

Crop photoperiodism model 2.0 for the flowering time of sorghum and rice that includes daily changes in sunrise and sunset times and temperature acclimation

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- **Background and Aims** Daylength determines flowering dates. However, questions remain regarding flowering dates in the natural environment, such as the synchronous flowering of plants sown simultaneously at highly contrasting latitudes. The daily change in sunrise and sunset times is the cue for the flowering of trees and for the synchronization of moulting in birds at the equator. Sunrise and sunset also synchronize the cell circadian clock, which is involved in the regulation of flowering. The goal of this study was to update the photoperiodism model with knowledge acquired since its conception.
- **Methods** A large dataset was gathered, including four 2-year series of monthly sowings of 28 sorghum varieties in Mali and two 1-year series of monthly sowings of eight rice varieties in the Philippines to compare with previously published monthly sowings in Japan and Malaysia, and data from sorghum breeders in France, Nicaragua and Colombia. An additive linear model of the duration in days to panicle initiation (PI) and flowering time using daylength and daily changes in sunrise and sunset times was implemented.
- **Key Results** Simultaneous with the phyllochron, the duration to PI of field crops acclimated to the mean temperature at seedling emergence within the usual range of mean cropping temperatures. A unique additive linear model combining daylength and daily changes in sunrise and sunset hours was accurately fitted for any type of response in the duration to PI to the sowing date without any temperature input. Once calibrated on a complete and an incomplete monthly sowing series at two tropical latitudes, the model accurately predicted the duration to PI of the concerned varieties from the equatorial to the temperate zone.
- **Conclusions** Including the daily changes in sunrise and sunset times in the updated photoperiodism model largely improved its accuracy at the latitude of each experiment. More research is needed to ascertain its multi-latitudinal accuracy, especially at latitudes close to the equator.

Key words: *Sorghum bicolor*, *Oryza sativa*, flowering time, panicle initiation, temperature acclimation, photoperiodism, daylength, sunrise, sunset.

INTRODUCTION

In plants and animals, reproductive cycles are synchronized through different means, among which photoperiodism, i.e. a response to the seasonal changes in daylength, plays an essential role (Thomas and Vince-Prue, 1997; Gwinner and Scheuerlein, 1998). This cue, caused by the movement of the earth around the sun, is highly stable across years. After the influence of daylength on the flowering time was understood (Tournois, 1912; Klebs, 1913), many experiments were conducted. Artificial stable daylengths and naturally changing daylengths were used alternatively to characterize the specific responses of each species and cultivar. This response to photoperiod is hereafter referred to as photoperiodism.

Sorghum and rice have been classified as short-day plants, in which flowering is proportionally accelerated by short days (Thomas and Vince-Prue, 1997). Vergara and Chang (1985) compiled a large number of experiments on rice photoperiodism and measured the duration to flowering in a large panel of rice varieties in four stable photoperiods (10, 12, 14 and 16 h light). The results showed substantial variability in the reaction to daylength, from insensitive to highly sensitive. Similar variability was documented in sorghum in 22 500 accessions of the International Crops Research Institute for the Semi-arid Tropics (ICRISAT) gene bank sown in fields in Hyderabad, India (17° N) in June and October (Grenier *et al.*, 2001). In tropical areas, photoperiod sensitivity was also evaluated through comparison of durations to flowering in response

to monthly sowings conducted over the year (Bezot, 1963; Miller *et al.*, 1968; Clerget *et al.*, 2004 for sorghum, and Dore, 1959; Dingkuhn *et al.*, 1995, 2015; Sié *et al.*, 1998 for rice). Less commonly, sowings were conducted in a greenhouse over the year at a temperate latitude (Kawakata and Yajima, 1995).

In both sorghum and rice species, annual series of monthly sowings exhibited large ranges in photoperiod sensitivity. Moderately photoperiodic varieties showed quantitative responses to the sowing date, typically modelled through a linear response to daylength (Major, 1980). Highly photoperiodic varieties showed a sudden large increase (up to 180 d) in the duration to flowering between two sowing dates occurring from January to March, depending on the variety (Miller *et al.*, 1968; Kawakata and Yajima, 1995; Clerget *et al.*, 2004). The response to daylength of this second group of varieties was classified as qualitative photoperiod-sensitive and modelled accordingly using a critical photoperiod threshold, above which flowering was strictly inhibited (Carberry *et al.*, 1992, 2001). In sorghum, it was additionally hypothesized that this threshold increased as the plant aged because panicle initiation (PI) occurred from July at a higher threshold than the critical threshold that caused the initial flowering inhibition, and that PI occurred immediately when the daylength reached this moving threshold (Folliard *et al.*, 2004; Dingkuhn *et al.*, 2008).

Models of photoperiodism generally assume that the crop progresses towards PI by accumulating daily progress equal to the inverse of the predicted duration to PI under the temperature and photoperiod of the day until reaching the value of 1 (Summerfield *et al.*, 1997). This concept of quantitative accumulation was strongly supported by the reciprocal transfer experiments at stable daylength (Collinson *et al.*, 1992; Ellis *et al.*, 1992). Plants were first grown in either long or short photoperiods and then transferred to the opposite photoperiod after variable durations. The duration to PI was a linear combination of the effect of each photoperiod multiplied by the proportion of time spent under each photoperiod.

A possible effect of decreasing daylength on the triggering of PI was tested on the dates of PI recorded in monthly plantings of three tropical varieties in Samanko, Mali (12°34' N), but could be successfully parameterized into only two varieties (Clerget *et al.*, 2004). In rice, modern varieties exhibit little photoperiod sensitivity; thus, no model was developed for the strongly photoperiodic flowering response. Thus, Dingkuhn *et al.* (2015) used the 2008 sorghum Impatience model for highly photoperiod-sensitive rice varieties. All current models are only valid at the latitude where they have been calibrated because photoperiods are different at other latitudes, although Abdulai *et al.* (2012) made a preliminary attempt to adjust the sorghum Impatience model with a latitude effect based on experiments from 11°13' N to 13°15' N.

The effect of the change in photoperiod with latitude on the flowering date has remained an unsolved question. Curtis (1968) showed that six Nigerian varieties sown at three latitudes from 7°30' N to 11° N headed simultaneously despite the difference in the perceived daylengths. At a fourth latitude, 12° N, sowings were delayed by the late onset of the rainy season and discarded. Conversely, Abdulai *et al.* (2012) showed that PI of seven sorghum varieties simultaneously sown in three locations was significantly earlier at 11°13' than at 12°39' or 13°25' N. Lafarge (1998) questioned the similar duration to PI of the

moderately sensitive sorghum variety 'E-35-1' sown simultaneously in May in Bamako, Mali (12°39' N) and Montpellier, France (43°39' N), despite the difference of 2–3 h in the photoperiods at the two locations.

The cue perceived by plants and animals at equatorial latitudes, where daylength is stably equal to 12 h 00 min, has intrigued many authors. In rice, Dore (1959) showed that the duration to flowering of the variety 'Siam 29' varied between 161 and 329 d with sowing month in Malacca, Malaysia (2°12' N), where annual photoperiod variation was only 14 min. Under an artificially stable photoperiod from 11 h 50 min to 12 h 50 min (20-min range), 'Siam 29' showed a strong photoperiodic reaction but the duration to flowering only varied from 80 to 150 d, much less than that in the monthly sowing experiment. At a larger scale, Borchert *et al.* (2005) gathered a large dataset on the flowering time of 41 species of forest trees in Central and South America that exhibited a synchronous bimodal flowering distribution in spring and autumn at equatorial latitudes, from 2.5° N to 5° S. In tropical zones at 10° N or 16° S, the flowering distribution was monomodal and synchronous with one of the equatorial flowering peaks. The authors pointed out that the bimodal distribution was synchronous with the peaks in the annual variation in the change in sunrise and sunset hours at the Equator, in March–April and September–October.

Indeed, as a consequence of the ellipsoidal orbit of the earth around the sun and of the inclination of the axis of rotation of the earth, variations in the times of sunrise (SR; Fig. 1A) and sunset (SS; Fig. 1B) result in symmetrical variation in daylength (photoperiod, PP; Fig. 1C) across the year. However, variations in SR and SS, as well as those of their daily derivatives (dSS and dSR), are asymmetrical across the year (Fig. 1D). All these vary with latitude. Similarly, Ramírez *et al.* (2010) reported that mango trees grown in La Mesa, Colombia (4°31' N), flowered twice a year in separate sections of the canopy.

