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Adaptation of sorghum: characterisation of genotypic flowering responses to temperature and photoperiod

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Abstract Sorghum [*Sorghum bicolor* (L.) Moench] is an important cereal crop grown in a wide range of tropical and temperate environments. This study was conducted to characterise the photothermal flowering responses of sorghum genotypes and to examine relationships between photothermal characteristics and environment of origin in order to better understand the phenological basis of adaptation to environment in sorghum. Twenty-four germplasm accessions and one hybrid from 24 major sorghum-growing areas were grown in a wide range of environments varying in temperature and photoperiod in India, Kenya and Mali between 1992 and 1995. Times from sowing to flowering (f) were recorded, and the responsiveness of $1/f$ to temperature and photoperiod was quantified using photothermal models. Times from sowing to flowering were accurately predicted in a wide range of environments using a multiplicative rate photothermal model. Significant variation in the minimum time to flower (F_m) and photoperiod sensitivity (critical photoperiod, P_c, and photoperiod-sensitivity slope, P_s) was observed among the genotypes; in contrast there was little variation in base temperature (T_b). Adaptation of sorghum to the diverse environments in which it is grown was largely determined by photoperiod sensitivity and minimum time to flower; photoperiod sensitivity determines broad adaptation to latitude (daylength), while variation in the minimum time to flower determines specific adaptation within smaller ranges of latitude, e.g. within the humid and sub-humid tropics.

Key words *Sorghum bicolor* · Flowering · Temperature · Photoperiod · Adaptation

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Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is an important and widely adapted small-grain cereal grown between 40°N and 40°S of the equator (Doggett 1988). It is mainly a rainfed crop of lowland, semi-arid areas of the tropics and sub-tropics and a post-rainy season crop grown on residual soil moisture, particularly in India. Sorghum is also grown in more temperate climates such as southern USA and China, and at mid- to high elevations in the tropics (e.g. Rwanda, Ethiopia). Cold-tolerant sorghums are also an important cereal in Central America.

Sorghum is a short-day plant (SDP), and variation in the response to photoperiod and temperature determines its adaptation to the wide range of different environments in which it is grown. Crop adaptation to latitude is generally determined by photoperiod responses. Tropical crops are normally SDPs but with decreasing photoperiod sensitivity if grown outside the tropics (Roberts et al. 1996), whereas temperate crops tend to be long-day (LDP) plants with decreasing photoperiod sensitivity if grown within the tropics (Erskine et al. 1990). Short-day plants within the tropics often show acute sensitivity to photoperiod, and the response is very closely adapted to latitude and the normal growing season (Curtis 1968a,b; Kassam and Andrews 1975; Roberts et al., 1996). For example, sorghum landraces grown in Nigeria always flower at approximately the

same calendar time (i.e. homeostasis of flowering date) at their location of origin, coincident with the end of the rains at that location, despite wide variations in the time of sowing both within and between years (Curtis 1968b; Kassam and Andrews 1975). When these particular landraces are grown at locations only a short distance (1 to 1.5° latitude, i.e. 110–165 km) south or north of their latitude of origin, flowering occurs earlier or later, respectively, than the end of the rains at the different locations, and yield relative to the locally adapted landrace is reduced (Curtis 1968a,b). While the environmental trigger is undoubtedly photoperiod, the details of the response have not been elucidated: variation in the critical photoperiod (i.e. that photoperiod above which in SPDs longer days delay time to flowering), photoperiod sensitivity, the number of short days after the longest day and photoperiod × temperature interactions have all been proposed as possible mechanisms (Curtis 1968b; Kassam and Andrews, 1975).

Matching phenology to the expected abiotic (water supply, temperature, nutrients) and biotic (pests, diseases) constraints is widely recognised as a prerequisite for good adaptation (e.g. Ludlow and Muchow 1990). Landraces that have evolved over millennia at a particular location should, as the example of sorghum in Nigeria illustrates (Curtis 1968a,b; Andrews 1973; Kassam and Andrews 1975), be well adapted to those particular locations or similar agro-ecological environments (Erskine et al. 1990). Therefore, characterising the flowering responses to temperature and photoperiod of landraces from a wide range of sorghum agro-ecological environments should improve our understanding of the photothermal basis of natural adaptation in sorghum. Furthermore, the study of a wide range of sorghum landraces should provide a more comprehensive description of genetic variation in responsiveness to temperature and photoperiod, and where geographically to find that variation, than has been available to date. Modelling responsiveness to temperature and photoperiod should also permit germplasm in breeding programs to be targeted more effectively to particular agro-ecologies (Lawn et al. 1995).

This paper reports an investigation in which the flowering responses to temperature and photoperiod of the USA hybrid RS610 and 24 landraces from a wide range of sorghum growing environments, including temperate and tropical, high and low elevations, rainy and post-rainy season, were quantified from field experiments in India, Kenya and Mali, and multivariate analyses used to examine relationships between the photothermal characteristics that determine time from sowing to flowering among genotypes and their agro-ecological environment.

Materials and methods

Agro-ecological environments and genotypes

Twenty-four agro-ecological environments covering the most important sorghum-producing areas were identified, and genotypes (germplasm accessions) from each agro-ecological environment selected (Table 1). These agro-ecological environments included

Table 1 Genotype number, grmplasm accession number and origin of genotypes used to study photothermal adaptation in sorghum

Number	IS no.	Geographical origin	Agro-ecological environment	Latitude (°)	Longitude (°)	Elevation (m)	Location
1	Sugar 20	45°N Russia	Temperate	45.40N	38.50E	(–)	Krasnodar, Russia
2	121	40°N USA	(Temperate)	(40.0N)[b]	(96.0W)	(–)	(Originated in Sudan)
3	RS610	40°N USA	Temperate	(40.0N)	(96.0W)	(–)	Nebraska
4	1212	40°N China	Temperate	(40.0N)	(115.0E)	(100)	Chu-Yeh-Ching
5	33094	15°N C. America	Tropical mid-elevation	(14.40S)	(86.30W)	(1000)	Honduras
6	33091	10°N C. America	Tropical lowland	(11.40S)	(85.30W)	(50)	Nicaragua
7	4516	20°N India[a]	Tropical lowland	19.50N	75.23E	580	Aurangabad, India
8	18421	20°N India	Tropical lowland	20.42N	77.20E	280	Akola, India
9	22068	15°N India	Tropical lowland	15.05N	76.32E	500	Teranagar, India
10	5374	10°N India	Tropical lowland	11.20N	76.59E	400	Coimbatore, India
11	20408	14°N W. Africa	Tropical lowland	(13.30N)	(2.10E)	(220)	Jonjari, Nigeria
12	24704	12°N N. Africa	Tropical lowland	11.56N	7.57E	540	Dayi, Nigeria
13	24853	10°N W. Africa	Tropical lowland	10.13N	9.28E	720	Bauchi, Nigria
14	33225	10°N C. Africa[a]	Tropical lowland	10.52N	14.46E	290	Cameroon
15	34969	8°N C. Africa	Tropical lowland	(8.24N)	(20.39E)	(510)	Bangoran, C. African Republic
16	34787	6°N C. Africa	Tropical mid-elevation	(5.58N)	(15.38E)	(1020)	Nana-Membere, C. Africa Republic
17	22365	14°N E. Africa	Tropical lowland	14.00N	35.18E	580	Gedaref Plain, Sudan
18	11758	10°N E. Africa	Tropical high-elevation	9.26N	41.55E	2000	Ethiopia
19	23508	8°N E. Africa	Tropical lowland	8.14N	34.38E	500	Abol, Ethiopia
20	32520	3°N E. Africa	Tropical lowland	3.80N	43.30E	450	Baidoa, Somalia
21	25557	2°S E. Africa	Tropical high-elevation	1.59S	30.40E	2000	Rwanda
22	23166	6°S E. Africa	Tropical mid-elevation	6.10S	35.46E	1120	Dodoma, Tanzania
23	27250	17°S S. Africa	Tropical mid-elevation	(16.47S)	(31.35E)	(960)	Madziwa, Zimbabwe
24	22233	24°S S. Africa	Tropical lowland	(24.40S)	(25.55E)	(90)	Kopong, Botswana
25	26717	28°S S. Africa	Tropical lowland	(27.0S)	(36.0E)	(1000)	Kwa Zulu, S. Africa

