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Characterization of different temperature and photoperiod responses in African sorghum cultivars

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Abstract — On the basis of studies conducted in Mali, we modeled the photoperiod response of two sorghum landraces by using daily minimum night temperatures. The two landraces differ in origin and adaptation with one rainy season kafir cultivar from South Africa (Is 9508) and the other a post rainy season durra from Senegal. The results validate the assumption that photoperiod effects on the vegetative duration of sorghum is well explained by using the daily night temperatures for computing thermal time. Moreover, the model characterizes the two landraces. The kafir Is 9508 appeared to be photo-insensitive. Growing in Mali under shorter photoperiods than its area of origin, Is 9508 was never in a position to exhibit photoperiod sensitivity. On the other hand, the durra Ssm 973 appeared very photosensitive, decreasing its vegetative thermal time until the shortest days of year. This trait and a low sensitivity to the cold night temperatures explain the adaptation of this post-rainy durra to the off-season. The comparison of the african landraces Is 7680, Is 9508 and Ssm 973 shows that: i) varietal photoperiod and temperature responses were related to agronomic adaptation, ii) varietal photoperiod and temperature responses seem to be independant. This latter result indicates that different levels of temperature and photoperiod sensitivity can be combined in selected lines.

Résumé — Caractérisation de différentes réponses à la température et à la photopériode de cultivars africains de sorghos. La modélisation de la réponse photopériodique des sorghos en fonction des températures minimum quotidiennes nocturnes a été appliquée à deux variétés, cultivées au Mali, très différentes par leur origine et leur utilisation culturale : un cultivar pluvial kafir d'Afrique du Sud Is 9508 et un sorgho de décrue durra du Sénégal Ssm 973. Les résultats valident l'hypothèse que l'effet photopériodique sur la durée des cycles végétatifs des sorghos est bien expliqué par une prise en compte des températures nocturnes. De plus, le modèle caractérise les réactions des deux cultivars. Le kafir est apparu non photopériodique ; poussant au Mali sous des longueurs de jours courtes par rapport à celles de sa zone d'origine, ce sorgho n'a pas été en situation de montrer une éventuelle sensibilité aux variations de longueurs du jour. En revanche, le durra est apparu très photopériodique en abaissant la durée thermique de son cycle végétatif même sous les jours les plus courts de l'année. Cette particularité, associée à un seuil bas de sensibilité aux températures nocturnes, expliquent son adaptation à la culture de décrue, culture de post hivernage. La comparaison des caractéristiques thermo-photopériodiques des cultivars guinea Is 7680, kafir Is 9508 et durra Ssm 973 montre que chacun est typé en fonction de ses aptitudes culturales. Il semble que la sensibilité à la photopériode s'établisse indépendamment de la sensibilité aux températures nocturnes. Ce résultat ouvre des perspectives pour la sélection de génotypes combinant différents niveaux d'expression de ces sensibilités.

Since sorghum was domesticated in Africa (Doggett, 1976), African sorghum landraces possess a great morphological diversity and include representatives of all the taxonomic groups of Harlan and de Wet (1972): the five basic races (bicolor, guinea, durra, caudatum and kafir) and the intermediate forms. The diversity of African cultivars is also high with respect to their agricultural uses. Sorghum is adapted to rainfed conditions with high or low rainfall, to irrigated conditions, to off-season cultivation as to high elevation areas. Because of the specific climatic constraints related to these agricultural uses, African sorghum landraces should have developed different kinds of temperature and photoperiod responses.

Little has been done to characterize them, however Miller *et al.* (1968) separated tropical and Us sorghums into five photoperiodic response classes on the basis of the critical photoperiod value. A recent study (Vaksmann *et al.*, 1998) showed that the photoperiod response of a West African guinea landrace (Is 7680) fits well to Major's pattern (Major, 1980) when the thermal time to panicle initiation is calculated by using daily minimum night temperatures. Thus, the photoperiod response of Is 7680 appeared to be that of a short-day plant with sensitivity to cold night temperatures. We think that this kind of response is shared by most of the West African guinea sorghum landraces.

In this study carried out at Samanko, Mali, the method developed to model the photoperiod behaviour of Is 7680 was applied to two African cultivars presenting distinctive features in phenology: Is 9508 and Ssm 973 respectively belonging to the kafir sorghum race and the West African post-rainy season durra. The particularity of kafir cultivars which have a Southern African origin is to become very late during the off-season cultivation conducted in tropical conditions (Reddy and Prasada Rao, 1993). In traditional cropping, the West African post-rainy season sorghums are grown without irrigation during the dry season when water is subsiding in the floodplains and the soils are drying out toward the end of the year (Sapin and Reynard, 1968). Maturing entirely on subsoil moisture, they must mature quickly in order to reproduce. Contrary to kafir sorghums, the post-rainy sorghums flower early in the off-season.