In birds, the annual cycles of reproduction, moulting and migration of high-latitude birds are rigidly controlled by seasonal variations in photoperiod (Gwinner and Scheuerlein, 1999). The stonechat birds living in Nakuru, Kenya (0°14' S), initiate breeding at the onset of the rains in March or April (Dittami and Gwinner, 1985), whereas other populations of the same bird species living at Mount Meru, Tanzania (3°23' S), start breeding in October (Scheuerlein and Gwinner, 2002). Goymann *et al.* (2012) demonstrated that the reproductive cycle of stonechats living indoors in Germany with 12 h 00 min of stable daylength and changes in the times of sunrise and sunset mimicking the changes in Nakuru was well synchronized among birds and with the cycle of wild birds living in Nakuru. Thus, they demonstrated the efficiency of the cue proposed by Borchert *et al.* (2005) (the daily change in sunrise and sunset times) in synchronizing the reproductive phase.

Since 2000, physiological studies have contributed much information on the relationships between the circadian clock and the seasonal triggering of reproduction in plants (Shim and Jang, 2020). The circadian clock in each cell is made up of antagonist molecule couples that translate the day–night alternation into molecular concentration alternations. Three main genes encode three proteins (TOC1, CCA1 and LHY) that interact in a series of interlocking transcriptional feedback loops (Barak *et al.*, 2000). Concentrations of CCA1 and LHY peak at dawn, whereas that of TOC1 peaks at dusk. The action of the feedback

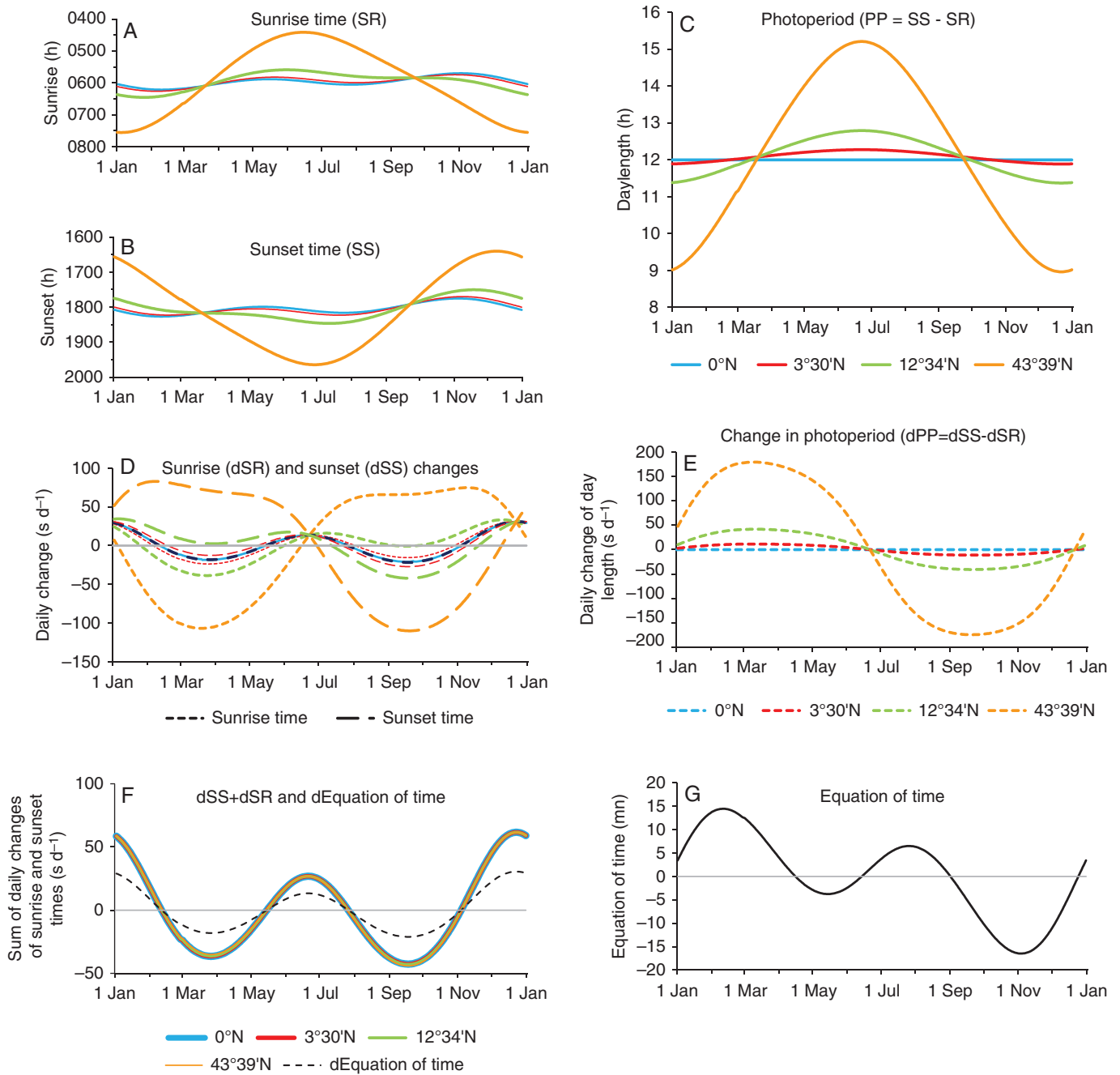


FIG. 1. Sunrise time (A), sunset time (B) and photoperiod (C) with the year date and their respective derivatives, the daily rates of change (D, E) at four latitudes from the Equator to Montpellier, France. At any latitude, the sum of the daily rates of change of sunrise and sunset times (F) was twice the derivatives of the equation of time (G).

loops is reversed at dawn and dusk, perceived through photoreceptors, including a blue photoreceptor, the cryptochrome, discovered in 1993 (Ahmad and Cashmore, 1993). Through a complex network of proteins with daily oscillating concentrations, the soluble FT protein (FLOWERING LOCUS T) is synthesized in leaf cells at concentrations that are adjusted by both photoperiod and temperature (Kinmonth-Schultz *et al.*, 2019). The FT protein moves to the stem apex, where it induces the transition to the reproductive phase.

The current paper relies on phenology data recorded during the last 26 years by sorghum and rice scientists from the French Agricultural Research Centre for International Development (CIRAD), who conducted their research programmes in various locations from equatorial to temperate latitudes. Sorghum is a staple food in West African Sahelian countries, where CIRAD and ICRISAT developed many partnerships for sorghum crop improvement. It soon appeared that photoperiod sensitivity was a key factor in the

adaptation of varieties in this part of the world and thus deserved a better understanding. CIRAD also conducted sorghum breeding activities in Nicaragua with the International Center for Tropical Agriculture (CIAT) and the Nicaraguan Institute of Agricultural Technology (INTA) and in Colombia with the Colombian Corporation for Agricultural Research (CORPOICA). CIRAD and the International Rice Research Institute (IRRI) share a long tradition of partnership in research for rice crop improvement. Complementary monthly sowings of rice were thus conducted at IRRI headquarters in the Philippines, which helped to link results from contrasting latitudes. After a long period of maturation, an improved and simple model emerged that synthesized current knowledge and could predict the response of sorghum and rice crops to photoperiod at any latitude. This model is described below.

MATERIALS AND METHODS

Data acquisition

Experiments were conducted in eight countries from four continents. These are listed in [Supplementary Data Table S1](#) and located on a world map in [Supplementary Data Fig. S1](#)).