[a] Post-rainy season (Rabi, Musquari) types
[b] Parentheses indicate incomplete data

temperate (e.g. 40°N in USA, Russia and China), tropical high- (>2000 m) (e.g. Rwanda, Ethiopia) and mid- (1000 m) elevation (e.g. Honduras, Zimbabwe) and tropical lowland (<1000 m) environments (e.g. West Africa, India). Among the tropical or subtropical lowland environments, which are the most important sorghum agro-ecological environments (Doggett 1988), a series of latitudinal transects between 10° and 20°N in India, 6° and 14°N in West and Central Africa, 3° and 14°N in East Africa and 2° and 28°S in East and Southern Africa were defined. Post-rainy season types from India (Rabi types) and Cameroon (Musquari types) were also included in the study.

In 1991 five germplasm accessions from each agro-ecological environment were grown at Patancheru under natural and extended daylength conditions. Accessions from each agro-ecological environment responded to photoperiod in a similar manner (not presented) and therefore one accession was selected to represent each agro-ecological environment, plus the hybrid RS610 as a check. Seed of each genotype was multiplied at Patancheru by growing and selfing seed from a single panicle of each accession and so the genotypes were thus fairly uniform.

Table 2 Latitude, longitude and elevation of the experimental locations

Location	Latitude	Longitude	Elevation (m)
Patancheru, India	17°30′	17°30′	545
Mtwara, Kenya	03°56′	39°45′	21
Kiboko, Kenya	02°30′	37°45′	980
Alupe, Kenya	02°29′	34°08′	1182
Katumani, Kenya	01°35′	37°14′	1575
Kabete, Kenya	01°15′	36°44′	1912
Muguga, Kenya	01°13′	36°38′	2003
Bamako, Mali	12°34′	07°55′	90

Locations

Experiments were conducted between 1992 and 1996 in India, and in 1995 in Kenya and Mali (Table 2). Experiments in India were all conducted at the ICRISAT Asia Center, Patancheru during the Rabi (mid October through January), summer (February to June) and Kharif (June to October) seasons. Experiments in Kenya were conducted during the short-rainy season (March to June) at six lo-

Table 3 Mean pre-flowering value of temperature (T) and photoperiod (P) and minimum, maximum and mean times from sowing to flowering of 25 genotypes of sorghum grown in India, Kenya and Mali between 1992 and 1995

Location	Sowing date	Mean T (°C)	Mean P (h day^{-1})	Days from sowing to flowering		
				Minimum	Maximum	Mean
Patancheru, India	28.09.92	25.3	12.5	45	86	63
Patancheru, India	28.09.92	25.3	13.6	46	>123[a]	84
Patancheru, India	28.09.92	25.2	14.3	49	>136	89
Patancheru, India	05.10.93	23.3	13.3	48	>131	82
Patancheru, India	05.10.93	23.3	13.6	48	136	86
Patancheru, India	05.10.93	23.3	13.9	51	142	92
Patancheru, India	19.06.94	26.3	13.8	45	>134	83
Patancheru, India	20.02.95	26.8	13.7	47	134	79
Patancheru, India	20.02.95	26.8	14.0	47	>135	76
Patancheru, India	20.02.95	26.9	14.4	48	>153	80
Patancheru, India	20.02.95	26.5	10.4	44	>95	63
Patancheru, India	29.04.95	31.2	13.8	44	>128	80
Patancheru, India	29.04.95	31.2	14.1	45	>129	82
Patancheru, India	29.04.95	31.3	14.6	45	>129	85
Patancheru, India	29.04.95	31.0	10.7	40	105	65
Patancheru, India	17.06.95	27.1	13.9	48	>157	96
Patancheru, India	17.06.95	27.1	14.2	48	>150	91
Patancheru, India	17.06.95	27.1	14.6	49	155	93
Patancheru, India	17.06.95	27.1	11.1	44	93	59
Patancheru, India	08.10.95	23.0	10.8	46	71	57
Patancheru, India	08.10.95	22.5	13.6	52	139	89
Patancheru, India	08.10.95	22.5	13.8	52	143	93
Patancheru, India	08.10.95	22.5	14.2	58	149	95
Patancheru, India	19.10.95	24.4	9.9	42	68	57
Patancheru, India	20.11.96	20.6	10.9	55	84	72
Patancheru, India	20.11.96	20.8	13.5	59	141	89
Patancheru, India	20.11.96	20.9	13.7	67	>126	90
Patancheru, India	20.11.96	21.0	14.1	65	>138	91
Alupe, Kenya	13.03.95	23.6	12.9	51	133	76
Kabete, Kenya	10.04.95	18.2	13.0	60	135	92
Kabete, Kenya	10.04.95	18.4	13.6	61	>169	105
Kabete, Kenya	10.04.95	18.3	14.2	61	>176	109
Kabete, Kenya	10.04.95	18.2	13.0	65	137	94
Katumani, Kenya	10.04.95	18.8	12.8	63	107	81
Mtwara, Kenya	28.04.95	26.4	12.7	47	108	68
Kiboko, Kenya	19.04.95	24.4	12.9	37	95	57
Kiboko, Kenya	19.04.95	24.1	13.8	46	159	92
Kiboko, Kenya	19.04.95	24.0	14.5	47	169	102
Kiboko, Kenya	19.04.95	24.3	13.0	44	107	69
Muguga, Kenya	08.04.95	13.7	12.9	60	>160	108
Bamako, Mali	26.06.95	27.2	13.4	49	144	92
Bamako, Mali	20.07.95	26.8	13.2	56	124	86

[a] > indicates that some genotypes did not flower before the end of the experiment

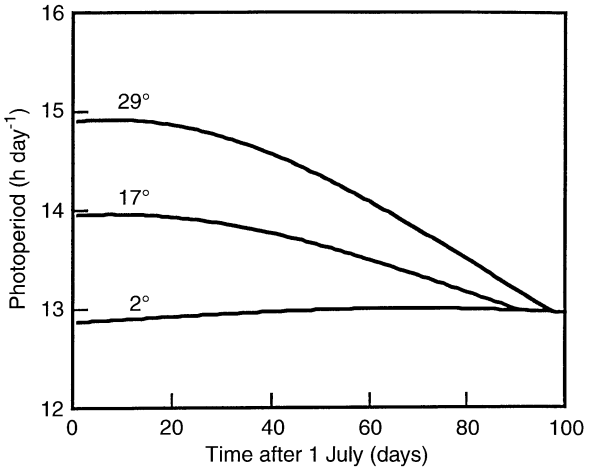

Fig. 1 Simulated photoperiods for a 1 July sowing date at latitudes 29° and 17°N, and the natural photoperiod at 2°N

cations at elevations from 20 to 2000 m. In Mali, experiments were grown at two sowing dates during the rainy season (June to October).

Daylength treatments

At Bamako in Mali and at Mtwara, Alupe, Katumani and Muguga in Kenya experiments were conducted under natural daylengths, while at Patancheru, India and at Kiboko and Kabete in Kenya, both natural and artificially extended daylength treatments were imposed (Table 3). In addition five short-day (10 h, artificially covered for part of the day) treatments were imposed at Patancheru.