The objective of this study was to validate the method applied to guinea Is 7680 on the chosen kafir and durra cultivars, and then to characterize them by estimating the genetic components of Major's photoperiod response pattern: the Bvp (Base vegetative phase), the Mop (Maximum optimal photoperiod) and photoperiod sensitivity (Major, 1980). On the basis of the results, a better understanding of the different adaptative abilities of the African sorghum landraces was expected.

Materials and methods

The sorghum cultivars representative of the kafir race and of the West African post-rainy season durra used in this study were respectively Is 9508 and Ssm 973 (from Cirad sorghum collection). Is 9508 comes from South Africa and Ssm 973 is a Senegal landrace adapted to traditional cultivation in the drying floodplains of the Senegal valley.

During three years (1994-1996), the two cultivars were sown at different dates in the field at the Samanko research station in Mali (8°70′ W, 12°33′ N, altitude 345 m). In total, observations were done on nineteen sowing dates for Is 9508 and eleven sowing dates for Ssm 973.

For each date of sowing and cultivar, the experimental plot consisted of one 6 m row with hills spaced at 0.30 m in the row and thinned to one plant per hill at about 10 days after seedling emergence. The plots received a standard level of fertilization and were irrigated when necessary.

For each experimental plot, six random plants were observed for the number of leaves produced during the vegetative phase and the time to flag leaf emergence.

During the period of experimentation, maximum and minimum daily air temperatures under shade were measured in a meteorological shelter at the Samanko station.

To model the photoperiod response of the two cultivars, we followed the method proposed for the guinea sorghum landrace Is 7680 (Vaksmann *et al.*, 1998).

For a given experimental plot and referring to the thermal time calculated following the Ceres sorghum model (Alagarswamy and Ritchie, 1991), the date of panicle initiation was situated at the calendar date when the thermal time from sowing achieved 0.6 x the thermal time from sowing to flag leaf emergence (Dttfl).

For each experimental plot, the thermal time to panicle initiation used in modelling the photoperiod response was established by accumulating daily minimum night temperatures to give the Nttini :

$\text{Nttini} = \Sigma_{i=1}^{n} (T_i\text{min} - \text{Tbase})$

where Nttini is the thermal time accumulated over n days from sowing to the estimated day of panicle initiation, $T_i$min = daily minimum temperature. When Tmin < Tbase the daily contribution was null.

The Tbase was estimated by means of least coefficient of variation (Cv) with Tbase changing by 1° from 0 to 6°C when the thermal times were related to the Bvp. When the thermal times were related to the photoperiod sensitivity phase, we tested the Tbase by means of highest correlation coefficient.

The effective photoperiods used to model the photoperiod reaction of the cultivars studied was assumed to be the lengths of the days at the estimated dates of panicle initiation. The lengths of these days were calculated for Samanko following the model of Forsythe *et al.* (1995) for a solar elevation > - 6 degrees.

Results and discussion

Field data and vegetative behaviour results are presented in tables I and II (for the durra Ssm 973, there is a lack of data for the sowings belonging to the 1995 year).

For the two cultivars, the phyllochron in number of days to produce one leaf tends to be longer when the mean daily temperatures are decreasing (tables I and II). In similar sowing conditions, the phyllochron of the durra Ssm 973 is always shorter than that of the kafir Is 9508. At the beginning of the rainy season,

Table I. Field data pertaining to the vegetative phase of kafir Is 9508 sown at different dates at Samanko from 1994-1996.

Sowing date	Sowing date in julian day	Number of days from sowing to flag leaf	Number of leaves	Phyllochron (day/leaf)	Mean daily temperature (sowing to flag leaf) (°C)
17/06/94	168	50.2	16.8	3.0	26.9°
01/07/94	182	47.0	17.5	2.7	26.3°
15/07/94	196	47.2	15.8	3.0	26.1°
29/07/94	210	47.0	16.3	2.9	26.3°
09/09/94	252	47.5	14.8	3.2	27.0°
16/12/94	350	106.2	25.2	4.2	24.1°
03/02/95	34	62.8	21.6	2.9	27.5°
23/06/95	174	50.8	17.3	2.9	27.6°
01/07/95	182	49.1	17.5	2.8	27.2°
09/07/95	190	49.6	16.7	3.0	26.6°
20/07/95	201	52.1	16.3	3.2	26.7°
11/09/95	254	48.1	15.6	3.1	27.5°
30/11/95	334	90.5	20.5	4.4	24.6°
03/01/96	3	67.4	20.0	3.4	26.0°
01/02/96	32	57.4	19.6	2.9	27.9°
13/06/96	165	52.0	19.2	2.7	27.8°
01/07/96	183	54.8	17.4	3.1	27.0°
22/07/96	204	58.8	15.8	3.7	26.0°
18/10/96	292	63.0	17.2	3.7	24.2°

