



## Modeling of sorghum response to photoperiod: a threshold–hyperbolic approach

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### Abstract

High photoperiod sensitivity is a singular trait for adaptation of sorghum to environmental constraints in sudano-sahelian West Africa. Difficulties encountered by selected models such as CERES-sorghum and STICS to simulate crop development may result from the representation of sorghum response to daylength during the photoperiod inductive phase. Four modeling approaches combining two temperature and photoperiod responses (linear, hyperbolic) and two calculation methods for development rates (cumulative, threshold) were evaluated to simulate time to panicle initiation (PI) in highly photoperiod sensitive *Guinea* sorghum variety CSM388. In the cumulative method, development rates were computed as summations of daily photothermal ratios, whereas in the threshold method accumulated degree days were tested against thermal time requirement to PI modulated by current photoperiod. Each model was calibrated based on observations from a Sotuba, Mali (12°39'N) planting date experiment spanning a 2-month period in 1996. Observed time from emergence to PI decreased from 54 to 22 days for a 20 min variation in daylength. Apparent higher performance by threshold methods was further tested against a 1994 independent dataset featuring three latitudes and a much wider range of sowing dates extending from February to September. Results validate the superiority of threshold over cumulative methods and confirm the better fit of a hyperbolic temperature and photoperiod response. A threshold–hyperbolic modeling approach is believed to be more consistent with crop physiology as it associates cumulative (temperature) processes and trigger (photoperiod) events that better reflect the concepts of quantitative plant growth and qualitative plant development. Its mathematical form and computational simplicity should ensure wide applicability for varietal screening over a large range of photoperiod sensitivities including neutral cultivars, and easy implementation into existing models.

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**Keywords:** Sorghum; Development rate; Photoperiod sensitivity; Phenological modeling

### 1. Introduction

Sorghum (*Sorghum bicolor* L. Moench) plays an important role as a major staple crop of semi-arid and

sub-humid tropical Africa. In Mali alone, sorghum accounts for up to 30% of total cereal production. Within this region, length of the growing period (LGP) is mainly a function of the date of the first rains (Sivakumar, 1988), which is delayed with latitude and varies widely from year-to-year. Sudano-sahelian agro-ecologies are prone to climatic risk and a good knowledge of cultivar development cycles is required

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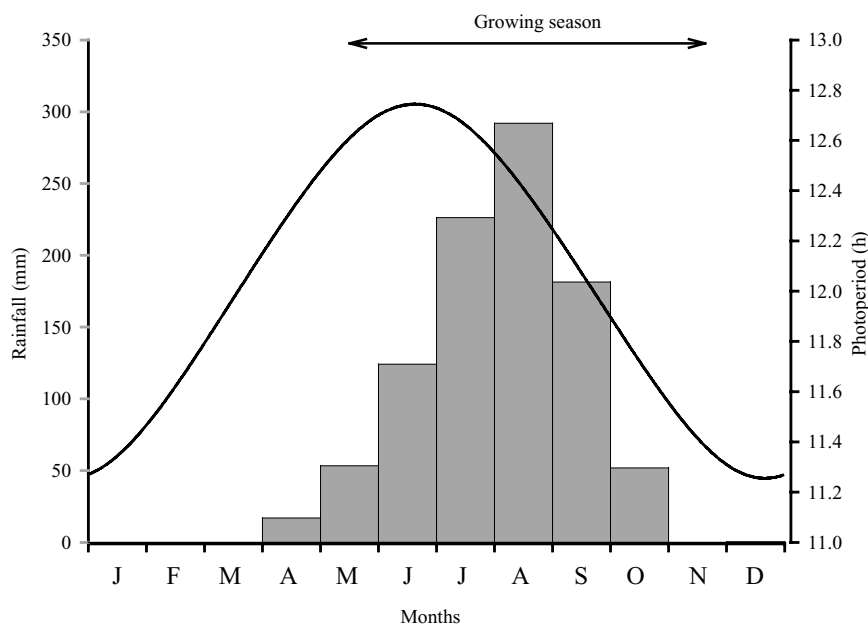


Fig. 1. Yearly variation of monthly rainfall and astronomical daylength in Sotuba, Mali ( $12^{\circ}39'N$ ,  $7^{\circ}55'W$ ). Most of sorghum growth occurs after summer solstice under decreasing daylength.

to best fit crop cycles to probable duration of the rainy season.

Sorghum is a short day photoperiod sensitive crop. Progress towards flowering is accelerated when daylength decreases. In West Africa, favorable conditions for sorghum cultivation usually extend from May to November. Most of the plant growth thus takes place under decreasing daylength (Fig. 1), explaining why cycle duration shortens when sowing is delayed.