The extended daylength treatments were designed to simulate daylength (including civil twilight) for a 15 June planting date at latitudes ranging from 10° to 29°N, and accordingly daylength was adjusted every 7 days to simulate the natural shortening of daylength (Fig. 1). The extended daylength treatments were imposed by suspending 100 W incandescent bulbs (in a 3 × 3-m grid) 1 m above the crop. At this height (which was adjustable up to a maximum height of 4 m) the level of light reaching the uppermost leaves was >20 lux, more than enough to saturate the photoperiod response of most crop plants (Summerfield and Roberts 1987). Lights were switched on in the morning and evening using electronic timers. The short-day treatments at Patancheru were imposed by covering plants with a mobile black-out facility covering an area of 40 m^2. The extended and short daylength treatments started 10–15 days after sowing, which is close to the time plants became sensitive to photoperiod (Caddel and Weibel 1972; Alagarswamy et al. 1998).

Experimental design

All experiments comprised single rows, 2 or 4 m long, of each genotype replicated twice. Within row spacing was 0.2 m. Where daylength extension treatments were imposed, a split-plot design was used with daylength as mainplots. Mainplots were separated by a 30-m border of sorghum or maize to ensure no border light effects. Sowing was done either mechanically (Patancheru) or by hand (Kenya, Mali), and recommended rates of fertilizer applied at each location. All experiments at Patancheru, India and at Kiboko, Kabete and Katumani in Kenya were given supplementary sprinker or furrow irrigation when necessary; the remaining experiments were all rainfed. All experiments were treated prophyllactically to prevent shoot fly (*Atherigona soccata*) and stem borer (*Chilo partellus*).

Observations and data analysis

Days from sowing to 50% seedling emergence and 50% flowering were recorded in all experiments. Daily minimum and maximum air temperature was recorded at the experimental site or at weather stations within 100 m of each experiment.

The effect of temperature and photoperiod on the rate of progress from sowing to flowering ($1/f$) was analysed using a multiplicative rate (DEVEL2) and an additive rate (RODMOD) photothermal model. In the multiplicative model, DEVEL2 (Holzworth and Hammer 1996)

$$1/f = R_{opt} \times f(temp) \times f(pp) \quad (1)$$

where R_{opt} is the rate of development under optimal temperature and photoperiod and f(temp) and f(pp) are modifying functions of temperature and photoperiod, respectively. The response to temperature was modeled using a broken-linear response function (Hammer et al. 1993) which defines the response to temperature in terms of a base (T_b), optimum (T_o) and maximum (T_m) temperature. The response to photoperiod was modeled using a triple broken-linear response function (Roberts and Summerfield 1987; Hammer et al. 1989, 1993) which defines the response to photoperiod in terms of a critical (P_c) and ceiling (P_{ce}) photoperiod, above and below which, respectively, increase in photoperiod reduces $1/f$ (i.e. delays flowering), and the slope between these values defines the sensitivity to photoperiod (P_s). Initial parameterisation of the model revealed that all genotypes had similar values for maximum temperature, T_m, between 40° and 47°C, and therefore T_m was fixed in subsequent runs at 42°C (Hammer et al. 1993). Similarly, the ceiling photoperiod, P_{ce}, was also about 18 h day^{-1} in all genotypes, and this value was therefore fixed at 18 h day^{-1}. After these values were imposed, the models were re-parameterized and quadratic functions used to estimate SE of the parameters. However, SE could not be estimated for all parameters.

In the additive rate model, RODMOD (Watkinson et al., 1994; Roberts et al., 1996), when mean temperature (T) is in the sub-optimal range (i.e. $T \leq T_o$), and mean photoperiod (P) is below P_c, then the 'thermal plane' is given by

$$1/f = a + bT \quad (2)$$

where a and b are genotype specific constants. When $P > P_c$, and photoperiod genes are expressed and delay flowering, then the 'photothermal plane' is given by

$$1/f = a' + b'T + c'P \quad (3)$$

where a', b' and c' are genotype specific constants. When $P \geq P_{ce}$ neither photoperiod or temperature have any further effect of the time of flowering

$$1/f = d \quad (4)$$

where d is a genotype specific constant. In genotypes insensitive to photoperiod only Equation (2) is needed, whereas in genotypes sensitive to photoperiod, and depending on photothermal environment, Equation (3) (e.g. lentils: Erskine et al., 1990) or Equations (2) and (3) (e.g. soybean: Roberts et al., 1996) suffice. Aside from the different modelling approaches detailed above, there are two other important differences between RODMOD and DEVEL2. First, RODMOD has no supra-optimal temperature response routines and therefore observations have to be limited to the sub- or near-optimal temperature range. Accordingly, all observations where T>28°C were excluded in the RODMOD analysis. Second, RODMOD uses mean pre-flowering values of temperature and photoperiod, whereas DEVEL uses a daily input time step.

The root mean square deviation (RMSD) was used to compare the fit of the two models, where

$$RMSD = \sqrt{1/n \sum (f_{obs} - f_{pre})^2} \quad (5)$$

where f_{obs} and f_{pre} is the observed and predicted days from sowing to flowering, respectively, and n is the number of observations.

Principal component analysis (PCA) and Cluster Analysis of the environments and photothermal parameters was carried out using Genstat 5 (Genstat V Committee, 1987).

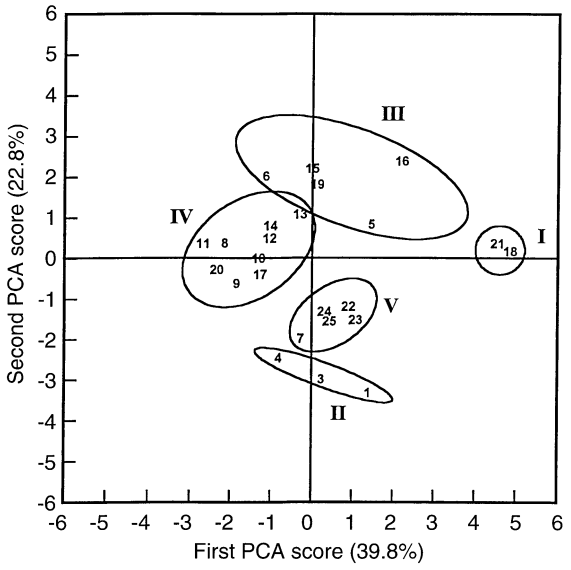

Fig. 2 First and second principal component analysis (PCA) scores for the characterisation of the environments from which the sorghum genotypes originated. The five groups of environments identified from the clustering analysis have been superimposed on the figure

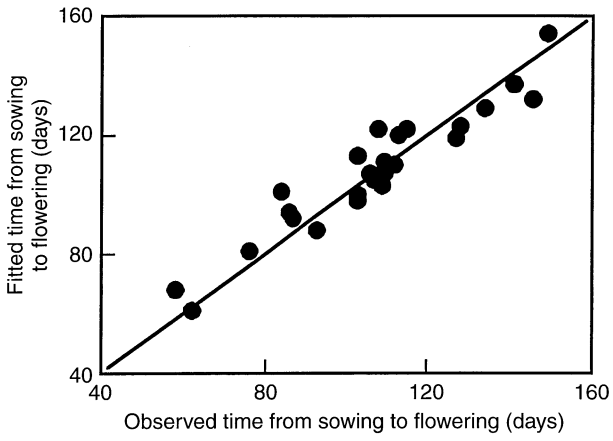

Fig. 3 Relation between fitted and observed times (days) from sowing to flowering in sorghum genotype IS5374. The *x = y line* shows perfect agreement between observed and fitted values

Results and discussion

Characterization of environments

The 25 genotypes originated from a wide range of environments covering latitudes 1° to 45°, altitudes of 50 to 2125 m and with seasonal rainfall totals of 170–1480 mm (Table 1). Indices describing the environments, such as latitude, altitude, the start, end and duration of the rainy season, seasonal rainfall, mean, minimum and maximum temperature and mean photoperiod were obtained from long term weather records (FAO 1984, 1987) for each location or closest location and grouped using PCA and clustering (average linking analysis) techniques.