Table II. Field data pertaining to the vegetative phase of durra Ssm 973 sown at different dates at Samanko from 1994-1996.

Sowing date	Sowing date in julian day	Number of days from sowing to flag leaf	Number of leaves	Phyllochron (day/leaf)	Mean daily temperature (sowing to flag leaf) (°C)
17/06/94	168	72.0	26.8	2.7	26.7°
01/07/94	182	72.0	27.2	2.6	26.3°
15/07/94	196	67.5	25.0	2.7	26.6°
29/07/94	210	61.8	24.7	2.5	26.5°
09/09/94	252	50.0	17.0	2.9	26.7°
16/12/94	350	78.8	19.8	4.0	22.3°
13/06/96	165	74.2	31.4	2.4	27.6°
01/07/96	183	75.0	26.0	2.9	27.1°
22/07/96	204	64.6	23.2	2.8	26.6°
18/10/96	292	48.0	16.2	3.0	24.5°
18/11/96	323	55.7	15.5	3.6	23.7°

the long vegetative duration of the durra associated with a low value of phyllochron explains that this cultivar produces a lot of leaves.

Varietal differences are observed in the response of the vegetative phase to flag leaf emergence (in days) depending on sowing dates all year long expressed in julian day (figure 1).

The kafir cultivar Is 9508 appears to be photoperiod insensitive during the rainy season (150-210th julian day): its vegetative phase is short and stable. At that time, the durra Ssm 973 responds to decrease in daylength by hastening its development. It shows the typical photoperiod response of a short-day plant. During the off-season, the kafir is more responsive and becomes later than the durra. Its vegetative phase increases about twofold compared to the situation observed in the rainy season (106 days in December vs about 55 days in the rainy season). At the same time, the vegetative phase of the durra is hardly longer than the longest of its vegetative phases measured in the rainy season.

Modeling photoperiod response by using daily minimum night temperature as done for the guinea Is 7680 allows a better characterization of the differences between the kafir Is 9508 and the durra Ssm 973.

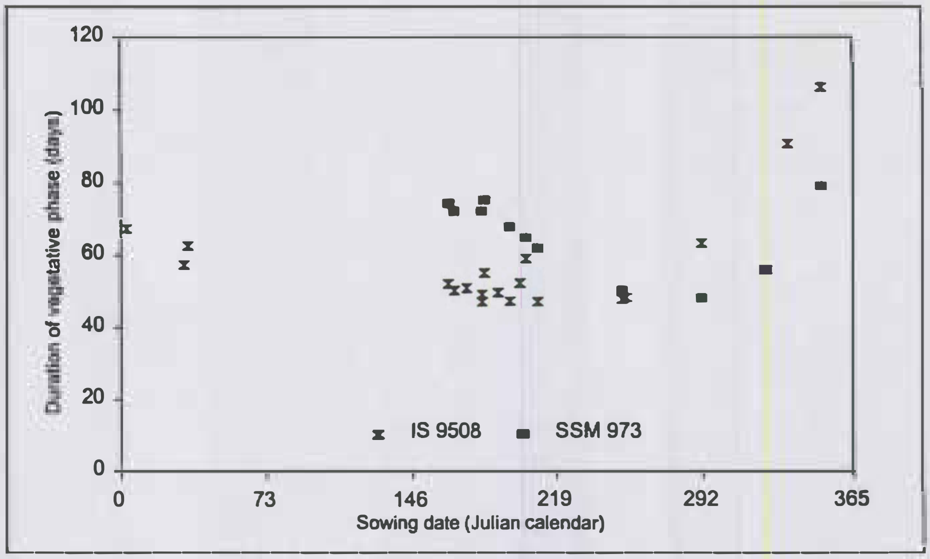

__Figure 1.__ Duration of vegetative phase (from sowing to flag leaf emergence) of kafir Is 9508 and durra Ssm 973 sown at different dates in Samanko (1994-1996).