Photoperiod sensitivity is a singular trait for adaptation to environmental constraints. In the sudano-sahelian zone, it allows for grouped flowering at the end of the rainy season for a wide range of planting dates (Traoré et al., 2000). This feature is useful to minimize grain mold and insect and bird damage that typically affect early maturing varieties, and to avoid incomplete grain filling, a problem for late maturing varieties faced with soil water shortage at end of season (Cochemé and Franquin, 1967; Curtis, 1968a,b; Kassam and Andrews, 1975; Vaksman et al., 1996).

However, photoperiod sensitivity traits are absent or faint in modern sorghum varieties. Removal of this characteristic has been a priority objective in breeding strategies (Doggett, 1986; Kouressy et al., 1998;

Major and Kiniry, 1991), notably to allow sorghum to produce in the longer daylengths of the temperate areas (Miller, 1982). Contrastingly, these enhanced varieties appear poorly adapted to West African agroecologies characterized by high LGP variability and climatic risk (Sivakumar, 1988) and where adoption rates remain very low (Stoop et al., 1981; Matlon, 1987).

The considerable role of photoperiod sensitivity for crop adaptation highlights the need for agricultural research to incorporate this trait as an important criterion for variety acclimation in this region. To do this, simulation models are useful research tools to investigate and understand genotype  $\times$  environment interactions in complex cropping systems of West Africa. Available models usually predict vegetative stage durations from sowing dates, but fail to simulate the development of strongly photoperiod sensitive sorghums of Mali.

For the purpose of our work, a suitable model is needed to simulate sorghum phenology under the range of conditions encountered in Mali. Genetic coefficients used by the model for each cultivar should be obtained through simple planting date experiments inside the growing season. The model should be usable

to screen large numbers of varieties, either for agro-climatic adaptation studies or for breeding purposes.

Sorghum phenology during the vegetative stage (from emergence to panicle initiation (EPI)) features two phases: a juvenile phase of 15–25 days, during which panicle initiation is not possible, regardless of daylength (Caddel and Weibel, 1972); a photoperiod sensitive phase which ends at panicle initiation. For short day plants, models generally consider that the duration of the vegetative phase increases with increasing daylength.

A first category of models relies on a linear relationship between vegetative phase duration and daylength initially described for rice (Vergara and Chang, 1985) and later generalized to other short or long day plants (Major, 1980) including sorghum (Ritchie and Alagarswamy, 1989). Another type of model features a very fast increase in vegetative stage duration with daylength using a hyperbolic function (Franquin, 1976; Hadley et al., 1983; Hammer et al., 1989; Vaksman et al., 1996).

The mode of calculation of crop development stage through daily iterations reveals another notable difference between models. In most cases, *crop development* is conceptualized in a manner similar to *crop growth* with the use of a daily cumulative photothermal age (Alagarswamy and Ritchie, 1991; Horie, 1994; Brisson et al., 2002; Stewart et al., 2003). Another procedure has been proposed for African sorghums (Vaksman et al., 1997). In that method, panicle initiation takes place when photoperiod drops below a cultivar-specific threshold which varies also depending on plant age.

This paper presents results to illustrate these different modeling approaches and discusses the opportunity to extend the validity of selected models to include highly photoperiod sensitive sorghum varieties.

## 2. Materials and methods

### 2.1. Driving variables

Thermal time after planting is computed using an algorithm by Jones and Kiniry (1986), considering that growth speed increases as a linear function of temperature between a base and an optimal temperature, and then decreases linearly between an optimal

and maximal temperature. Values published by Ritchie and Alagarswamy (1989) for sorghum are employed (base, 8 °C; optimal, 34 °C; and maximal, 44 °C temperatures).

Daylength used is civil daylength, which includes periods when the sun is 6° below the horizon to account for photoperiod response during twilight (Aitken, 1974). Calculations are made using formulae published by Baille et al. (1983). For the main experimental site of Sotuba, daylength varies from 12 h 9 min on 21 December to 13 h 39 min on 21 June.

### 2.2. Relationship type

The *linear relationship* employed in CERES-sorghum (Alagarswamy and Ritchie, 1991) considers that below a threshold P2O of the photoperiod  $P$ , the duration of the vegetative stage  $f(P)$  is a constant, is minimum and equals the duration of the juvenile phase P1. Above P2O, the duration of the vegetative stage  $f(P)$  increases as a linear function of daylength with slope P2R (Fig. 2a). This model corresponds to quantitative plants that will eventually flower even if photoperiod remains high (Thomas and Vince-Prue, 1997).