The first two PCA scores accounted for 62.6% of the variation in environments (Fig 2). The first PCA score (39.8%) discriminated environments on the basis of temperature, with positive loadings for cool minimum, maximum and mean temperature, and high altitude. The second PCA score discriminated environments on the basis of total rainfall, daylength and latitude, with positive loadings for high rainfall, short days and low latitude. The cluster analysis suggested that there were five Groups of environments (at 85% level), and these have been imposed on Fig. 2.

Group I environments were characterized by high elevation and cool temperature and included geographical origins 18 and 21 from 1700 and 2125 m in Rwanda and Ethiopia, respectively. Group II environments, covering geographical origins 1–4, were characterized principally by long days and high latitude, with below average rainfall, shorter growing season and average temperatures, i.e. as temperate environments. Group III environments, covering geographical origins 5, 6, 15, 16 and 19, were characterized as high rainfall, short daylength and warm to average temperatures, i.e humid tropical environments. Group IV environments were characterized as warm, low-elevation, short-day environments with average to low rainfall, i.e. lowland sub-humid to semi-arid tropical environments, and comprised 9 geographical origins. Lastly, Group V environments were characterized as moderately long-day, cool sub-tropical environments and comprised geographical origins from the mid-elevation (1000 m) savannas of southern Africa.

Photothermal modeling of genotypes

Mean pre-flowering temperatures and photoperiods varied substantially across experiments, resulting in considerable variation in times from sowing to flowering (Table 3). Mean pre-flowering temperature ranged from 13.7°C at Muguga in Kenya to 31.3°C in the summer sowings at Patancheru, India and photoperiod from 9.9 h day^{-1} in an artificially shortened daylength treatment at Patancheru to 14.6 h day^{-1} in a simulated daylength at latitude 29°N. These variations in photothermal environment resulted in mean times from sowing to flowering ranging from 57 to more than 109 days (Table 3). The mean minimum time from sowing to flowering ranged from 40 days in warm, short-day genotypes (31°C/10.7 h day^{-1}) to 67 days in cool, long-day ones (21°C/13.7 h day^{-1}) and the mean maximum time from sowing to flowering from 68 days, also in warm, short-days (31°C/10.7 h day^{-1}), to more than 160 days (i.e. some genotypes never flowered) in cold, short-days (13.7°C/12.9 h day^{-1}) and cool, long-days (18°C/>13.6 h day^{-1}).

Both the multiplicative and additive rate models quantified the response of $1/f$ to temperature and photoperiod well in most genotypes over the wide range of photothermal environments imposed, with the coefficient of determinant (R^2) of the models ranging from 0.60 to 0.95 and 0.36 to 0.94, respectively. In the additive model, only Equation (3), i.e. a photothermal plane, was

needed to quantify the response of 1/*f* to temperature and photoperiod, as in the example of lentils (Erskine et al., 1990). However, the multiplicative model more accurately predicted the observed values of *f* (Fig. 3), with values of R^2 ≥0.80 in 20 out of 25 genotypes, and with RMSD values of less than 10% of the latest flowering time in most genotypes (Table 4). In addition, the parameters from the multiplicative model are more useful (in terms of understanding the responses affecting adaptation) than the constants from the additive model and can be easily coupled to existing crop models, and therefore the remainder of this paper will concentrate on parameters from the multiplicative model, DEVEL2.

The minimum time from sowing to flowering (F_m), the inverse of the rate of development, R_{opt}, should reflect differences between genotypes in inherent earliness if it is determined in warm, inductive photothermal environments, i.e. environments where temperature is near optimal and photoperiod is below the critical photoperiod, P_c. The value of P_c in sorghum lies mostly between 12.5 and 13.5 h day^{-1} (Alagarswamy and Ritchie 1991; Hammer et al. 1989), and therefore a number of artificially shortened daylengths of less than 12 h day^{-1} were included in the present investigation to ensure F_m was accurately determined (Table 3). Under inductive short days at 24°–25°C F_m varied by 25 days, ranging from 42

Table 4 Minimum (F_m) and maximum (F_{mx}) values of *f* (days), rate of development at optimal photoperiod and temperature (R_{opt}), base (T_b) and apparent optimum (T_{ao}) temperature (°C), critical photoperiod (P_c, h day^{-1}), photoperiod sensitivity slope (P_s, day^{-1} h^{-1}), coefficient of dtermination of the model (R^2) and RMSD (days) of observed and fitted values of *f* for 25 genotypes of sorghum grown in India, Kenya and Mali between 1992 and 1995. Standard errors of parameters are given where they were estimated

Genotype	F_m	F_{mx}	R_{opt} (×10^3)	T_b	T_{ao}	P_c	P_s (×10^2)	R^2 (n)	RMSD
Sugar 20	45	79	24.6 (0.54)	8.3	30.5 (0.11)	16.1	–25.0 (3.29)	0.82 (33)	5.9
IS121	44	87	21.2 (0.86)	9.4	22.7 (0.63)	14.9	–23.6 (1.45)	0.75 (32)	5.4
RS610	44	93	26.7 (0.44)	10.0	30.0 (0.06)	17.5	–35.2 (0.08)	0.95	4.5
IS1212	45	80	25.1 (0.31)	8.7	29.1	17.1	–26.4	0.86 (36)	5.1
IS33094	55	160	16.6 (0.82)	11.9	20.3 (0.68)	11.3 (1.02)	–19.9 (0.34)	0.60 (27)	18.2
IS33091	59	167	18.3 (2.33)	8.4	20.6 (0.80)	11.1	–24.0 (0.79)	0.85 (22)	11.5
IS4516	60	112	17.1 (0.32)	8.9	26.2 (0.06)	14.1	–20.2 (1.67)	0.92 (35)	4.4
IS18421	51	106	19.0 (0.80)	9.0	22.3 (0.22)	12.2	–11.5 (0.24)	0.78 (36)	6.7
IS22068	53	102	17.6 (3.26)	9.3 (0.53)	24.8 (0.09)	14.4 (0.15)	–18.8 (0.72)	0.83 (37)	5.3
IS5374	58	149	17.4 (1.72)	10.4	21.0 (0.36)	11.5 (0.45)	–19.6 (0.52)	0.88 (31)	7.7
IS20408	42	113	26.0 (1.64)	9.5	21.6 (0.68)	11.1 (0.24)	–14.0 (0.29)	0.77 (34)	8.8
IS24704	50	168	21.7 (2.44)	10.2 (2.74)	22.6 (1.81)	10.9 (0.62)	–22.6 (1.35)	0.84 (30)	12.2
IS24853	52	151	23.7 (1.74)	10.6 (0.40)	20.2 (0.74)	10.7 (0.16)	–21.5 (1.97)	0.82 (28)	13.9
IS33225	57	177	19.8 (3.20)	9.8	24.6 (0.60)	10.9	–19.8 (0.34)	0.85 (20)	13.5
IS34969	58	153	18.9 (2.74)	8.7	20.1	10.5	–19.4 (0.49)	0.80 (20)	13.0
IS34787	54	165	20.2 (1.39)	8.8	22.2 (0.51)	10.7	–22.5 (0.27)	0.84 (23)	12.6
IS22365	52	134	22.5 (4.75)	9.5	20.6 (2.28)	11.2 (0.73)	–14.2 (1.45)	0.81 (35)	10.4
IS11758	67	118	16.4 (1.51)	8.9 (0.17)	24.0 (1.25)	11.8 (0.27)	–9.9 (6.6)	0.82 (33)	6.5
IS23508	56	99	17.6 (0.42)	9.2	22.9 (0.11)	12.5	–8.3 (0.09)	0.65 (38)	5.9
IS32520	49	105	22.7 (1.04)	9.5 (0.06)	23.0 (0.21)	11.4 (0.13)	–12.5 (1.21)	0.79 (38)	6.8
IS25557	54	122	22.8 (0.00)	10.5	20.8 (0.34)	11.3	–20.0 (0.31)	0.81 (32)	9.8
IS23166	45	145	24.7 (1.58)	12.2 (0.39)	20.1 (1.09)	10.2 (0.31)	–17.7 (1.63)	0.87 (31)	10.6
IS27250	52	142	21.2 (3.58)	9.4	20.8 (0.55)	10.5 (0.16)	–16.8 (0.99)	0.80 (28)	11.6
IS22233	49	94	21.7 (0.51)	8.6	28.8 (0.18)	14.5 (0.10)	–22.7 (3.46)	0.89 (38)	7.6
IS26717	54	110	18.2 (0.25)	9.0	27.0 (0.07)	14.6 (0.64)	–23.6	0.92 (34)	4.9