For each sowing date and cultivar, table III shows the components of the modelling with the dates of panicle initiation estimated at 0.6 x thermal time from sowing to panicle emergence calculated following Ceres model. It also presents the photoperiods at the estimated dates of panicle initiation and the thermal times from sowing to estimated dates of panicle initiation computed by accumulating daily minimum night temperatures. These thermal times are calculated with Tbase = 1° C which gives the best fitting of the data tested by means of Cv (case of Is 9508) or by means of correlation coefficient (case of Ssm 973) (Table IV).

For each cultivar, the visual relationship between thermal time to panicle initiation and photoperiod at panicle initiation leads to graphs which are in agreement with the Major's photoperiod response pattern (figures 2 and 3). Thus, the photoperiod response of the kafir Is 9508 is clearly that of a photoperiod insensitive cultivar with Bvp estimated at 634° and Tbase = 1° (figure 2). The photoperiod response of the durra Ssm 973 is that of a short-day plant for which the range of daylength at Samanko is not enough to put in evidence its Mop (photoperiod threshold) and *a fortiori* its Bvp (figure 3). Only its photoperiod sensitivity can be evaluated by the photoperiod sensitivity coefficient: 442° day/h with Tbase = 1° C.

The mathematical coefficients which evaluate the fitting of data to the Major's photoperiod response pattern are satisfactory: Cv = 8.7% with the kafir Is 9508 and coefficient of correlation = 0,99 with the durra Ssm 973. They validate the calculation of the vegetative thermal time by using daily minimum night temperature to account for the photoperiod response of sorghum.

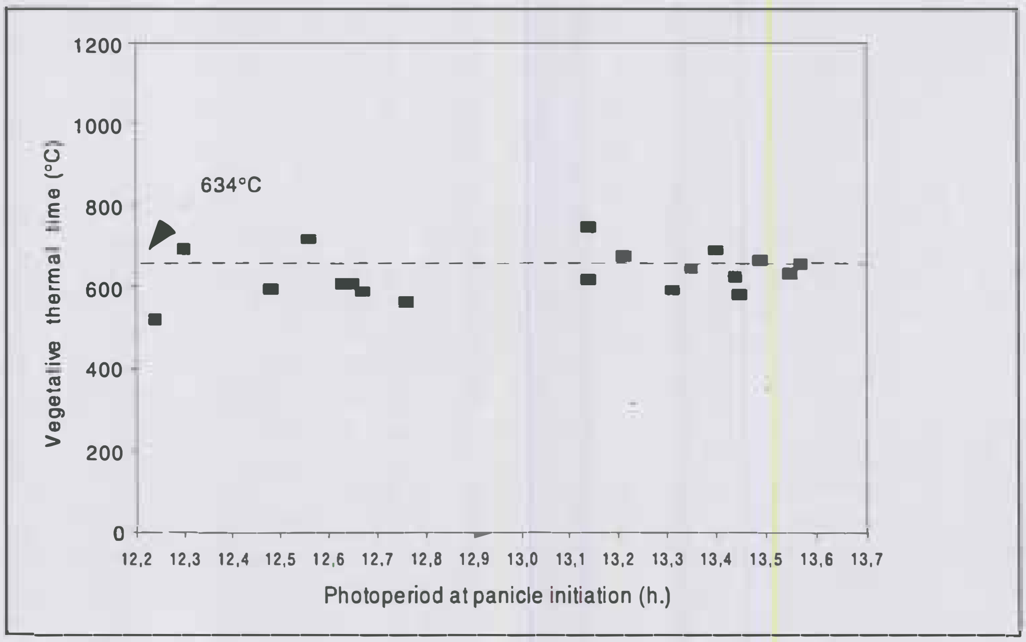

__Figure 2.__ Thermal time to panicle initiation calculated by using night temperature plotted against photoperiod at panicle initiation of kafir Is 9508 sown in Samanko (1994-1996).

Table III. Estimation of dates, photoperiods and thermal times at panicle initiation of Is 9508 kafir and Ssm 973 durra sown at different dates in Samanko from 1994-1996.