Monthly sowings of sorghum in Mali. Four series of monthly sowings on approximately the tenth day of each month were conducted from July 2000 to October 2008 at the Samanko ICRISAT research station near Bamako, Mali (12°34' N, 8°04' W, 330 m asl). Three tropical sorghum cultivars, 'CSM 335', 'IRAT 174' and 'Sariaso 10', were used during the first series (26-month study; Clerget *et al.*, 2004, 2008) and 12 new cultivars, plus 'CSM 335' as a control, were used during a second series (29-month study; Dingkuhn *et al.*, 2008). Seven East African cultivars plus 'CSM 335', 'IRAT 174' and 'Sariaso 10' were used during a third series (12-month study). Finally, six cultivars from two distinct genetic clusters of durra sorghums (Deu *et al.*, 2006) were tested during the last series (15- to 18-month study) ([Supplementary Data Table S2](#)). Individual plots consisted of four 5-m-long rows, sown at 0.75 m × 0.20 m spacing. Split fertilization doses were applied to secure the optimum growth of the plants (gypsum at 100 kg ha⁻¹ and N-P-K at 128, 92 and 60 kg ha⁻¹ as urea, diammonium phosphate and KCl, respectively, during the first 45 d. Then, in late varieties, N at 46 kg ha⁻¹ was applied as urea monthly until flag-leaf appearance). Soil moisture was never limiting because of twice-weekly irrigation during the dry season. Hand-weeding and insecticide were applied when required. Ten plants of the two central rows per plot were specifically labelled and the numbers of leaves that emerged from the whorl on the main culm were recorded weekly. From seedling emergence to PI, two plants per variety were sampled every week and after a longer interval for very late varieties. The plants were dissected to count the number of leaves initiated at the apex and to record the PI date.

Additionally, a sorghum core collection of 210 accessions established by CIRAD and ICRISAT scientists (Grenier *et al.*, 2001) was sown in Samanko, Mali, on 13 November 2007 in an irrigated field. Plots consisted of one 3-m-long line distributed in an unbalanced incomplete block design, including six repeated checks. Adequate fertilization and irrigation were

applied to secure optimum growth, as described above. Dates at which 50 % of the plants had reached flag-leaf expansion, heading and flowering were recorded in each plot.

Simultaneous sorghum sowings in France and Mali. In France, sorghum experiments were managed by the CIRAD sorghum breeding programme for the adaptation of tropical resources to temperate environments in Montpellier, France. Sorghum trials were sown in the GEVES Lavalette Research Station (43°39' N, 3°52' E) from mid-May. After ploughing, 300 kg ha⁻¹ of fertilizer compound (N-P-K: 0-23-19) was applied, sowing was conducted at 75 × 20 cm, and sprinkler irrigation was applied every 2 weeks when required. Three N fertigation at 40 kg ha⁻¹ N each were applied at ~30, 60 and 90 d after sowing.

From 1994 to 1997, two photoperiod-sensitive sorghum varieties ('SSM 973' and 'IS 9508') and one photoperiod-insensitive variety ('IS 2807') were sown both in Samanko, Mali (17 June, 1, 15 and 29 July 1994; 23 June, 1, 9 and 20 July 1995; 16 June, 1 and 22 July 1996) and in Montpellier, France (18 May and 8 June 1994; 15 May and 17 June 1997), and the dates of flag-leaf appearance and flowering were recorded.

In 2001, 'CSM 335', 'IRAT 174' and 'Sariaso 10' were sown simultaneously in Samanko and Montpellier on 11 May, 7 June and 3 July. Leaf appearance kinetics and PI were recorded as described above for monthly sowing experiments in Mali.

In 2006, five sorghum varieties ('CSM 335', 'IRAT 174', 'IRAT 204', 'Sariaso 10' and 'Souroukoku') were simultaneously sown in Samanko, Mali, and Montpellier on 19 May, 22 June and 20 July. Leaf appearance and PI were also recorded and all 111 remaining plants of the late varieties were dissected on 17–18 October 2006, before the beginning of the cold season, to determine their reproductive stage. From 2008 to 2017, additional observations of flowering dates were conducted in Montpellier for the varieties 'Sariaso 10' and 'Sariaso 14' with sowing dates in approximately mid-May.

Sorghum in Nicaragua and Colombia. From 2002 to 2008, CIRAD conducted a regional participatory sorghum breeding programme based in Nicaragua, in partnership with the INTA, the CIAT, national NGOs and local farmer organizations, targeting resource-poor farmers in drought-prone areas where sorghum is an important staple crop. Local cultivars from Nicaragua, known as criollo or maicillon, generally grown in intercropping systems with maize and/or beans, are very late and highly photoperiod-sensitive and the quantification of the photoperiod-sensitivity was included in the research programme. African varieties ('Sariaso 14' and 'Souroukoku') were included in these experiments.

From 2008 to 2011, CIRAD and the CORPOICA (now AGROSAVIA) implemented a research project to develop sweet sorghum hybrids adapted to four targeted agro-ecologies of Colombia. In the framework of this project, phenology as well as other adaptive and productivity traits of a large collection of diverse cultivars and inbred lines were recorded at three low-latitude locations (Palmira, 3°30' N; Espinal, 4°26' N; and Monteria, 8°44' N). A large database was thus established, from which data for some cultivars grown both in Nicaragua and in Colombia with multiple sowing dates were selected.

Monthly sowings of rice in the Philippines. Published results of monthly rice sowings in Malaysia, close to the equator

(Dore, 1959), and in Japan, at a temperate latitude (Kawakata and Yajima, 1995), constituted a good basis for comparison with monthly sowings conducted in the tropics. The six varieties from the Japanese experiment were obtained from the IRRI's gene bank and rejuvenated in four pots per variety, which were sown in December 2011. Plants were then grown in a greenhouse at the IRRI farm, Los Baños, Philippines (14°11' N, 121°15' E) using a protocol as similar as possible to the original protocol. On or close to the 10th of each month, 12 sowings were conducted during 12 consecutive months, starting on 10 May 2012. For each variety, three plants were grown in two 13-L pots filled with soil from the IRRI upland farm. Fertilizers were applied in each pot (0.16 g P as SSP, 0.16 g K as KCl and 0.06 g ZnSO₄ at sowing; 0.16 g N as urea at 18 and 30 d after sowing and then monthly). Soil water content was kept at the saturation point for 2 weeks; then, the water level was maintained ~3 cm above the soil surface. Leaf appearance was recorded for the main stem of each of the six plants until the flag leaf expanded.

The second series of 15 consecutive monthly sowings from 14 March 2014 only involved the variety 'Siam 29', used by Dore (1959). Seeds from two accessions of 'Siam 29', 'IRGC 13741' and 'IRGC 27' were obtained from the IRRI's gene bank, but 'IRGC 27' was later discarded because of the earliness of the plants. The first sowing was conducted in six 13-L pots placed in the IRRI greenhouse, as in the series described above. All the following sowings were conducted in a small 6 × 6-m IRRI screenhouse, i.e. a field space covered with a 2-m-high metallic structure covered with a metallic mosquito net. Each month, six plants were sown at 20 × 20 cm in a 1 × 1-m bonded plot and managed as in the previous series. Leaf appearance was recorded on the main stem of each of the six plants until the flag leaf expanded. In December 2015 and January 2016, simultaneous experiments were conducted in the greenhouse and the screenhouse to check for a possible effect of the enclosures.

Data analysis

Duration from sowing to PI. The duration of the vegetative phase until the induction of flowering varies with photoperiod and temperature during the vegetative phase. Thus, the duration to flowering induction, i.e. PI in Poaceae, must be either known or carefully estimated before it can be related to the factors responsible for its variation. Panicle initiation was recorded in all sorghum experiments conducted in Samanko, where both leaf initiation and leaf appearance kinetics were recorded. In rice, the leaf appearance kinetics were recorded in all experiments conducted in Los Baños and the data were sufficient to accurately estimate the time of PI. For data from other sources, only the duration to heading or flowering was recorded. The duration

to PI was then estimated with bilinear relationships parameterized from the large Samanko and Los Baños databases, as described below.

Ex post estimation of PI date from the leaf appearance kinetics in rice. In the monthly sowings of rice conducted in Los Baños, only the flowering dates were recorded because the *ex post* estimation of the PI date from the leaf appearance kinetics was easy and highly reliable in this species. In this specific species, a stable, re-checked number of four developing leaves is hidden inside the leaf sheaths at any time during the vegetative phase until the time of PI (Yoshida, 1981).