days in IS20408 to 67 days in IS11758 (Table 4). In contrast, under natural days (12.9 h day^{-1}), at the same mean temperature, F_m ranged from 37 to 95 days (Table 3), emphasizing the importance of using appropriate photothermal environments for screening.

The range in F_m of 25-days found here, which should largely reflect variation in the length of the juvenile or basic vegetative phase (BVP) rather than the panicle development phase (Alagarswamy et al. 1998), was greater than the range in juvenile phase reported by Alagarswamy and Ritchie (1991), Ellis et al. (1997) and Alagarswamy et al. (1998) of 5 to 13 days. This greater range in F_m probably reflects the wider range of germplasm used in our study, though it is possible that the short-day treatments of 10 h day^{-1} were not below P_c in all cases or that the short-day treatments started after plants become inductive, between 5 and 9 day according to Alagarswamy et al. (1998). In general, values of F_m were smallest (<45 days) (i.e. rate of development was fastest) in photoperiod-insensitive genotypes such as Sugar 20, RS610, IS121 and IS1212 and greatest (>55 days) in genotypes originating from latitudes 8°-10°N (e.g. IS11758, IS33091) and in post-rainy season genotypes (IS4516 and IS33223).

The broken-linear temperature function described the response to temperature well, and it was clear that time to flowering was delayed in the warmest temperature regimes and that T_o was exceeded. Although the maximum mean pre-flowering temperature of 31.5°C was close to published values for T_o (30°C: Hammer et al. 1989, 1993) the maximum daily temperature exceeded this value in many experiments and reached a maximum value of 43.0°C in May at Patancheru, and therefore T_o was certainly transgressed during the pre-flowering period at some locations. Similarly, although the T_b in sorghum is about 8–12°C (Hammer et al. 1989, 1993; Alagarswamy and Ritchie 1991), and the lowest mean temperature 13.7°C, daily minimum temperatures below this threshold were recorded at Muguga (0.6°C) and T_b was therefore also transgressed at some locations. At Muguga, the coolest location, predicted values of *f* were always earlier that observed values of *f*, confirming observations of frost damage, and accordingly these data were excluded from the analysis.

There was very little variation in T_b among genotypes (mean 9.5°±0.98°C, Table 4), with all values lying between 8° and 11°C except for IS33094 (11.9°C) and IS23166 (12.2°C), despite the wide range of agro-ecological environments, and particularly different elevations, from which the landraces originated. These results support experiments with the same genotypes in controlled environments (Craufurd et al. 1998) and other data which suggests that T_b is very conservative in sorghum (e.g. Hammer et al. 1989). However, in other crops such as soybean (Roberts et al. 1996) and rice (Dingkuhn and Miezen 1995) there appears to be more variation in T_b among genotypes.

In contrast to T_b, values of T_o varied significantly among genotypes (Table 4), from 30.5°C in Sugar 20 to 20.1°C in IS34969 and, in general, T_o was higher in photoperiod-insensitive genotypes (e.g. Sugar 20, RS610) than in photoperiod-sensitive genotypes. However, because of the interaction between photoperiod and temperature (Yan and Wallace 1996), wherein the response to photoperiod modifies the response to temperature, the values of T_o are better termed as the 'apparent optimum temperature', T_{ao}. The variation in T_{ao} therefore reflects variation in photoperiod sensitivity rather than variation in the response to temperature *per se*, and this is illustrated by the strong relationship between T_{ao} and P_c (Fig. 4), discussed below. It is therefore only in genotypes insensitive or relatively insensitive to photoperiod such as Sugar 20, IS1212 and RS610 that the value of T_{ao} is close to T_o. The value for T_o for RS610 of 30°C is similar to the values of 27.4°-32.8°C reported for the same hybrid by Hammer et al. (1989, 1993).

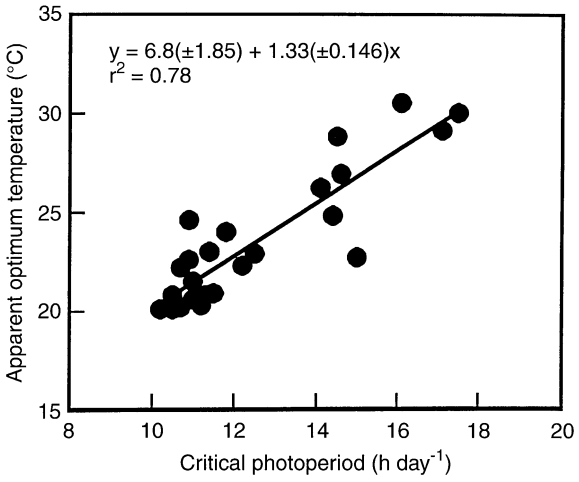

Fig. 4 Relation between the apparent optimum temperature (T_{ao}, °C) and the critical photoperiod (P_c, h day^{-1}) among 25 genotypes of sorghum

The response to photoperiod was well defined by the triple broken-linear model and the critical photoperiod, P_c, varied from 17.5 h day^{-1} in RS610 to 10.2 h day^{-1} in IS23166 and the photoperiod-sensitivity slope, P_s, from –0.083 (day^{-1} h^{-1}) in IS23508 to –0.352 (day^{-1} h^{-1}) in RS610 (Table 4). In the multiplicative model used the value of P_c, which determines when the photoperiod function [f(pp)] is switched on, is the major determinant of sensitivity to photoperiod and therefore genotypes with low values of P_c (i.e. <14 h day^{-1}) were the most sensitive to photoperiod and those with high values of P_c (>14.5 h day^{-1}) were relatively insensitive to photoperiod. Thus Sugar 20, IS1212, RS610, IS26717 and IS22233 were all relatively insensitive to photoperiod, while genotypes similar to IS24853 and IS33091, for example, were all acutely sensitive to photoperiod.