Sowing date	Is 9508 kafir			Ssm 973 durra		
	Estimated date of panicle initiation (1)	Photoperiod at estimated date of panicle initiation (2)	Nttini: (Tbase = 1° C) (3)	Estimated date of panicle initiation (1)	Photoperiod at estimated date of panicle initiation (2)	Nttini: (Tbase = 1° C) (3)
17/06/94	17/07/1994	13.55	637°	30/07/1994	13.44	910 °
01/07/94	29/07/1994	13.45	583°	14/08/1994	13.29	926°
15/07/94	12/08/1994	13.31	594°	25/08/1994	13.16	868 °
29/07/94	27/08/1994	13.14	617°	05/09/1994	13.03	802°
09/09/94	08/10/1994	12.65	610°	10/10/1994	12.63	651°
16/12/94	25/02/1995	12.56	719°	06/02/1995	12.37	506°
03/02/95	15/03/1995	12.76	563°	-	-	-
23/06/95	24/07/1995	13.49	667°	-	-	-
01/07/95	30/07/1995	13.44	628°	-	-	-
09/07/95	08/08/1995	13.35	647°	-	-	-
20/07/95	21/08/1995	13.21	677°	-	-	-
11/09/95	10/10/1995	12.63	610°	-	-	-
30/11/95	27/01/1996	12.30	693°	-	-	-
03/01/96	17/02/1996	12.48	596°	-	-	-
01/02/96	07/03/1996	12.67	590°	-	-	-
13/06/96	14/07/1996	13.57	657°	27/07/1996	13.47	931°
01/07/96	03/08/1996	13.40	692°	15/08/1996	13.27	943°
22/07/96	27/08/1996	13.14	747°	31/08/1996	13.09	828°
18/10/96	24/11/1996	12.24	521°	15/11/1996	12.29	429°
18/11/96	-	-	-	23/12/1996	12.16	378°

(1) Date at 0.6 x ddtfl from Ceres model.
(2) In hours and decimals.
(3) Vegetative thermal time by summation of minimum temperatures (sowing to panicle initiation) (° Celcius).

Table IV. Tbase value tested by means of coefficient of variation (Cv) associated to the Bvp of Is 9508 kafir and coefficient of correlation associated with the photoperiod sensitivity phase of Ssm 973 durra.

Tbase for calculation of vegetative thermal time using daily minimum night temperature	-Is 9508 kafir - Coefficient of variation associated to Bvp	- Ssm 973 durra- Coefficient of correlation associated to photoperiod sensitivity phase
0°	8.92	0.985
1°	8.66	0.986
2°	8.70	0.986
3°	9.13	0.983
4°	10.06	0.979
5°	11.70	0.979
6°	13.70	0.975

Another validation of our approach is the following: the photoperiod characteristics of the kafir Is 9508 and the durra Ssm 973 are in accordance with their origin or agricultural use.

The area of origin of the kafir Is 9508 is South Africa at high latitude (about 25° S) for tropical sorghums. At Samanko, variation in photoperiod is low compared to the variation in its area of origin and below its likely Mop. In these conditions, the vegetative growth of the kafir Is 9508 at Samanko reveals only its intrinsic earliness. The kafir is never in a position to exhibit a possible photoperiod sensitivity which explains its apparent photopheriod insensivity. The important increase of the vegetative phase of the kafir Is 9508 during the off-season, is due to the fact that the vegetative thermal time remains constant and high (634°). Although the kafir Is 9508 appears insensitive to cold with Tbase estimated at 1°C, the natural decrease of night temperature suffices to explain the delay in flowering: in terms of night