The first step was to determine the parameters of leaf appearance kinetics in each variety. Depending on the variety and the sowing date, the dynamics of leaf emergence were linear, bilinear or trilinear and were fitted with linear or broken-linear segmented models, as previously detailed (Clerget et al., 2008). In short, observed leaf number (LN) (initiated, emerged, ligulated or senesced) was regressed against the elapsed thermal time from emergence (TT) using the following equation in the case of trilinear kinetics:

$$LN = a + b_1 \times \min(TT, TT_1) + b_2 \times \min(TT_2 - TT_1, \max(0, TT - TT_1)) + b_3 \times \min(TT_3 - TT_2, \max(0, TT - TT_2)) \quad (1)$$

where a is the number of leaves at emergence, b_1 , b_2 and b_3 are the first, second and third rates of development, and TT_1 , TT_2 and TT_3 are the thermal times when either the change in the rate occurred or development terminated. Parameters were estimated iteratively using the procedure NLIN in SAS (2012). Phyllochrons were calculated as the reciprocal of the slope coefficients for leaf emergence.

Then, when for instance leaf appearance was trilinear, the thermal time at PI (TT_{PI}) was estimated as the thermal time at the appearance of the leaf (N-4), with N being the total number of leaves produced by the main stem:

$$TT_{PI} = [N-4 - a - b_1 \times TT_1 - b_2 \times (TT_2 - TT_1)]/b_3 + TT_2 \quad (2)$$

Relationship between duration to flowering and duration to PI. Bilinear relationships between either the observed or the estimated duration to PI and the duration to flowering were fitted for sorghum in Samanko and rice in Los Baños data from the monthly sowings, as:

$$dur_PI = c_0 + c_1 \times \min(thr_1, dur_flower) + c_2 \times \max(0, (dur_flower - thr_1)) \quad (3)$$

where dur_PI is the duration from sowing to PI, dur_flower is the duration to flowering and c_0 , c_1 , c_2 and thr_1 are parameters (Supplementary Data Fig. S2 and Table 1). This relationship was used to estimate the date of PI from the flowering date in datasets in which PI was not recorded.

TABLE 1. Parameters and statistics of the bilinear relationship duration to PI = f(duration to flowering) plotted in Supplementary Data Fig. S2

Species	c_0	c_1	thr_1	c_2	n	R^2	RMSD
Sorghum	-12.68	0.689	135.8	0.892	859	0.969	8.52
Rice	-9.54	0.569	111	1.024	94	0.9877	3.36

Once the duration to PI was computed, the reverse relationships allowed the estimation of duration to flowering, as follows:

$$\text{dur_flower} = -c_0/c_1 + 1/c_1 \times \min(\text{dur_PI}, (c_0 + c_1 \times \text{thr}_1)) + 1/c_2 \times \max(0, \text{dur_PI} - (c_0 + c_1 \times \text{thr}_1)) \quad (4)$$

Using the sunrise and sunset times in modelling the date of PI at any latitude. The more recent models for the duration to flowering in response to the photoperiod used photoperiod thresholds that determined the onset and end of the period during which flowering initiation was inhibited in qualitative photoperiodic varieties (Carberry et al., 1992; Folliard et al., 2004; Dingkuhn et al., 2008). Therefore, several attempts were conducted to replace the photoperiod thresholds by (dSR + dSS) thresholds that would be similar at every latitude. However, the simpler additive model using PP, dSR and dSS fitted the observations better than any of the other, more sophisticated models and was thus retained.

The 2.0 photoperiod model was built based on the model proposed by Major (1980). Seedling emergence is followed by a juvenile phase, known as the basic vegetative phase (BVP). At the end of the BVP begins the photoperiod-sensitive phase (PSP), which has a genetically determined duration and ends at PI. Under stable photoperiod and controlled environments, PI occurs immediately after the end of the BVP when the daylength (PP) is below the base photoperiod (Pb_1). Otherwise, when PP exceeds Pb_1 , the duration of the PSP increases linearly with PP as a product of a photoperiod-sensitivity coefficient (Ps), with the difference between the actual photoperiod and Pb_1 being ($Ps \times (PP - Pb_1)$) in varieties with a quantitative short-day response.

In natural environments, the expected duration of PSP on a specific day, $\text{PSP}(\text{day}) = f(\text{PP}, T)$, changes every day with PP and T (the mean daily temperature); thus, it was assumed that plants accumulate daily progress towards PI, according to the equation $\text{dPI} = 1/f(\text{PP}, T)$ (Summerfield et al., 1992). PI occurs when the daily sum of progress reaches 1.

The daily change in sunrise and sunset times is a sufficient cue to trigger flowering in trees and to synchronize the circannual reproductive rhythms of birds living at the equator at similar dates as in congeners living in tropical areas (Borchert et al., 2005; Goymann et al., 2012). Thus, an additive effect of each of these two factors (dSR and dSS) was introduced in crop photoperiodism model 2.0, by multiplying them by the respective sensitivity coefficients, SRs_1 and SSs_1 . These two effects were assumed to act on any day of the year, whereas the PP effect acts only when $PP > Pb_1$, leading to the general model equation:

$$\text{PSP}(\text{day}) = \max(1, Ps \times \max(0, PP - Pb_1) + SRs_1 \times \text{dSR} + SSs_1 \times \text{dSS}) \quad (5)$$

This model could fit the data of the extremely photoperiod-sensitive rice variety ‘Siam 29’ when grown close to the equator with June to December sowings but not with January to May sowings. During the latter time interval, the duration to PI decreases by 1 month between each monthly sowing date, indicating the absence of any progress towards PI. The modelling solution was to hypothesize that $\text{PSP}(\text{day})$ was very long from approximately the

spring equinox to the summer solstice, when both the photoperiod (PP) is above a specific threshold Pb_2 and $\text{dSS} > \text{dSR}$ because of a stronger response to dSR and dSS with larger coefficients SRs_2 and SSs_2 . During approximately the 3 months of spring, the model equation for ‘Siam 29’ was as follows:

if ($PP > Pb_2$ and $\text{dSR} < \text{dSS}$) then

$$\text{PSP}(\text{day}) = \max(1, Ps \times \max(0, PP - Pb_1) + SRs_2 \times \text{dSR} + SSs_2 \times \text{dSS}) \quad (6)$$

The concept was then re-used in modelling the specific response of ‘IRAT 204’ with sowings from July to September, the time when $PP > Pb_2$ and $\text{dSR} > \text{dSS}$, and by extension to improve the model fit of nearly every sorghum and rice variety. Thus, from the summer solstice to a date determined by the optimized Pb_2 parameter, SRs_2 and SSs_2 replaced the coefficients SRs_1 and SSs_1 in the general equation (eqn 5) for all varieties with a defined Pb_2 value, except ‘Siam 29’.

Lastly, it appeared that in rice grown in the greenhouse all three effects act only when $PP > Pb_1$. The duration to flowering could be estimated from the duration to PI with eqn (4).

The time unit was changed from thermal time to day based on further detailed results and discussion. In summary, the PI of plants simultaneously sown in Samanko (Mali) and Montpellier (France) occurred on close dates but after a longer thermal time for plants grown in Mali. The duration in days to PI of the daylength-insensitive variety ‘IRAT 204’ was additionally insensitive to the variation of the mean temperature between Samanko and Montpellier. These results were attributed to acclimation of the duration to PI to the temperature at seedling emergence, which was able to buffer the effect of temperature on the plant development rate within a large range of temperatures. Given the current knowledge, it thus appeared more accurate to assume the insensitivity of the duration to PI in days to the temperature under the usual cropping conditions than the contrary, even if this was not entirely true.