It is difficult to judge whether the range in photoperiod-sensitivity observed in our study is similar or greater than that reported elsewhere because of differences in analytical procedures (e.g. calendar or thermal time, rates), development stage (panicle initiation or flower-

Table 5 Principal components of axes 1, 2 and 3, and the prcentage variation accounted for by each axis, for the photothermal parameters minimum time to flowring (F_m), base (T_b) and apparent optimum (T_{ao}) temperature, critical photoperiod (P_c) and photoperiod-sensitivity slope (P_s)

	Principal component axes		
	1	2	3
F_m	0.30	–0.57	–0.66
T_b	0.30	0.68	–0.07
T_{ao}	–0.58	–0.16	0.02
P_c	–0.59	0.06	0.07
P_s	–0.36	0.43	–0.75
% variation	50.3	25.7	13.5

ing) and because sensitivity is determined by both P_c and P_s (and in the model used here by T_{ao} as well). Alagarswamy and Ritchie (1991) quantified the response of panicle initiation to photoperiod, using the equivalent thermal time rather than rate approach, and found P_s, at values of P_c of 11–12 h day^{-1}, to vary from approximately –0.05 to –0.50 while Hammer et al. (1989) reported a mean P_s of –0.19 (P_c=13.2h day^{-1}) for eight sorghum hybrids. In general and allowing for the different model used, the range in photoperiod-sensitivity found among the wide range of landraces investigated here appears to be similar to that previously documented.

Characterisation of photothermal parameters

A PCA was carried out on the photothermal model parameters (Table 4) quantifying the response of 1/*f* to temperature and photoperiod, namely F_m, T_b, T_{ao}, P_c and P_s, to examine genotypic variation in *f*. The PCA scores and latent vectors for axes 1, 2 and 3 are presented in Table 5, and axes 1 and 2 plotted in Fig. 5.

The first PCA score (50.3% variation) discriminated genotypes largely on the basis of T_{ao} and P_c and is therefore separating genotypes on the basis of whether they are relatively insensitive to photoperiod (negative loading), i.e. have a high value for P_c and a high value for $T_{ao,}$ or sensitive to photoperiod (positive loading), i.e. have a low value of P_c and T_b (Table 5). The latent vectors for P_c and T_{ao} both have the same direction and strength, and the latent vector for P_s is within 90° of P_c and T_{ao}, indicating that all three vectors discriminate in a similar manner. Accordingly, genotypes 1, 3 and 4 are insensitive to photoperiod, genotypes 2, 7, 9, 24 and 25 are relatively insensitive to photoperiod, while all the remaining genotypes are sensitive to photoperiod.

The second PCA score (25.7% variation) has positive loadings for T_b and P_s and negative loadings for F_m, and therefore discriminates between those genotypes that are inherently late flowering and have a lower T_b (e.g. genotypes 15, 18 and 19) and those that are inherently early flowering and have higher T_b (e.g. genotypes 5, 13 and 22). The latent vectors F_m and T_b formed an angle greater than 90° relative to each other, indicating that they

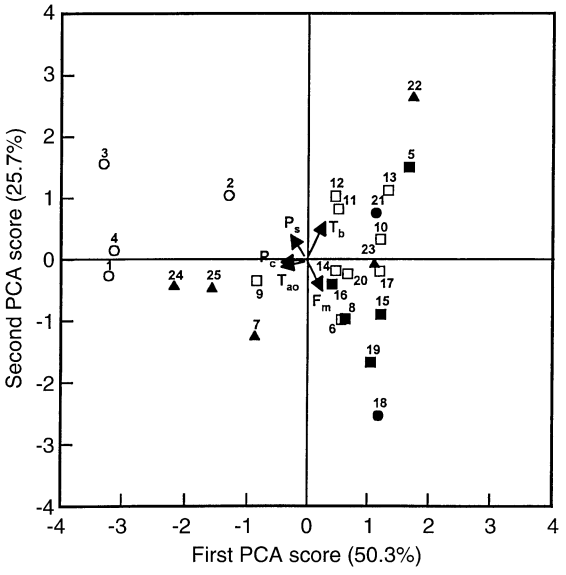

Fig. 5 First and second principal component analysis (PCA) scores for the characterisation of photothermal parameters among 25 genotypes of sorghum. The direction of the latent vectors T_b, T_{ao}, P_c, P_s and F_m are shown by *arrows*. Individual genotypes are identified by their *number* (see Table 1) and their environmental group (see **Fig. 2**) by the symbols: ● Group I, ○ Group II, ■ Group II, □ Group IV, ▲ Group V

were not discriminating in a similar manner, and some genotypes had high value F_m and T_b. In contrast, F_m and T_b formed an angle of approximately 180° with P_s and P_c/T_{ao}, respectively, indicating that they discriminated in the opposite direction to P_s and P_c/T_{ao}. The third PCA score accounted for 12% of the variation and contrasted those genotypes with low value for P_s and early F_m (e.g. 8, 11 and 19) with high value P_s and late F_m (e.g. 6, 10 and 14).

The genotype responses identified in the PCA of the photothermal parameters were largely in accord with the environmental groupings identified previously (Fig. 2). In general, genotypes from temperate (Group II: open circles) and the mid-elevation tropics (Group V: solid triangles) were insensitive or relatively insensitive to photoperiod, temperate genotypes more so, while those from the humid (Group III: solid squares) and sub-humid (Group IV: open squares) tropics and high-elevation areas (Group I: solid circles) were sensitive to photoperiod. Temperate genotypes also tended to have a smaller F_m than mid-elevation genotypes. Similarly, among the photoperiod-sensitive genotypes, those from the humid lowlands (Group III) had later F_m and lower T_b than those from sub-humid and semi-arid lowlands (Group IV).

Environmental adaptation of sorghum

This analysis suggests that there are two major mechanisms controlling time from sowing to flowering, and hence adaptation, in sorghum; first, whether genotypes

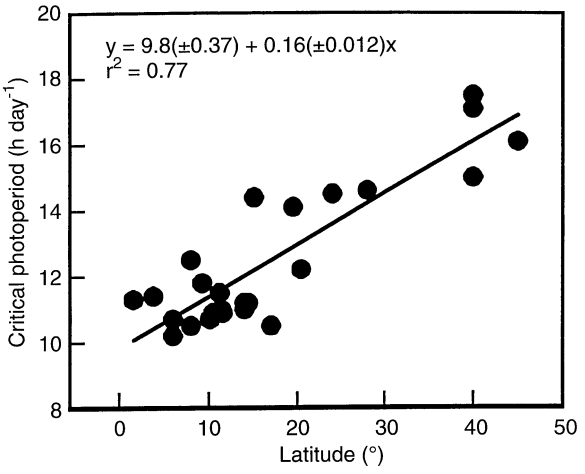

Fig. 6 Relation between the critical photoperiod (P_c, h day^{-1}) and latitude of origin among 25 genotypes of sorghum

are sensitive or insensitive to photoperiod and, second, whether genotypes are inherently early/late flowering or have low/high T_b. Given that photoperiod sensitivity is the most important mechanism governing adaptation, and that this environmental signal or trigger is fixed in relation to latitude, it is not surprising that there is a strong relationship (r^2=0.77, P<0.001) between photoperiod-sensitivity (given by P_c) and latitude of origin (Fig. 6), with photoperiod sensitivity increasing at lower latitudes. A similar relationship between latitude of origin and photoperiod sensitivity has been reported previously in soya bean, also an SDP (Roberts et al. 1996), and the reverse relationship (i.e. photoperiod sensitivity increasing with latitude) in the LDP lentil (Erskine et al. 1990).