The *hyperbolic relationship* employed in STICS (Brisson et al., 2002) also considers that below a threshold photoperiod  $P_{\text{sat}}$ , the duration of the vegetative stage  $f(P)$  is a constant, is minimum and equals the duration of the juvenile phase P1. Above  $P_{\text{sat}}$  however, the duration of the vegetative stage  $f(P)$  increases as a hyperbolic function of daylength until an asymptote is reached for  $P = P_{\text{base}}$  (Fig. 2b). For values of  $P$  larger than  $P_{\text{base}}$ , flowering is not possible anymore and development is stopped. This model is appropriate for qualitative plants (Thomas and Vince-Prue, 1997). For such plants, vegetative stage can continue for as long as daylength conditions are not met (Belliard, 1982).

### 2.3. Calculation of daily development rate

For any given day  $j$  of the considered phenological stage, daily development rate  $DR_j$  is computed as a function of thermal time and photoperiod. Panicle initiation occurs when  $DR_j = 1$ . Two approaches are possible for the calculation of  $DR_j$ . In the first approach, which we call the *cumulative method*,  $DR_j$  is the daily summation of a photothermal ratio

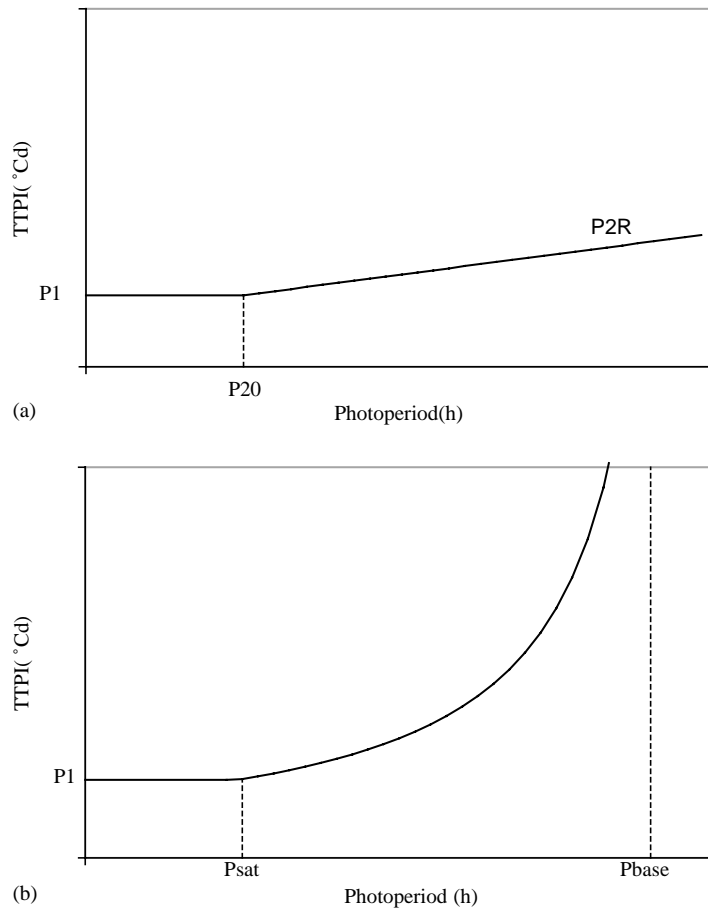


Fig. 2. Relationship type between the duration of the vegetative stage  $f(P)$  expressed as thermal time to panicle initiation TTPI (°C days), and photoperiod: (a) linear and (b) hyperbolic.

expressed as follows:

$$DR_j = \sum_{i=1}^j \frac{dti_i}{f(P_i)} \quad (1)$$

where  $dti_i$  is the daily thermal time and  $f(P_i)$  is the thermal time required for panicle initiation. In the second approach, which we call the *threshold method*,  $DR_j$  is computed as follows:

$$DR_j = \frac{1}{f(P_j)} \sum_{i=1}^j dti_i \quad (2)$$

In this case, initiation occurs when the sum of temperatures  $\sum dti_i$  meets the demand expressed by  $f(P_j)$ .

Apparently similar, these formulae have different physiological meanings. The cumulative method

(Eq. (1)) would imply that the plant progresses every day towards flowering with a variable rate, function of temperature and photoperiod. In that case, higher photoperiods typically delay plant development. On the contrary, the threshold method (Eq. (2)) requires that daylength conditions be met for flowering to take place.