Finally, the 2.0 model can be summarized as below:

In the field:

if ($PP > Pb_2$ and $\text{dSR} > \text{dSS}$) then

$$\text{PSP}(\text{day}) = \max(1, Ps \times \max(0, PP - Pb_1) + SRs_2 \times \text{dSR} + SSs_2 \times \text{dSS})$$

$$\text{else } \text{PSP}(\text{day}) = \max(1, Ps \times \max(0, PP - Pb_1) + SRs_1 \times \text{dSR} + SSs_1 \times \text{dSS}).$$

Exception for ‘Siam 29’: replace $\text{dSR} > \text{dSS}$ with $\text{dSR} < \text{dSS}$.
In the greenhouse:

$$\text{if } PP > Pb_1 \text{ then } \text{PSP}(\text{day}) = \text{same as in the field, else } \text{PSP}(\text{day}) = 1$$

then, $\text{dPI}(\text{day}) = 1/\text{PSP}(\text{day})$; if $\sum \text{dPI}(\text{day}) \geq 1$ then $PI = 1$ (PI is triggered);

$$\text{dur_PI} = \text{BVP} + \text{PSP} \text{ and } \text{dur_flower} = f(\text{dur_PI}) \text{ where } f = \text{eqn (4)}.$$

Daily photoperiod and sunrise and sunset times were calculated using the equations from Laureanno (1992) (Supplementary

Excel File). Variety parameters for the model were issued from an iterative optimization using the evolutionary solving method in Microsoft Excel Solver to minimize the sum of square errors (predicted – observed). When data were available from several latitudes, those from one or two latitudes were used to calibrate the parameters of the model [‘C’ in the Use column in the tables of parameters (Tables 2 and 3), Supplementary data, Tables S4 and S5]. The parameterized model was then validated using the remaining data from the other latitudes (‘Val’ in the Use column).

The accuracy of the prediction of the duration to PI was assessed using the coefficient of determination (R^2) derived from the regression of observed and predicted days to PI, and the root mean square deviation (RMSD), which represents a mean weighted difference between predicted and observed data. The RMSD was calculated as $\text{RMSD} = [\sum(\text{observed} - \text{predicted})^2/n]^{0.5}$. Two R^2 and RMSD values were computed for each variety at each location. Firstly, all sowing dates were used. Secondly, the dataset was reduced to that of eight sowing months, from March to October, to discard the highly contrasting durations to PI observed from November to February sowings in some highly photoperiod-sensitive varieties.

Prediction of the duration to PI for daily sowing dates was then computed using the model with the optimized parameters in SAS data steps. Proc GLM (SAS, 2012) was used to compute the ANOVAs.

RESULTS

Universal solar cue from the Equator to the Polar Circles

Daylength and its derivative, the daily change in daylength, have symmetrical yearly variations centred on the equinoxes (21 June and 21 December) (Fig. 1C, E). The daily change in daylength is also the difference, $dSS - dSR$, whereas the sum of the daily changes in the sunrise and sunset hours, $dSS + dSR$, has the same daily value everywhere on earth from the Equator to the polar circles (Fig. 1F). $dSS + dSR$ is equal to twice the daily derivative of the equation of time, i.e. twice the difference between the solar time (indicated by sundials) and the mean solar time (shown by clocks) (Fig. 1G). Similar to daylength, $dSS + dSR$ has symmetrical variations centred at the equinoxes, which led to investigation of the utility of $dSR + dSS$ as a universal cue to improve the photoperiod models. However, in this study thresholds of $dSS + dSR$ were unsuccessfully tested as replacements for the previous thresholds of the photoperiod in qualitative photoperiod-sensitive varieties.

Durations of the vegetative phase in monthly sowings in the tropics

Monthly sowings of sorghum in Samanko, Mali. Photoperiod sensitivity is a major trait of adaptation of sorghum varieties in West Africa, which justifies the need for research to precisely and exhaustively describe the variabilities, both within the species and between years, of this trait. The 28 sorghum varieties that were sown monthly in Samanko, Mali, from 2000 to 2008 showed a larger range of responses to the

sowing date than reported by the previous authors (Bezot, 1963; Miller et al., 1968) (Fig. 2 and Supplementary Data Fig. S3). Results for the 14 varieties sown between 2000 and 2005 have been reported previously (Clerget et al., 2004; Dingkuhn et al., 2008). Another set of 14 varieties was sown from 2005 to 2008. Eight varieties were selected that covered the entire range of observed patterns of photoperiodic responses of the duration to PI to the sowing date, from insensitive to highly sensitive varieties (Fig. 2A–H). The duration to PI of the variety ‘IRAT 204’ was short and stable during the eight sowing months from November to June but was prolonged from July to October (Fig. 2A). ‘CSM 63-E’ showed a short and stable duration to PI for sowings from May to October and prolonged durations for sowings from November to April (Fig. 2B). Figure 2C–G show varieties with increasing photoperiod sensitivity for sowings from January to September. ‘Sima’ and ‘Ouéni’ were moderately photoperiod-sensitive, whereas ‘IRAT 174’, ‘Kaura D-12’ and ‘IS 15401’, with a breakpoint in the annual pattern between two early sowing dates in the year, showed high photoperiod sensitivity. The shorter duration to PI occurred for the September and October sowings in every variety. The duration to PI was much longer for November and December sowings in the varieties ‘CSM 63-E’, ‘IRAT 174’ and ‘Ouéni’.

A new pattern was observed for the first time in four landraces from South Tanzania (‘IBS 19’, ‘IBS 30’, ‘IBS 40’ and ‘IBS 582’) (Fig. 2H and Supplementary Data Fig. S3O–Q). In these highly photoperiod-sensitive varieties, the PI of the November and December sowings could be delayed until July or August of the next year, with large inter-annual variation. The PI of all sowings from January to July occurred during August. This November threshold in the photoperiodic reaction was confirmed by the duration to flag leaf observed for 207 accessions of the sorghum core collection sown at Samanko on 13 November 2007, which ranged from 59 to 350 d. Sixteen accessions of this diversity panel flowered after 1 September 2008, i.e. 9.5–12 months after the sowing date (Supplementary Data Table S3).

Monthly rice sowings in Los Baños, Philippines. Latitude and year to date have combined effects on daylength; thus, data on the effect of the sowing date carried out at contrasting latitudes were needed to decorrelate the two factors.

The series of 12 sowings in the greenhouse replicating the experiment of Kawakata and Yajima (1995) was fully successful. The five Japanese rice varieties and ‘IR 72’ sown monthly in Los Baños showed only small changes in the duration of the vegetative phase in response to the sowing date, with a maximum duration for the May sowing and a minimum duration for the September to February sowings (Fig. 3A–F). Conversely, the duration to PI of the Indian rice variety ‘Co 26’ strongly reacted to the sowing date with a maximum duration for the March sowing and a minimum duration for the December sowing (Fig. 3G).

Only the first eight monthly sowings of the rice variety ‘Siam 29’ in the series replicating the experiment of Dore (1959), from March to December 2014, were successful. None of the following sowings could be maintained until PI because of stem borer damage to the January and February sowings. Then, Tungro virus infestation damaged all the