The reasons why photoperiod sensitivity should change systematically with latitude have been discussed in detail by Roberts and Summerfield (1987) and Roberts et al. (1996). Briefly, seasonal variation in photoperiod (including civil twilight) decreases with latitude from 3.95 h day^{-1} at 30° to 1.16 h day^{-1} at 10°, while in the tropics variation in temperature is small and temperatures are warm and near optimal for development from sowing to flowering. Under these circumstances, genotypes that are relatively insensitive to photoperiod flower and mature too early in the tropics to accumulate sufficient biomass for high seed yield (Mayers et al. 1991). For example, the photoperiod-insensitive genotype RS610 would flower after 40 days in the tropics (i.e. at 30°C and 12–13h day^{-1}) compared with about 90 days and more than 140 days in the moderately and strongly photoperiod-sensitive genotypes IS20408 and IS24853, respectively (see Fig. 7, which shows isopleth maps of days from sowing to flowering in relation to mean temperature and photoperiod generated from the photothermal model parameters). Therefore, in order to ensure a long enough crop duration and/or homeostatis of crop duration in the tropics where the strength of the signal (photoperiod) is weak, sensitivity to that signal must be increased.

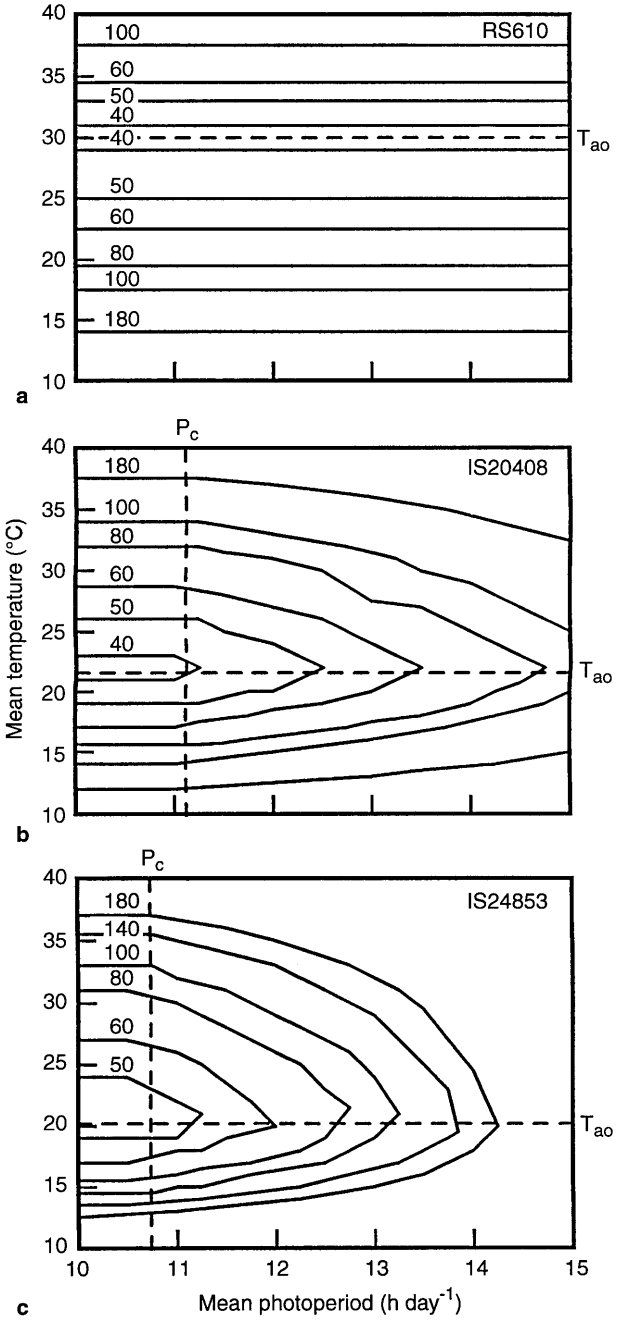

Fig. 7a–c Isopleths showing time from sowing to flowering (days) as a function of temperature (°C) and photoperiod (h day^{-1}) in sorghum genotpyes: **a** RS610, **b** IS20408, **c** IS24853

The relationship between F_m and latitude was much weaker (r=–0.48, P<0.05), and among the tropical sorghums (i.e. excluding those from >30°N) there was no relationship (r=–0.06). However, when the relationship between F_m and latitude is examined across the series of transects in North and Central America, India, West and East Africa and southern Africa a clearer picture emerges (Fig. 8). In the transects from 10° to 40°N in America, 10° to 20°N in India and between 8° and 15°N in West and East Africa F_m decreases as latitude increases. How-

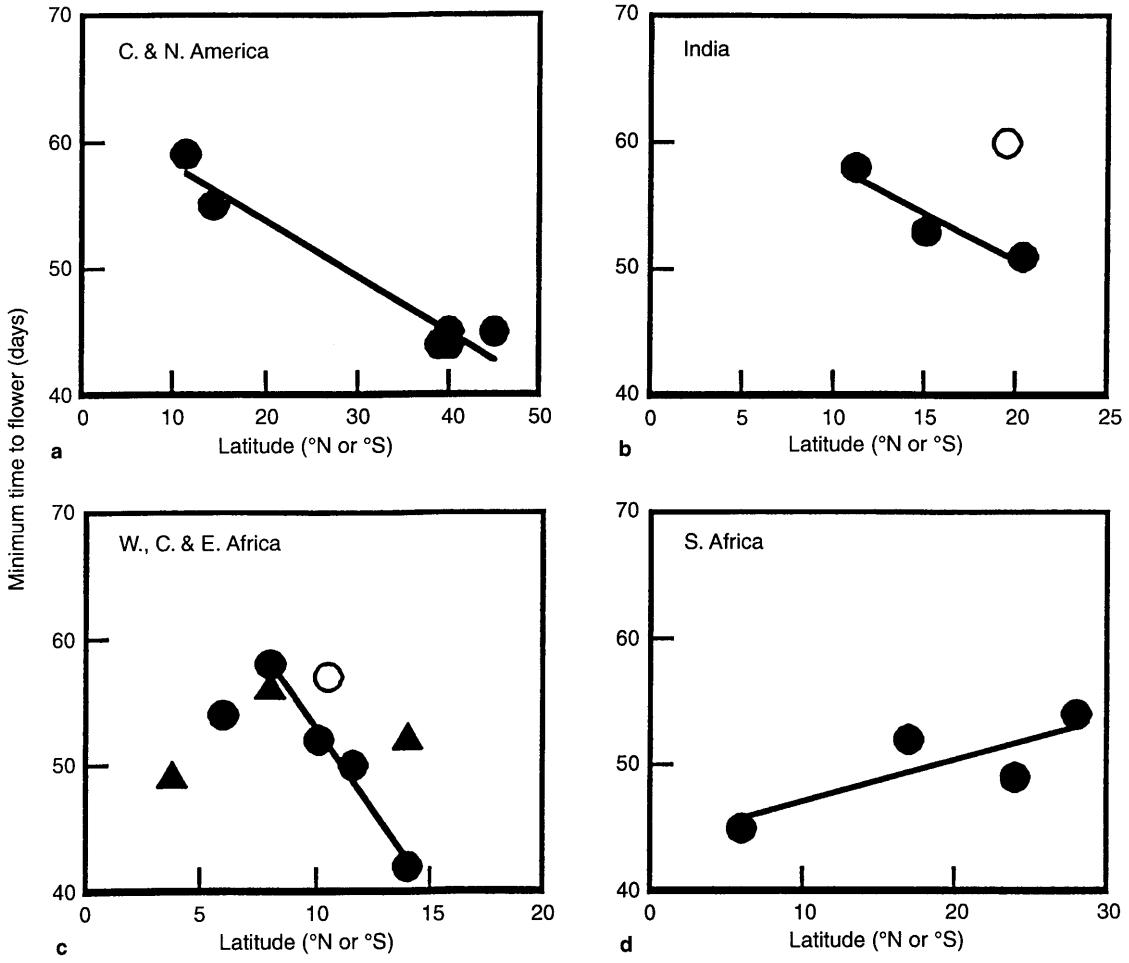

Fig. 8a–d Relation between minimum time to flower (F_m, days) and latitude of origin for genotypes originating in: **a** Central and North America, **b** India, **c** West and Central (●) and eastern (▲) Africa, **d** southern Africa. *Open symbols* in **b** and **c** are post-rainy season genotypes

ever, at latitudes <8°N in west and east Africa, in post-rainy season genotypes and in southern Africa the relationship was different.