#### 2.4. Practical implementation

Sorghum development is simulated using the four possible combinations of relationship type (linear, hyperbolic responses) and daily rate calculation approach (cumulative, threshold methods). For convenience, we keep the parameter names used in CERES-sorghum for the linear responses, and those

employed in STICS for the hyperbolic responses. It is understood that both P2O and  $P_{\text{sat}}$  refer to the same photoperiod below which there is no daylength induced delay in plant development.

For the *cumulative linear case* (as in CERES-Sorghum), phenological stage is assumed to start at the end of the juvenile phase and  $f(P_i)$  is computed as follows (Alagarswamy and Ritchie, 1991):

if  $P_i > \text{P2O}$  then  $f(P_i) = 102 + \text{P2R}(P_i - \text{P2O})$ ,  
otherwise  $f(P_i) = 102$

The constant above corresponds to minimum thermal time required for panicle initiation under optimum daylengths after the end of the juvenile phase (constant for all sorghum varieties). Hence, thermal time duration of the juvenile phase P1 plus 102 °C days equals the duration of the basic vegetative phase (BVP: Major and Kiniry, 1991).

For the *cumulative hyperbolic case* (as in STICS), phenological stage is assumed to start at emergence and  $f(P_i)$  is computed as follows (Brisson et al., 2002):

if  $P_i > P_{\text{sat}}$  then  $f(P_i) = \text{P1} \left( \frac{P_{\text{sat}} - P_{\text{base}}}{P_i - P_{\text{base}}} \right)$ ,  
otherwise  $f(P_i) = \text{P1}$

A  $j$  subscript is used instead of the  $i$  in the above formulas for the *threshold linear case* and the *threshold hyperbolic case*, respectively.

## 2.5. Calibration of models

Experimental data used for calibration of the four models were collected at the Regional Agronomic Research Center of Institut d'Economie Rurale (IER) in Sotuba, Mali (12°39'N, 7°55'W). The cultivar used was CSM388, a Guinea sorghum variety from the Mali sorghum collection, with an average cycle duration of 130 days. Observations were gathered during a 1996 planting date experiment, with five sowing dates on 10 June, 25 June, 10 July, 25 July and 10 August. Experimental plot followed a randomized complete block design with two repetitions for the five planting dates. Each sub-plot consisted of seven rows with 12 hills. Hill spacing was 75 cm × 75 cm. Daylength on the first planting date was 13 h 38 min. The longest day was 21 June with 13 h 39 min. From that date onward, daylength gradually decreased to reach 12 h 39 min on 8 October when the last heading was observed.

Table 1

Screening ranges and increments used for each parameter to estimate genetic coefficients

Parameter	Minimum value	Maximum value	Increment
P2O, $P_{\text{sat}}$ (h)	5	23	0.05
$P_{\text{base}}$ (h)	$P_{\text{sat}}$	23	0.05
P2R (°C h <sup>-1</sup> )	10	5000	10

Panicle initiation was monitored by periodic dissections every 5 days, including a count of the total number of leaves generated. Panicle initiation was considered to be effective when no new leaf was observed on the apex.

Juvenile phase duration P1 for CSM388 has been determined previously by Vaksman et al. (1996) who observed that panicle initiation coincided with the end of the juvenile phase for a sowing on 10 August, and estimated a value P1 = 413 °C days.

Genetic coefficients have been estimated by statistical adjustment, by screening all possible combinations of (P2O, P2R) and ( $P_{\text{sat}}$ ,  $P_{\text{base}}$ ) using the following ranges and increments for each parameter (Table 1).

For every pair of values, date of panicle initiation is simulated for the five planting dates of the Sotuba 1996 experiment and compared to observations. The set of values that minimizes the root mean square error (RMSE: Willmott, 1982) is selected as the best estimate for the parameters. RMSE is defined here as

$$\text{RMSE} = \left[ n^{-1} \sum (\text{EPI}_{\text{calc}} - \text{EPI}_{\text{obs}})^2 \right]^{0.5}$$

where  $n$  is the number of planting dates, EPI the number of days from emergence to panicle initiation, and the subscripts calc and obs, respectively, stand for calculated and observed.

