, sowing time and daily minimum and maximum air temperature. The reliable prediction of time to flowering helps optimize the choice of dolichos bean cultivars with different GDD requirement and sowing and harvesting dates to target production environments. To the best of our knowledge this is the first study aimed at modelling time to flowering of PS genotypes in response to photoperiod and temperature variation, and comparative analysis of critical minimum and maximum and optimum photoperiod and GDD and T_b for PS and PIS genotypes for time to flowering in dolichos bean.

1. Shorter, R., Lawn, R. J. and Hammer, G. L., Improving genotypic adaptation in crops – a role for breeders, physiologists and modelers. *Exp. Agric.*, 1991, **27**, 155–176.
2. Lawn, R. J. *et al.*, Towards the reliable prediction of time to flowering in six annual crops. VI. Applications in crop improvement. *Exp. Agric.*, 1995, **31**, 89–108.
3. Fox, G. A., Consequences of flowering-time variation in a desert annual: adaptation and history. *Ecology*, 1989, **70**, 1294–1306.
4. Ehrmann, T. and Cocks, P. S., Reproductive patterns in annual legume species on an aridity gradient. *Vegetation*, 1996, **122**, 47–59.
5. Hadley, P., Roberts, E. H., Summerfield, R. J. and Minchin, F. R., Effects of temperature and photoperiod on flowering in soya bean [*Glycine max* (L.) Merrill]: a quantitative model. *Ann. Botany*, 1984, **53**, 669–681.
6. Ellis, R. H. *et al.*, Toward the reliable production of time to flowering in six annual crops. V. Chickpea (*Cicer arietinum*). *Exp. Agric.*, 1994, **30**, 271–282.
7. Summerfield, R. J., Roberts, E. H., Ellis, R. H. and Lawn, R. J., Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Exp. Agric.*, 1991, **27**, 11–31.
8. Shanmugasundaram, S. and Tsou, S. C. S., Photoperiod and critical duration for flower induction in soybean. *Crop Sci.*, 1978, **18**, 598–601.
9. Wang, Z., Reddy, V. R. and Quebedeaux, B., Growth and photosynthetic responses of soybean to short-term cold temperature environment. *Exp. Agric.*, 1997, **37**, 13–24.
10. Omanga, P. A., Summerfield, R. J. and Qi, A., Flowering of pigeonpea (*Cajanus cajan*) in Kenya: responses of early-maturing genotypes to location and date of sowing. *Field Crops Res.*, 1995, **41**, 25–34.
11. Roberts, E. H. and Summerfield, R. J., Measurements and prediction of flowering in annual crops. In *Manipulation of Flowering* (ed. Atherton, J. G.), Butterworths, London, 1987, pp. 17–50.
12. Schaaffhausen, R. V., Dolichos lablab or hyacinth bean: its use for feed, food and soil improvement. *Econ. Bot.*, 1963, **17**, 146–153.
13. Vishwanatha, S. R., Shivashankar, G. and Manjunath, A., Nonseason-bound dolichos lablab with new plant type. *Curr. Sci.*, 1971, **40**, 667–668.
14. Purseglove, J. W., *Tropical Crops Dicotyledons*, Longman, London, 1977, pp. 273–276.
15. Shivashankar, G. and Kulkarni, R. S., Field bean (*Dolichos lablab* Linn. var. Lignosus Prain). *Indian J. Hortic.*, 1989, **34**, 24–27.
16. Ison, R. L. and Hopkinson, J. M., Pasture legumes and grasses of warm climate regions, In *Handbook of Flowering* (ed. Halevy, A. H.), CRC Press, Boca Raton, Florida, 1985, pp. 203–251.
17. Girish, G. and Gowda, M. B., Inheritance of qualitative characters in Dolichos bean *Lablab purpureus* L. Sweet. *Environ. Ecol.*, 2009, **27**(2), 571–580.
18. Yin, X., Kropff, M. J. and Ellis, R. H., Rice flowering in response to diurnal temperature amplitude. *Field Crops Res.*, 1996, **48**, 1–9.
19. Yang, S., Logan, J. and Coffey, D. L., Mathematical formulae for calculating the base temperature for growing degree days. *Agric. For. Meteorol.*, 1995, **74**, 61–74.
20. Arnold, C. Y., The development and significance of the base temperature in a linear heat unit system. *Proc. Am. Soc. Hortic. Sci.*, 1959, **74**, 430–445.
21. Nuttonson, M. Y., A comparative study of lower and upper limits of temperature in measuring the variability of day-degree summations of wheat, barley and rye. American Institute of Crop Ecology, Washington, DC, 1956.
22. Chandraratna, M. F., Genetics of photoperiod sensitivity in rice. *Genetics*, 1955, **53**, 215–223.
23. Weller, J. L. and Ortega, R., Genetic control of flowering time in legumes. *Frontiers Plant Sci.*, 2015, **6**, 1–13.
24. Maurer, A. *et al.*, Modelling genetic architecture of flowering time control in barley through nested association mapping. *BMC Genet.*, 2015, **16**, 1–12.
25. Iannucci, A., Terribile, M. R. and Martiniello, P., Effects of temperature and photoperiod on flowering time of forage legumes in a Mediterranean environment. *Field Crops Res.*, 2008, **106**, 156–162.
26. Papastylianou, P. and Bilalis, D., Flowering in Sulla (*Hedysarum coronarium* L. cv. Carmen) and Persian clover (*Trifolium resupinatum* L. cv. Laser) as affected by sowing date in a Mediterranean environment. *Australian J. Crop Sci.*, 2011, **5**(10), 1298–1304.
27. Kim, S. E., Okubo, H. and Kodama, Y., Growth response of dwarf lablab bean (*Lablab purpureus* (L.) Sweet) to sowing date and photoperiod. *J. Japan Soc. Hortic. Sci.*, 1992, **61**(3), 589–594.
28. Kim, S. E. and Okubo, H., Control of growth habit in determinate *Lablab* bean (*Lablab purpureus*) by temperature and photoperiod. *Sci. Hortic.*, 1995, **61**(3–4), 147–155.
29. Upadhyay, A. P., Ellis, R. H., Summerfield, R. J., Roberts, E. H. and Qi, A., Characterization of photothermal flowering responses in maturity isolines of soybean [*Glycine max* (L.) Merrill] cv. Clark. *Ann. Bot.*, 1994, **74**, 87–96.
30. Monks, D. P., Moot, D. J. and Scott, W. R., Photoperiod affects the flowering time of field-sown balansa clover. *Crop Pasture Sci.*, 2010, **61**, 639–644.
31. deRuiter, J. M. and Taylor, A. O., Annual cool-season legumes for forage. III. Effects of temperature, photoperiod and vernalization on flowering. *NZ J. Exp. Agric.*, 1979, **7**, 153–156.
32. Hall, A. E., *Crop Response to Environment*, CRC Press, New York, Washington, DC, 2001, pp. 83–91.
33. Silim, S. N., Gwataa, E. T., Cocb, R. and Omanga, P. A., Response of pigeonpea genotypes of different maturity duration to temperature and photoperiod in Kenya. *Afr. Crop Sci. J.*, 2007, **15**(2), 73–81.
34. Hill, G. D., A requirement for chilling to induce flowering in dolichos lablab cv. Rongai. *Papua New Guinea Agric. J.*, 1967, **19**, 16–17.
35. Acock, M. C. and Acock, B., Photoperiod sensitivity during soybean flower development. *Biotronics*, 1995, **24**, 25–34.

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