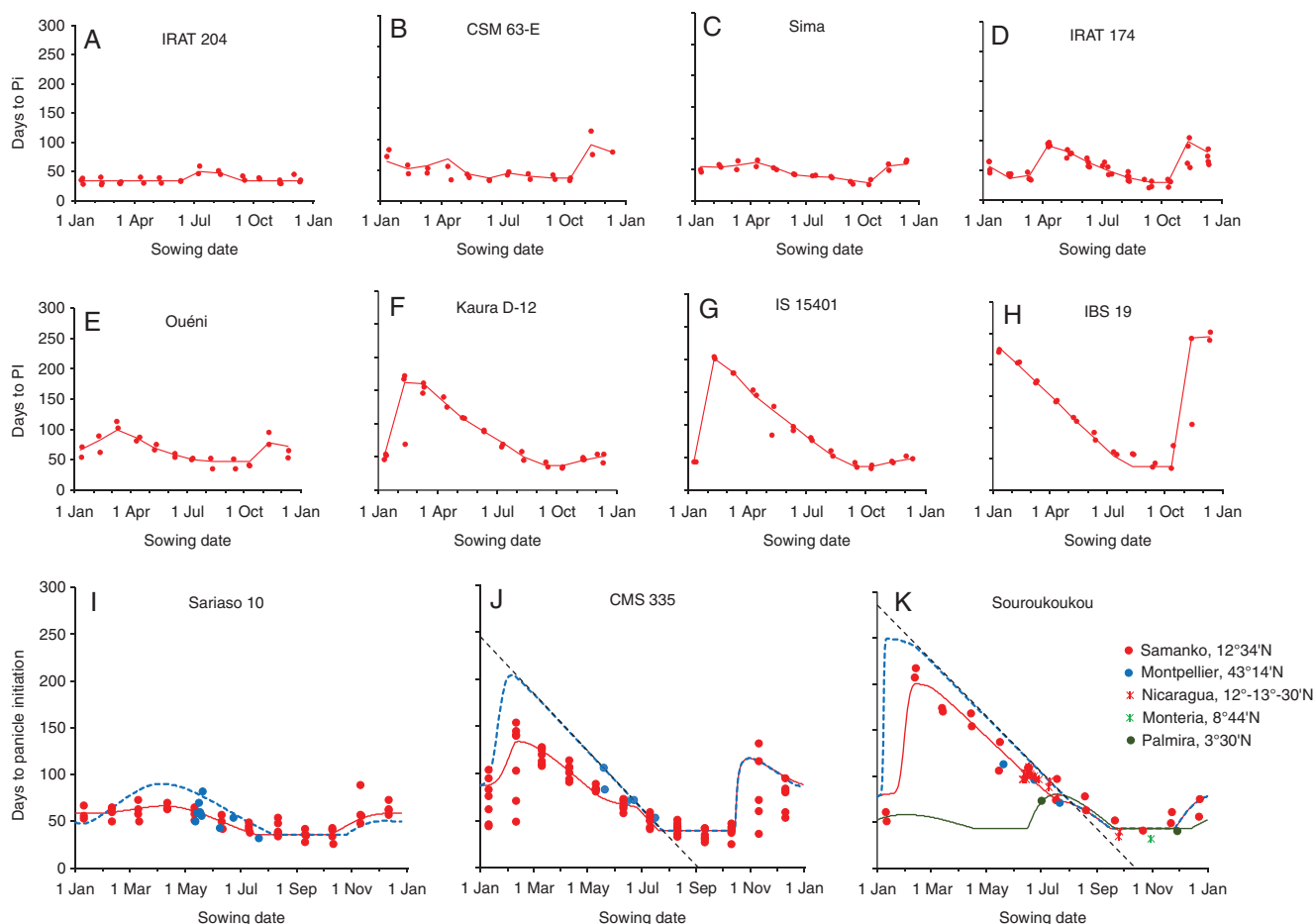


FIG. 2. Observed duration to panicle initiation in 2-year monthly sowing series of eight sorghum varieties (A–H), covering the whole of the observed range of photoperiod sensitivity, grown in the field in Samanko (Mali) (12°34' N) and in three sorghum varieties sown monthly in Samanko and additionally observed on the usual planting date at either one other latitude (I, J) or four other latitudes (K). The model predictions are plotted with solid lines for the locations used for calibration of the variety parameters and with dashed lines for the locations used for model validation. The –1:1 line is drawn as a black dashed line for late varieties.

plants from the next sowings. The time to PI was at a maximum for the March sowing and decreased for the next sowings until reaching its minimum for the September to December sowings (Fig. 3H).

Comparison of the duration to PI from the Equator to temperate latitudes

Simultaneous dates of PI in Samanko and Montpellier for sorghum. Panicle initiation of sorghum varieties sown at close year-to-dates in Samanko and Montpellier often occurred at close dates; however, the accrued thermal time was much higher in Samanko than in Montpellier. Thus, 'IRAT 204' is reputed to be non-photoperiod-sensitive but showed a response in the duration of the vegetative phase for the sowing dates from July to October in Samanko (Fig. 4A). For the eight remaining sowing dates, the duration of the vegetative phase was stable when expressed in days (mean = 33.4 d) and was consequently correlated with the monthly mean temperatures when expressed in thermal time (Fig. 4B, C). The duration in days to PI was also insensitive to latitude and consequently

to both daylength and temperature when sown in mid-May in Montpellier, where mean temperatures are always lower than those in Samanko (mean = 35 d) (Fig. 4A, C). For the eight sowings from November to June, the slope of the regression between the duration to PI and the mean temperature did not significantly differ from zero ($-0.22 \text{ d } ^\circ\text{C}^{-1}$, $P = 0.36$), within a 19–31.5 °C range of mean temperature (Fig. 4D).

The PI of the moderately photoperiodic sorghum varieties 'Sarioso 10', 'Sarioso 14', 'IS 2807' and 'SSM 973' occurred in the first fortnight in July for May sowings and in late July to early August for June sowings, independently of the latitude of the location, either 12–14° N or 43°39' N (Fig. 5A–D). In such situations, less thermal time had accrued before PI in cooler Montpellier than in Samanko. Thus, in 2001, Sarioso 10 was sown on 7 and 10 May in Montpellier and Samanko, respectively, and reached PI after 50 d or 502 °Cd and mean daylength of 15 h in Montpellier and after 54 d or 904 °Cd and mean daylength of 13 h 35 min in Samanko (Supplementary Data Table S4). The range of variation in the durations to PI of 'Sarioso 10' sown in May was ~1 week in Samanko and 2 weeks in Montpellier (Fig. 5A). However, in 2006 tropical varieties flowered exceptionally late in both locations and PI occurred

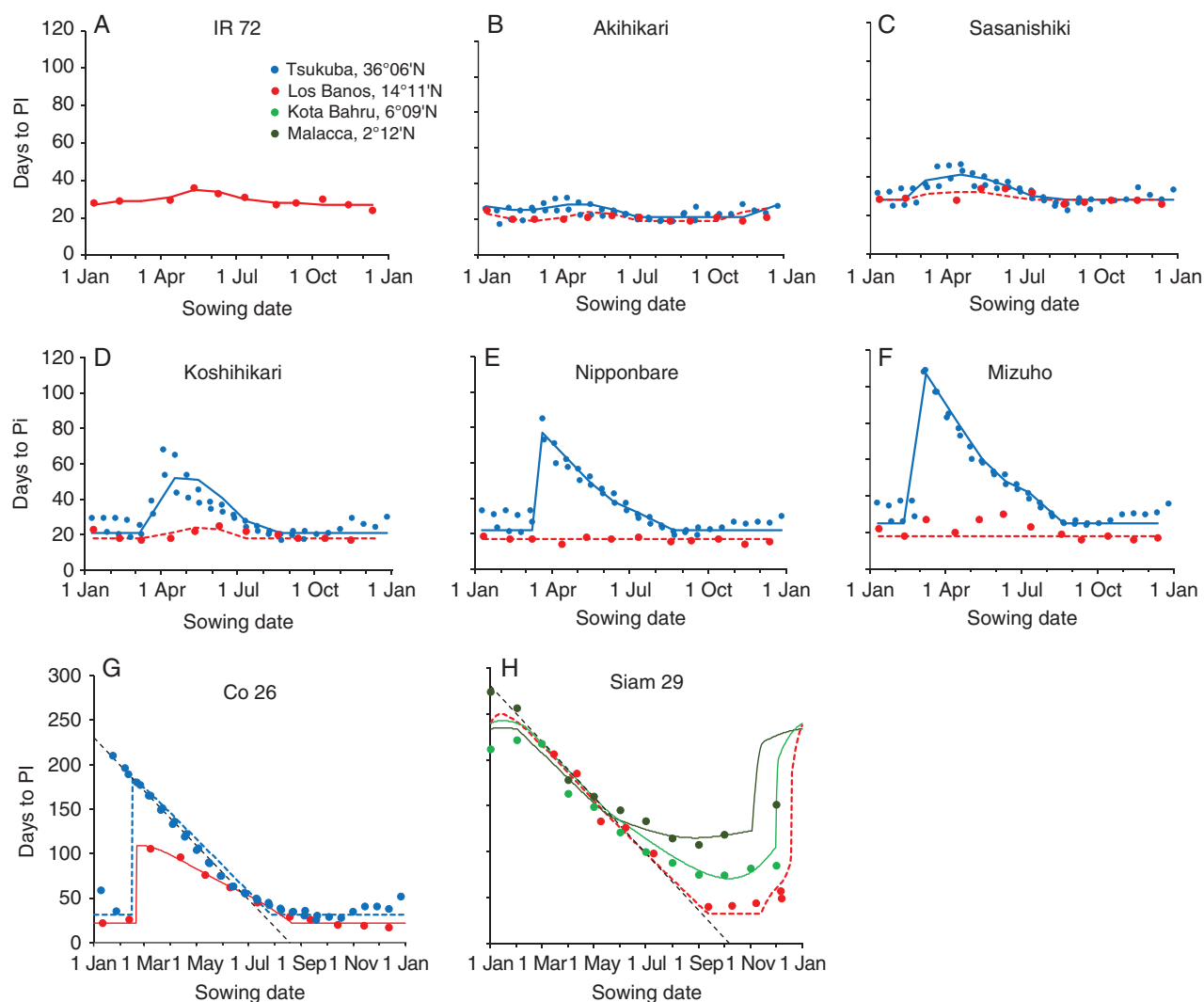


Fig. 3. Duration to panicle initiation for a 1-year monthly sowing series of seven rice varieties (A–G) grown in a greenhouse in Los Baños (14°11' N), for a 2-year fortnightly sowing series of six rice varieties (B–G) grown in a greenhouse in Tsukuba (36°06' N), and for a 1-year series of one variety (H) grown in the field at three latitudes. The model predictions are plotted with solid lines for the locations used for the calibration of the variety parameters and with dashed lines for the locations used for model validation. The –1:1 line is drawn as a black dashed for late varieties.

at similar thermal times. ‘Sariaso 10’ was sown simultaneously on 20 May 2006 in both locations and reached PI after 82 d or 984 °Cd in Montpellier and 60 d or 978 °Cd in Samanko.