In general genotypes of sorghum originating from higher latitudes were both less photoperiod sensitive and were inherently earlier than those from lower latitudes, confirming similar relationships found in soya bean (Roberts et al. 1996). Apparently, the spread into more sub-tropical and temperate latitudes, where temperature as well as rainfall is the major determinate of season length (Evans 1993), has required short duration genotypes with a high degree of homeostatis of crop duration (e.g. RS610; Fig. 7) and this could only be achieved by both photoperiod insensitivity and inherent earliness. Indeed, in soya bean there is a strong relationship between the length of the juvenile (pre-inductive phase) and the presence of the photoperiod-sensitivity genes E_{1-3} (Roberts et al. 1996). However, although photoperiod insensitivity and inherent earliness are correlated in soya bean and sorghum, in rice insensitivity to photoperiod is often associated with a longer basic vegetative phase or F_m (Vergara and Chang 1985; Dingkuhn and Miezen 1995).

Sorghum evolved in West and East Africa (Dogget 1988), and it is among genotypes from these regions that the greatest variation in F_m, 20 days between latitudes 8° and 14°N, occurs. Furthermore, all the genotypes from this region (11–20, excluding 18) were photoperiod sensitive, most highly so (Table 4). Because of oscillation of the Inter-Tropical Convergence Zone the duration of the rainy period in West Africa declines from about 200 days at 7°N to 80 days at 13°N, with the end of the rains being far less variable than the start of the rains (Kowal and Knabe 1972). Furthermore, variation in mean temperature during the growing season at latitudes 7° to 13°N is small, temperature averaging 25 to 27°C (Kowal and Knabe 1972). Sorghum, and other crops originating in West Africa such as cowpea (Wien and Summerfield 1980), have, therefore, had to adapt to a variation in season length with latitude coupled with variable sowing dates, but also to comparatively stable end to the rainy period at a given latitude (Curtis 1968a,b; Andrews 1973).

Photoperiod sensitivity provides a mechanism contributing to the homeostatis of flowering at a given location that is independent of variable sowing dates (Curtis 1968b; Andrews 1973; Roberts et al. 1996), and it is no-

table that genotypes from 8° to 12°N (e.g. IS33091, IS5374, IS24853, IS33225 and IS 34969) all have the same acute photoperiod sensitivity (Table 4). Interestingly, the most photoperiod-sensitive genotypes of cowpea are also found at latitudes 8°–11°N (Wien and Summerfield 1980). Thus, given that mean temperatures during the growing season are similar and genotypes have a similar photoperiod sensitivity, then genotypes at 8°N would flower sooner than genotypes at 12°N because mean and absolute photoperiods are shorter (e.g. compare *f* at 13 and 13.5h day^{-1} in IS24853; Fig. 7c). However, a longer F_m would compensate for the shorter daylength at lower latitudes and hence increase time to flowering for the longer growing season found at lower latitudes. Similarly, adaptation to the short growing season of the Sahel at 14°N, where daylengths are correspondingly longer, is achieved by lower photoperiod sensitivity, thus still ensuring some homeostasis of flowering date, coupled with a much shorter F_m (e.g. IS20408; Fig. 7b). Thus, at Niamey (14°N), which has a rainy season of approximately 90 days (Sivakumar et al., 1993), the genotype originating from that zone, IS20408, would flower in about 90—100 days at the prevailing mean temperatures and photoperiods of close to 30°C and 13.7 h day^{-1}, respectively (Fig. 7b). Similarly, at Bauchi (10°N), which has a rainy season of approximately 130 days, the genotype originating from that zone, IS24853, would flower in about 140—160 days at the prevailing mean temperatures and photoperiods of close to 27°C and 13.4 h day^{-1}, respectively (Fig. 7c).

Two post-rainy season (Rabi in India Musquari in Cameroon) genotypes (IS4516 and IS33225) were included in this study and both had a longer F_m (5–10 days) than rainy season genotypes from the same latitude and environment (Fig. 8, open symbols). Although these differences in F_m are not large, it is logical that F_m should be longer (and photoperiod sensitivity less) in post-rainy season types since they are usually sown into short, inductive daylengths (e.g. November in India) and therefore some mechanism is needed to prevent precocious flowering. However, temperatures are usually cooler in the post-rainy season, which would also contribute to a delay in flowering.

In contrast to the negative relations between F_m and latitude observed for genotypes from the northern hemisphere, the relationship among genotypes from southern Africa was generally positive (Fig. 8). These 4 environments formed a distinct group (Group V: Fig. 2) in the PCA and clustering analysis, characterised by cooler temperatures and generally lower rainfall totals than for lowland tropical environments (Group IV), as well as a different growing season. However, mean photoperiods were similar, and it is difficult to see why F_m should be longer at higher latitudes in the southern hemisphere, since environmental conditions are essentially the mirror of conditions in the northern hemisphere during the growing season. The two genotypes from lower than 8° latitude from Central and East Africa also had a shorter F_m than genotypes from 8° or higher and therefore did not follow the trend observed in West Africa, India and America. This reduction in F_m with latitude was not associated with a concomitant increase in photoperiod sensitivity, which Roberts et al. (1996) have argued would be needed to stabilise crop duration at such latitudes.

An alternative explanation for these different relations between F_m and latitude lies in the length of the growing season. For example genotype 20 from latitude 3.8°N in Somalia (Fig. 8c) is from an area with a particularly short growing season (<90 days) where the premium would undoubtedly be on earliness *per se*, while the length of the growing season is about 140 days at 6°S (Tanzania) and 16°S (Zimbabwe), 90 days at 24°S (Botswana) and 172 days at 28°S (Kwa-Zulu). Therefore, some of the variation in F_m may reflect adaptation to particularly short season environments and aross all environments there was a significant (r=0.44, P<0.05), but not strong, relationship between F_m and growing season length.

There was little variation among genotypes T_b (Table 4) and this was therefore not an important adaptive mechanism among the genotypes studied, despite the inclusion of temperate adapted genotypes and 2 genotypes from a high elevation close to the equator (genotypes 18 and 21) where long term seasonal minimum and mean temperatures were 12°–14°C and 17°–18°C, respectively. One possible explanation for this is that in the lowland tropics of West Africa, which is an important centre of diversity of sorghum (Doggett 1988), there is not much variation in mean temperature during the growing season (Kowal and Knabe 1972), and therefore variation in T_b did not evolve in this environment, since such a mechanism would be redundant. However, given the almost universal value for T_b of about 10°C in other tropical cereals and legumes (though not maize where more intensive selection for highland and lowland types has occurred), the conservative response to temperature observed here may simply reflect a conservative response of enzymes to temperature.

In conclusion, this study has shown that the time from sowing to flowering, *f*, in diverse sorghum genotypes can be accurately predicted in a wide range of environments using a multiplicative rate photothermal model. Significant variation in the minimum time to flower (F_m) and photoperiod sensitivity (critical photoperiod, P_c, and photoperiod sensitivity slope, P_s) was observed among the genotypes; in contrast there was little variation in base temperature (T_b). Adaptation of sorghum to the diverse environments in which it is grown is determined largely by photoperiod sensitivity and minimum time to flower; photoperiod sensitivity determines broad adaptation to latitude (daylength) while variation in the minimum time to flower determines specific adaptation within smaller ranges of latitude, e.g. within the humid and sub-humid tropics.

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