## 2.6. Validation of models

The four models and their sets of coefficients were run against an independent set of observations collected during 1994 agronomic trials for validation purposes. In these experiments, variety CSM388 was planted along a latitudinal transect including Bamako (12°39'N), Cinzana (13°15'N) and Kopro (14°14'N) locations, and with planting dates spread over an even wider period of time extending from 15 February to 15 September. Relevant information on

Table 2

1996 experimental observations used for calibration. All durations were computed from emergence

Sowing date	Photoperiod at PI (h)	TTPI, thermal time to PI (°C days)	EPI, days to PI (days)	EFL, days to flag leaf (days)	TLN, total leaf number
10 June 96	13.37	1063	54	87	32
25 June 96	13.31	851	44	76	30
10 July 96	13.19	756	40	68	26
25 July 96	13.10	603	32	56	18
10 August 96	13.03	413	22	47	16

crop development available from these trials is limited to the average date of flag leaf expansion observed among 10 plants and over two repetitions. Thermal time from emergence to flag leaf (EFL) expansion TTEFL has been shown to be linearly related to thermal time to panicle initiation TTEPI by Ritchie and Alagarswamy (1989) after phenology data reported by Schaffer (1980). Vaksman et al. (1996) found the following relationship for CSM388:

$$\text{TTEFL} = 1.24 \times \text{TTEPI} + 425$$

This formula is applied to model outputs  $\text{TTEPI}_{\text{calc}}$  to yield  $\text{TTEFL}_{\text{calc}}$ . The number of days from emergence to flag leaf expansion is derived from  $\text{TTEFL}_{\text{calc}}$  and used for comparison with observations. Finally, concurrent computation of RMSE and examination of scatterplots of calculated versus observed values arguably provides a fair overall evaluation of model performance (Yan and Wallace, 1998).

### 3. Results

#### 3.1. Model calibration

Observed time from emergence to panicle initiation, and corresponding thermal time (TTPI) are presented in Table 2 alongside total leaf number (TLN) and time from emergence to flag leaf.

Over the 2-month range of planting dates, EFL decreased from 87 to 47 days and TLN from 32 to 16. For this relatively small variation in daylength (0.33 h), EPI decreased from 54 to 22 days.

Table 3 shows results from the statistical adjustment obtained by screening all possible combinations of (P2O, P2R) and ( $P_{\text{sat}}$ ,  $P_{\text{base}}$ ). For the hyperbolic model, there was only a 0.85 h difference between  $P_{\text{base}}$  and  $P_{\text{sat}}$ . This illustrates the high sensitivity of

cultivar CSM388 to daylength. As a comparison, Brisson et al. (2002) showed ( $P_{\text{base}} - P_{\text{sat}}$ ) differences of some 12 h in long day and low photoperiod sensitive wheat. Similarly, P2R slopes in the linear model were much steeper ( $1160 \text{ } ^\circ\text{C days h}^{-1}$ ) as compared to those of less photoperiod sensitive varieties studied by Alagarswamy et al. (1998) for example, where P2R did not exceed  $221 \text{ } ^\circ\text{C days h}^{-1}$ .

#### 3.2. Model validation

Emergence-flag leaf durations calculated using the four possible modeling approaches ( $\text{EFL}_{\text{calc}}$ ) were tested against observations gathered during the 3-location 1994 agronomic experiment ( $\text{EFL}_{\text{obs}}$ ). Scatterplots (Fig. 3) show best agreement between calculated and observed values for the threshold hyperbolic case, with the lowest RMSE of 8 days (Fig. 3d). For short EFL durations of up to about 120 days, all four approaches performed satisfactorily with their respective sets of adjusted coefficients. However, for longer cycles, duration of the vegetative phase was best predicted by the threshold hyperbolic approach. Both linear and hyperbolic models failed to simulate

Table 3  
Model calibration

Model type	Coefficients		RMSE
	P2O (h)	P2R (°C days h <sup>-1</sup> )	
Cumulative-linear case	13.05	1160	2.7
Threshold-linear case	13	1660	1.2
	$P_{\text{sat}}$ (h)	$P_{\text{base}}$ (h)	
Cumulative-hyperbolic case	13.05	13.9	2.0
Threshold-hyperbolic case	12.85	13.7	1.7

Best estimate of genetic coefficients for the four model types.