Simultaneous dates of PI from the equator to the temperate latitudes for sorghum. The date of PI of highly photoperiod-sensitive varieties grown from the Equator to the temperate latitudes depended only on the sowing date and not on latitude or temperature. Thus, the Malian sorghum landrace ‘Souroukoku’ was grown in six locations in Africa, Europe and Central and South America, covering a range of latitudes from 3°30' N to 43°39' N, and showed similar responses to the sowing date in the duration to PI at all latitudes, including at low latitude in Palmira, Colombia (Fig. 2K). Six late sorghum varieties from Nicaragua grown at four latitudes from 3°30' N to 13° N showed the same independence of latitude in the response of the duration to PI from the sowing date as for ‘Souroukoku’ especially for the varieties ‘99 PREEIME

117’ and ‘EIME 119’ (Supplementary Data Fig. S4). Indeed, the duration to PI was shorter in Palmira for four varieties sown during late June than that in the other locations.

Divergent responses to latitude in the duration to PI of the rice varieties. Moderate to highly photoperiod-sensitive varieties reached PI earlier at lower latitude, whereas the extremely photoperiod-sensitive variety ‘Siam 29’ showed the reverse pattern.

Thus, the IRRI-bred rice variety ‘IR 72’ and the five Japanese varieties chosen for their contrasting photoperiod sensitivity in Japan were insensitive to the sowing date when grown in a greenhouse at the tropical latitude of Los Baños (Fig. 3A–F). Conversely, the Indian ‘Co 26’ tropical rice variety was highly sensitive to the sowing date at both temperate and tropical latitudes (Fig. 3G). The estimated dates to PI of ‘Co 26’ were earlier in the Philippines (14°11' N) than in Japan (36°06' N) for March to May sowing dates and were similar for other sowings.

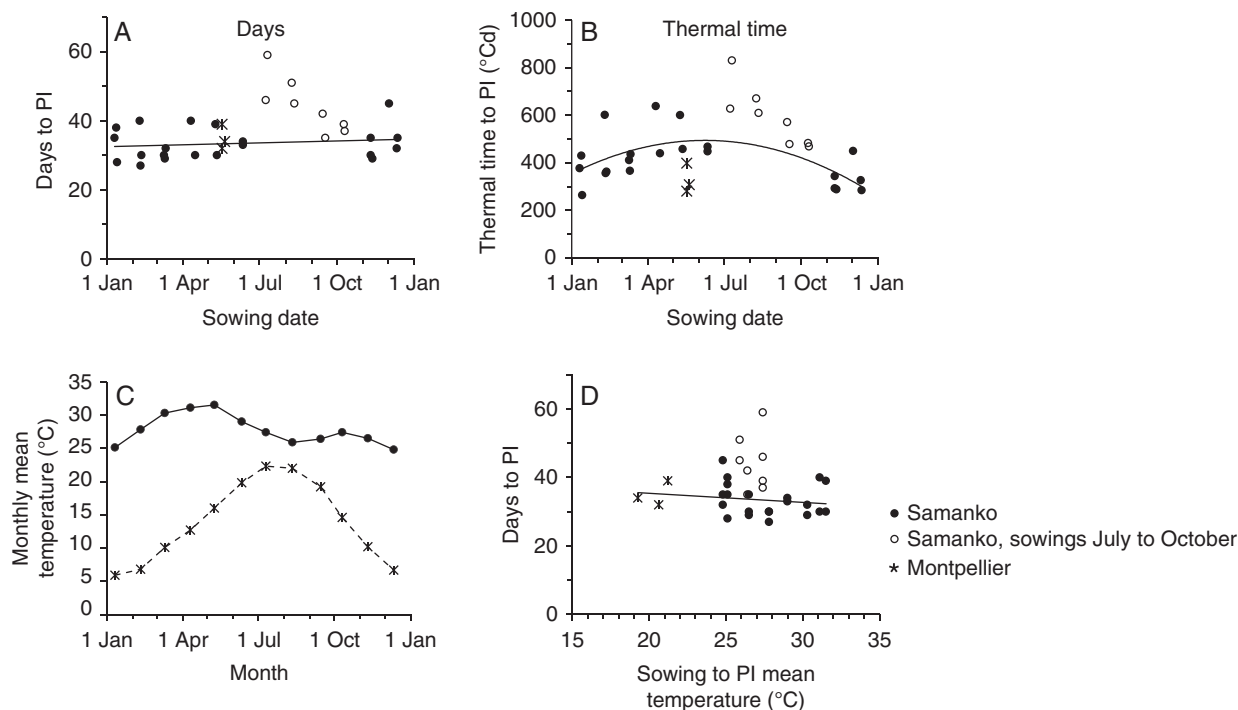


FIG. 4. Observed durations to panicle initiation in days (A) and in thermal time (B) by sowing date of the non-photoperiodic sorghum variety 'IRAT 204' sown monthly in Samanko, Mali, from 2003 to 2005 and in May 2001, 2010 and 2017 in Montpellier, France. In Samanko, a photoperiodic reaction was observed in sowings from July to October (○). (C) Monthly mean temperatures at both locations and (D) relationship between mean temperature and observed durations to PI.

The Malayan rice landrace 'Siam 29', known for its high sensitivity to sowing date at latitudes close to the Equator, showed an even stronger response to sowing date when sown in the field at the tropical latitude of Los Baños (Fig. 3H). The PI dates of 'Siam 29' were late and synchronous in Malaysia and the Philippines for sowings from March to June–July. For sowings from July–August to December, the sowings in Los Baños confirmed that PI occurred earlier at higher latitudes, where the photoperiod is shorter during this period in the year.

Temperature acclimation of the phyllochron in sorghum. In sorghum, the phyllochron acclimated to the prevailing temperature during seedling emergence. Phyllochron1, set at seedling emergence, was shorter in Montpellier (35 °Cd) than in Samanko (47 °Cd) for 'Sarioso 10' in May 2001 (Supplementary Data Table S4). Similar differences were observed for June sowings and the varieties CSM 335 and IRAT 174. However in 2006, phyllochron1 was longer in Montpellier (41 °Cd) than in Samanko (37 °Cd). In Montpellier, temperatures were exceptionally high (up to 34 °C) during the last week of May 2006 and again during the last 10 d in June 2006 (up to 36.8 °C) for the times of seedling emergence for May and June sowings. For May and June sowings, PI date was delayed from the average date by 1 month and 1 fortnight, respectively. Location and year had significant effects on phyllochron1, thermal time to PI and the total number of leaves.

Crop photoperiodism model 2.0 fitted any type of photoperiodic response at any latitude

Monthly sorghum sowings in Samanko. For all sorghum varieties, a set of optimized parameters permitted the proposed

model to fit the data well at every sowing date, which was not feasible with the previous models for photoperiodism (Fig. 2, Supplementary Data Fig. S3, Table 2, and Supplementary Data Table S5). In particular, the parameterized model was notably well fitted to the longer duration to PI for sowings in November and December regardless of the amplitude of the increase without any temperature input. The November breakpoint in varieties such as 'IBS 19' and the specific pattern of 'IRAT 204' from July to October were also well fitted. The respective roles of daylength and the changes in the sunset and sunrise times in the daily-predicted duration to PI were plotted for three sorghum varieties grown at several latitudes (Fig. 6A–G). Daylength often played the main role, which was modulated by dSR and dSS, although the respective weights of the components could be balanced, as in 'CSM 335' in Samanko. The Ps coefficient, expressed in $d h^{-1}$, had much higher values than the SRs_1 , SRs_2 , SSs_1 , and SSs_2 coefficients, expressed in $d^2 s^{-1}$, because the choice of the units ensured that the different products in the linear model had homogeneous orders of magnitude.