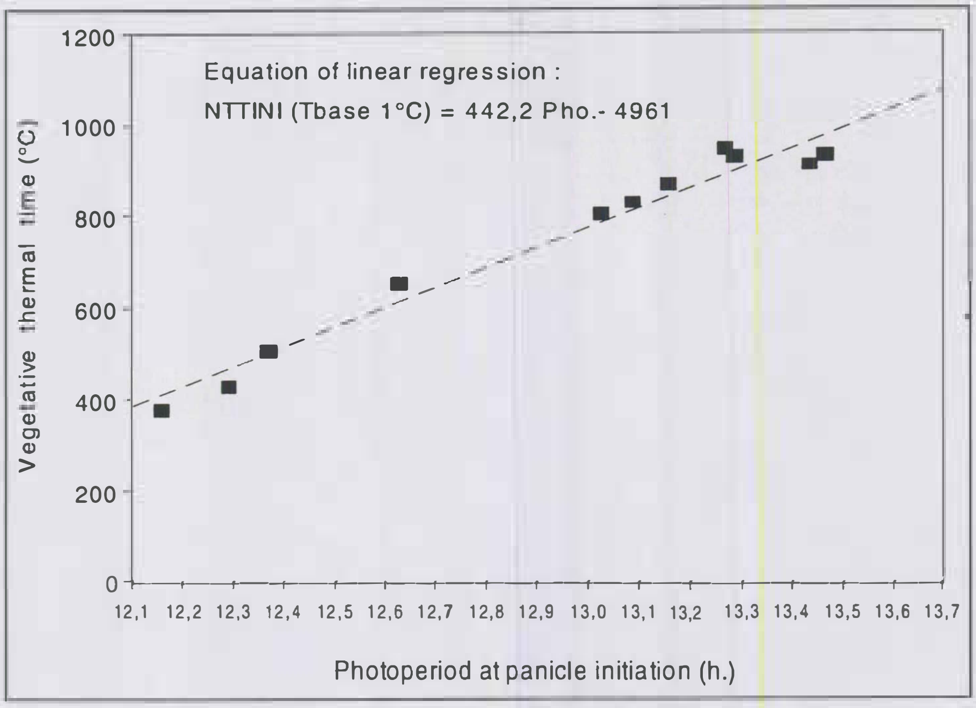

***Figure 3.** Thermal time to panicle initiation calculated by using night temperature plotted against photoperiod at panicle initiation of durra Ssm 973 sown in Samanko (1994-1996).*

temperatures, its needs time to achieve the Bvp: the days of December or January appear only half as efficient to conduct to flowering as the days of the rainy season.

As we already said, the durra Ssm 973 is a post-rainy season sorghum from Senegal growing on residual subsoil moisture. In our study, we verified that it has the advantage of flowering quickly in the off-season and we established the components which ensure this advantage: a high photoperiod sensitivity with a very low Mop (lower than lowest photoperiod observed at Samanko) and an insensitivity to cold night temperatures quantified by a low value of Tbase (Tbase = 1°). With these features, the influence of the off-season night temperatures to delay flowering is minimized by the cold insensitivity of the kafir Is 9508 and compensated by its vegetative thermal time shorter than in the rainy season. Here, we probably identified the specific traits of the adaptation to off season of African post-rainy season sorghums and Cameroon transplanted sorghums which mostly belong to durra race.

This type of thermal and photoperiod response is different from that of the guinea Is 7680 characterized by high photoperiod sensitivity in the rainy season, Bvp achieved for the September days and constant in the off-season, and sensitivity to cold night temperatures (Tbase = 6° C) (Vaksmann *et al.*, 1998).

According to Major's model, the characteristics of the thermal and photoperiod responses of the guinea Is 7680, the kafir Is 9508 and the durra Ssm 973 are resumed in table V. In comparison with Major's model, table V presents an additional genetic constant: the Tbase or efficacy threshold of night temperature.

With only three cultivars, table V shows important differences in the values assigned to the components of the temperature and photoperiod varietal response. Moreover, it seems that independence exists between these components. Thus, insensitivity to cold night temperatures can be associated to photoperiod insensitivity (kafir Is 9508) as well as to photoperiod sensitivity (durra Ssm 973). In the same way, photoperiod sensitivity can be associated to both cold night

Table V. Characteristics of the thermal and photoperiod responses of three African cultivars.

Components of thermal and photoperiod characterization	Guinea Is 7680	Kafir Is 9508	Durra Ssm 973
Bvp : Base Vegetative Phase (C°)	453°	634°	If it exists < 400°
Mop : Maximum optimal photoperiod (h)	12.95 h	If it exists > 13.60 h	If it exists < 12.10 h
Photosensitivity (°C day/h)	625° days/h	[illegible]	442° days/h
Efficacy threshold of night temperatures (°C)	6°	1°	1°

temperature sensitivity (guinea Is 7680) and cold night temperature insensivity (durra Ssm 973).

As reported in the study of Vaksmann *et al.*, 1998, it appears that temperature acts differently in the growth and development phases of the studied sorghum cultivars. During the growth phase, what is important is the daily mean temperature mainly to explain phyllochron. On the other hand, it is efficient to consider the daily night temperatures to explain time to panicule initiation.

More investigations among African landraces would certainly identify new kinds of temperature and photoperiod responses related to particular uses in traditional cropping systems. They would also accurately define the scope of variation of the different components of the temperature and photoperiod varietal response. For now, our results broaden the photoperiod sensitivity coefficients that Ritchie and Alagarswamy (1989) found in modelling the phenology of selected Us cultivars.

A better understanding of sorghum development strategies related to their agronomic uses is anticipated. If the genetic independence in the components of the temperature and photoperiod varietal response is verified, we will have new breeding tools to combine different levels of temperature and photoperiod sensitivity in selected lines.

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