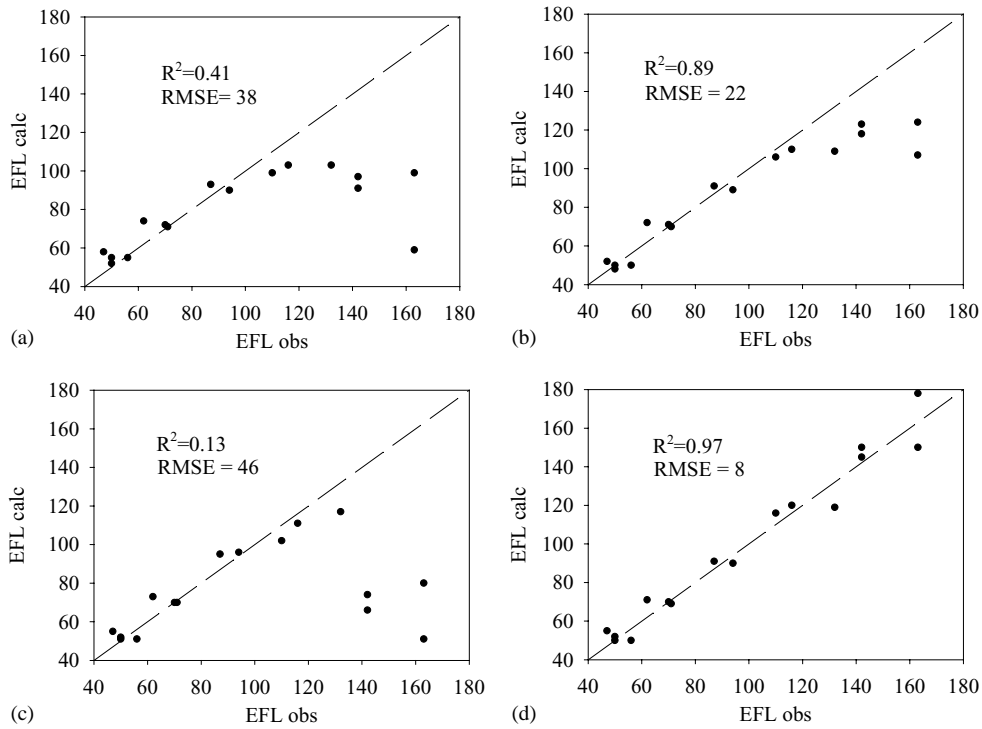


Fig. 3. Model validation. Scatterplots of calculated emergence-flag leaf expansion durations ( $EFL_{calc}$ ) against observations from the 1994 experiment ( $EFL_{obs}$ ). Dashes identify the 1:1 line, RMSE is the root mean square error,  $R^2$  is the determination coefficient: (a) cumulative linear; (b) threshold linear; (c) cumulative hyperbolic; (d) threshold hyperbolic.

long cycles when implemented with the cumulative method (Fig. 3a and c). The hyperbolic model was the most responsive to change in the method for DR calculation (Fig. 3c and d).

Fig. 4 illustrates the time evolution of EFL predictions by each of the four models compared to six observations gathered for the Sotuba site during the 1994 planting date experiment. Validation data here

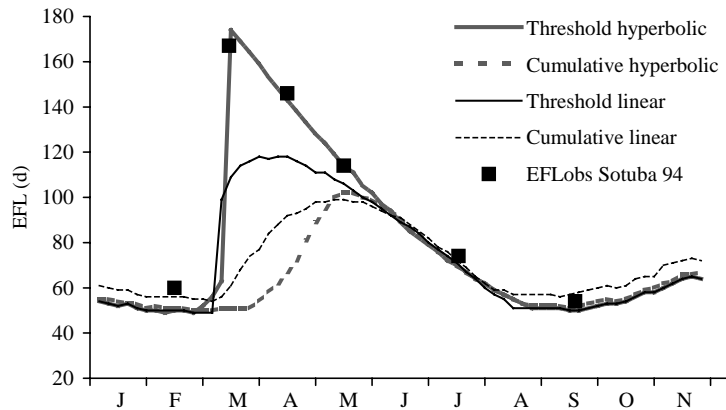


Fig. 4. Predictions of EFL as a function of planting dates for the four approaches, as compared to six observations ( $EFL_{obs}$ ) from the 1994 experiment in Sotuba, Mali.



involves a larger range of EFL values (range = 107 days) than calibration where planting was restricted to rainy season (range = 40 days, see Table 2). While all models reasonably match EFL durations observed during the 1996 calibration experiment, the threshold hyperbolic approach is the only one capable of predicting longer EFL durations for unseasonal sowing dates in March and April. Reliance on a threshold method allows models to adequately simulate the abrupt transition between short days and long days conditions, with EFL varying from 60 to 167 days for a small interval in planting dates in late February/early March.

#### 4. Discussion

Results show that two existing models relying on simple mathematical representations of sorghum response to temperature and daylength can largely underestimate the duration of the vegetative phase for sorghum cultivar CSM388, and therefore fail to simulate the development of this highly photoperiod sensitive variety. CSM388 is quite typical of local varieties of the semi-arid and sub-humid tropics of West Africa where other indigenous cereals such as pearl millet (*Pennisetum typhoides*: Belliard, 1982), and legumes such as bambara groundnut (*Vigna subterranea*: Brink et al., 2000) demonstrate similar adaptation traits through unique responses to temperature and photoperiod. Deriving from a natural selection process dictated by unusual environmental variability, these special features allow for evaluation of model performance towards the limits of their original 'definition domain'.

Indeed, numerous crop models have not been initially developed for cultivars adapted to, and conditions prevailing in, low-input, semi-arid tropical agricultural systems. When simulating sorghum growth and development in such environments, model calibration alone is often not sufficient to accurately predict the duration of phenological stages (Birch et al., 1990). Modeling of sorghum response to photoperiod and temperature has often shown to be problematic (Ellis et al., 1997; Alagarswamy, pers. commun.), and may benefit from larger efforts targeted at conceptual improvements that reflect an increasing understanding of plant physiology (e.g. Adams et al., 2001).

While the preferred use of temperature-based development rates over phase durations has been widely adopted as a concept arguably more consistent with basic plant physiology (Major and Kiniry, 1991), handling of photoperiod  $\times$  temperature interactions has inspired different approaches. Typically a distinction can be made between additive models (Summerfield et al., 1997), multiplicative models (Cober et al., 2001), or a combination of the two (Yan and Wallace, 1998). Depending on whether these models can mimic photoperiod  $\times$  temperature interactions or not, Bertero et al. (1999a) differentiate them as interactive or non-interactive.

In spite of their computational complexity, one interesting feature of additive models is that they allow for the simulation of 'obligate' photoperiodic responses typical of qualitative plants (Summerfield et al., 1997), accounting for the fact that short daylengths constitute an obligate requirement for short day plants if the plant is not to remain permanently vegetative. This capability is absent from most simple multiplicative models which seem to have been tailored to quantitative responses where daylength determines time to flowering, but cannot prevent the latter. Interesting results from Carberry et al. (2001) indicate that pigeonpea has a clear qualitative response to photoperiod, similar to sorghum. They further suggest that it can be simulated relying on a linear function, although explicit description of model photoperiod  $\times$  temperature interaction is not included in that paper.

One questionable assumption in multiplicative models such as CERES and STICS is the association of cumulative processes (thermal time response) and other phenomena which may not be cumulative (photoperiod sensitivity) into single 'photothermal' units, a concept viewed by some as incorrect from a genetic standpoint: '[. . .] The thesis that crops require a fixed amount of heat (accumulated degree-day) or photothermal units is not correct and [. . .] the values of these so-called summation constants are not genetical characteristics of the crops' (Robertson, cited by Franquin, 1974). Such models seem to work satisfactorily in most cases, but this apparent performance may hide a limited validity as illustrated by results on highly photoperiod sensitive CSM388. The concept of development rates based on photothermal ratios may be misleading one to think that floral initiation is 'programmed' and will occur sooner or later, whereas



photoperiod sensitivity studies demonstrate that plants not only retard, but somehow pull away from, flowering under increasing daylengths—to eventually regress to vegetative stage in extreme cases.

The proposed combination of a hyperbolic response and a threshold iteration whereby the current thermal age of the plant is tested daily against a thermal time requirement for panicle initiation (modulated by photoperiod and potentially infinite for highly sensitive varieties) constitutes a robust simplified framework for sorghum modeling which is more consistent with our understanding of photoperiodicity in plants. Its relatively simple mathematical formulation can accommodate all sensitivity ranges (including of course the particular case of neutral plants) through appropriate fitting of the  $P_{base}$  parameter on a cultivar basis. From a computational standpoint, it only involves minor modifications in existing models. In CERES-sorghum for

example, one parameter ( $P2R$ ) is replaced (by  $P_{base}$ ) and only three lines in the source code require changes.

It may be argued that since they can only delay flowering, photoperiod genes are inhibitors of an otherwise autonomous development process as suggested by Yan and Wallace (1998). However, the assumption that an appropriate photoperiod is required to induce flowering appears difficult to challenge for photoperiod sensitive plants, where other phenomena (e.g. circadian rhythms) could provide physiologically based explanations for this inhibition effect (Heller, 1985). Hammer et al. (1989) suggested that day time could be associated with the accumulation of an inhibitor, and night time with the accumulation of a promoter, with floral initiation triggered at some critical hormone level or ratio. It seems that photoperiodicity is more a function of shifts in hormonal balances than of florigen accumulation, and that even

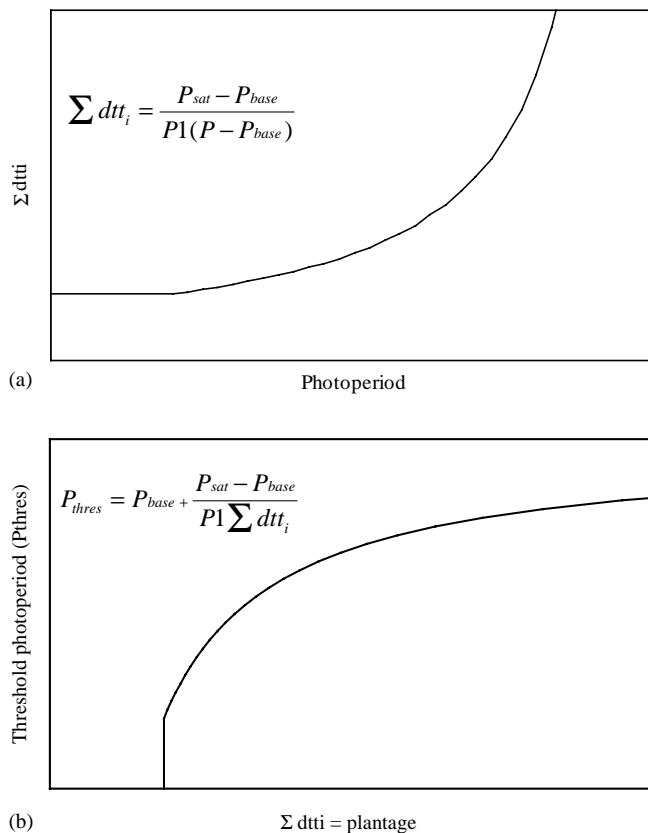


Fig. 5. Traditional approach of cumulative thermal age as a function of photoperiod (a) can be reversed to consider a threshold daylength, function of thermal age more consistent with the definition of photoperiodism (b).

quantitative plants are subject to a ‘trigger effect’ (Franquin, 1976) consistent with this proposed threshold concept. The traditional way of looking at the relationship between thermal age and photoperiod (Fig. 5a) may be reversed to consider a threshold daylength, function of plant thermal age (Fig. 5b).

A better understanding of plant physiology in development models may also help reduce the lack of consistency in terminology pointed out by Adams et al. (2001). Depending on the sources, ‘basic vegetative phase’ (BVP) can relate to the photoperiod insensitive stage (e.g. Yin et al., 1997) or to the minimum period from emergence to flowering (e.g. Bertero et al., 1999b). Similarly, ‘critical photoperiod’ often refers to the daylength below which there is no photoperiod induced delay in development (e.g. Summerfield et al., 1997), or sometimes to the extreme non optimum daylength above which flowering will not occur in qualitative plants (e.g. Major and Kiniry, 1991). The latter remark also applies to ‘base photoperiod’ (Cober et al., 2001; Brisson et al., 2002).

This modeling work eventually reminds us that critical photoperiod sensitivity traits can be incorporated in breeding strategies through simple planting date experiments. Kouressy et al. (1998) showed that photoperiod sensitivity was affected by dominant alleles of one major gene, equivalent to the Ma5 or Ma6 maturity loci identified by Aydin et al. (1997). With a single early June sowing, Mendelian disjunction allows to screen insensitive germplasm out of large populations. Different maturity lines can be fixed, and their relevant genetic parameters can be determined with two to three sowing dates. Coupled with a GIS and a water balance model, the proposed threshold–hyperbolic approach can then be used to determine geographical recommendation domains for each parameterized variety. In Mali, these would roughly correspond to areas where flowering occurs 20 days on average before the date of the last rains. Conversely, this model can be applied to screen populations and select varieties that best fit a particular agro-ecological environment.

## 5. Conclusion

Introduction of photoperiod sensitivity traits in breeding strategies for West Africa is only relatively

recent and might explain the observed low adoption rate of ‘enhanced’ varieties to a large extent. High environmental variability and associated climate risk has dictated selection by generations of farmers, and resulted in West Africa being a primary center of biodiversity for sorghum and other crops. In spite of this, agricultural extension services often show limited awareness and understanding of the role of these traits in cultivar adaptation, highlighting the need for simple screening methods.

Results show that successful simulation of sorghum development in the vegetative phase can be attained by the calculation of development rates based on the combined use of a hyperbolic response to photoperiod and a daily threshold iteration procedure easy to implement in existing models. This convenient approach allows for quick varietal screening by comparison of accumulated thermal time  $\sum dti$  with photoperiod at panicle initiation to derive a simple  $\sum dti = f(P)$  relationship, hence reducing dependency upon heavy experimental designs and statistical approximation procedures. It is also suggested that while modeling of *quantitative crop growth* can rely on concepts such as accumulated degree days, derived concepts like photothermal ratios should not be used for simulating *qualitative plant development*.

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