The predicted duration to PI of 'IRAT 204' and 'CSM 63-E' did not respond to daylength (Ps and Pb were undetermined) but only to the additive effects of the sunrise and sunset changes (SRs and SSs coefficients in Table 2). As expected, the daylength parameter (Ps) was larger in varieties with a longer duration to PI, with the noticeable exception of the IBS series. In the four IBS varieties, the SRs_1 and SSs_1 coefficients were much higher than in other varieties and stable over all sowing dates (no SRs_2 and SSs_2). The basic vegetative phase varied from 19 to 50 d and Pb_1 from 8.2 to 12.3 h, with no relationship with the level of photoperiod sensitivity.

In many varieties, such as 'Kaura D-12' and 'IBS 19', data fitting was better for the sowings from March to October than

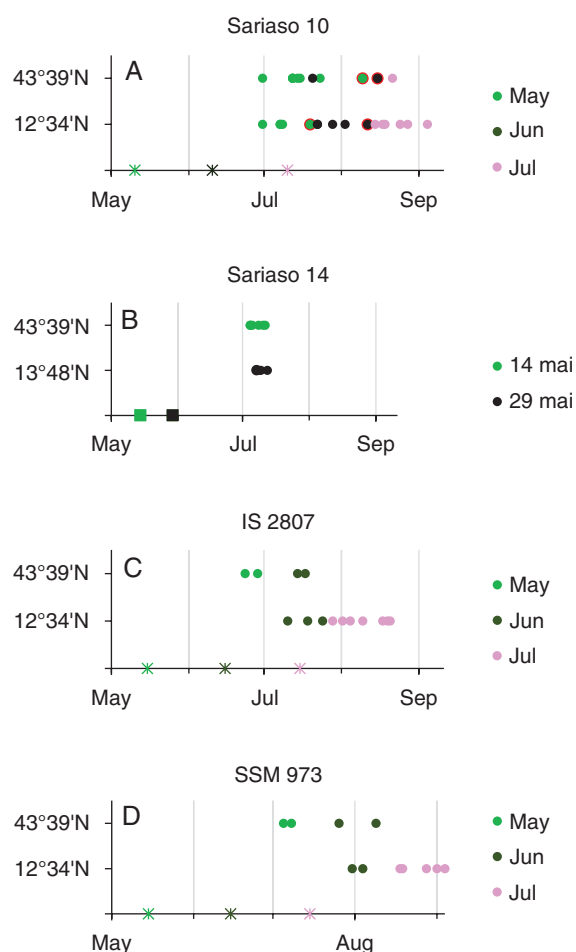


FIG. 5. Distribution of the dates of panicle initiation of four sorghum varieties (A–D) simultaneously sown in Montpellier (43°39' N) and either Samanko (12°34' N) or Somoto, Nicaragua (13°48' N) from May to July between 1994 and 2017. Divergent results from 2006 are marked with red circles around the symbol for 'Sariaso 10' (A).

for data from the 12 sowing months because of high inter-annual variability in the duration to PI in some sowings from November to February (Fig. 2 and Table 2).

Sorghum varieties sown at several contrasting latitudes. Once calibrated with data from monthly sowings in Samanko, the model was run with data for daylength and its changes in Montpellier, and the predictions were compared with the observations (Fig. 2I–K and Table 2). For 'CSM 335' and 'Sariaso 10', RMSD values in Montpellier were higher than those in Samanko because the predictions of the duration to PI in Montpellier for May to July sowings were too long. Conversely, RMSD was very low for 'CSM 335' in Montpellier (two observations in 2006). Data from both Samanko and Palmira were needed to accurately calibrate the model for the variety 'Souroukoku'. Once done, the model well predicted the duration to PI in Montpellier for May to July sowings, and in Nicaragua at latitude close to that in Samanko. The duration to PI equal to the BVP was also accurately predicted for the October sowings in Monteria. However, the availability of only two sowing dates in Palmira was not enough to guarantee the validity of the yearly-predicted duration to PI, plotted prospectively.

Monthly rice sowing series at several contrasting latitudes. In rice, two long-time published monthly series from Malaysia and Japan over a long period were complemented with two similar monthly sowing series in Los Baños, Philippines. Data from 20 additional sowing dates in 1989 completed the 1988 series of the Japanese experiment (Fig. 3B–H). Thus, comparisons between monthly sowing series at several latitudes were available.

For the five Japanese varieties from the Tsukuba series, the response of the duration to PI to the sowing data was either null or very small in Los Baños (Fig. 3B–F) and the model was consequently calibrated with the data from Tsukuba (Table 3). Conversely, the duration to PI of the Indian variety 'Co 26' responded strongly to sowing date in both locations and the model was calibrated with data from Los Baños because it resulted in a better fit of the data from both locations. No parameters were able to fit well with the observations for the five Japanese varieties. The highly variable duration to PI for January and February sowings of 'Co 26' grown in Tsukuba argued in favour of a breakpoint of the yearly pattern in early January, whereas the duration to PI of the other five varieties was minimal for sowings from September to February or March. The absence of increased duration to PI during this 5-month period in all rice varieties (except for one observation in 'Co 26') was opposite to the behaviour observed in sorghum. However, in the monthly sowing of rice variety panels conducted in paddy fields in northern Senegal, the duration to PI and to flowering was minimal for August–September sowings and prolonged for October–February sowings (Supplementary Data Fig. S5) (Dingkuhn *et al.*, 1995, 2015). Unlike the Tsukuba series, observations from the Senegal series were well fitted to crop photoperiodism model 2.0 with no temperature input (Fig. 3 and Supplementary Data Table S6). It was thus hypothesized that the greenhouse modified the perception by the plants of the lighting cues for sowings from November to February or even March when the photoperiod was below Pb_1 . Under this additional constraint, the model fitted well the observations from Tsukuba. In 'Akihikari', 'Sananishiki', 'Koshihikari' and 'Co 26', Pb_1 was estimated at 9.97, 12.0, 12.08 and 12.57 h, respectively, and the model predicted a response of the duration to PI to the sowing date in Los Baños, where the maximum PP was 12.89 h (Fig. 3B–D, G and Table 3). Conversely, for the two other Japanese varieties ($Pb_1 = 12.57$ and 12.77 h), the model predicted the absence of a response to the sowing date, as observed and despite a strong dSR – dSS component similar to 'Mizuho' (Fig. 6H).

In 'Siam 29', crop photoperiodism model 2.0 calibrated with data from Malacca and Kota Bahru fitted well the monthly sowing series at the three contrasting latitudes (Fig. 3H and Table 3). The components dSR and dSS were hypothesized to cause the main lengthening of the predicted PSP, and thus to play the main role in the very long durations to PI observed at low latitudes for sowings from January to June (Fig. 6J–K). At a tropical latitude, in Los Baños, the addition of the responses to PP, dSR and dSS resulted in a very long predicted PSP (day) (Fig. 6L).

DISCUSSION

Duration to PI acclimates to temperature

Durations are expressed in thermal time in the phenological models because temperature is a major factor in any plant metabolic activity, including the duration to flowering (Summerfield

TABLE 2. Parameters of crop photoperiodism model 2.0 and data fitting of (A) eight sorghum varieties representative of the range of photoperiod sensitivity observed in Samanko, (B) two sorghum varieties grown in Samanko and Montpellier, and (C) one late sorghum variety grown in Samanko, Montpellier and Cali. When data from several locations were available, they were used for either calibrating (C in Use column) or validating (Val) the model. Data fitting was computed either for all data from 12 sowing months or for data from only 8 sowing months, from March to October

Variety	Location	Use	Parameter							Data fitting				
			BVP (d)	Pb ₁ (h)	Ps (d h ⁻¹)	SRs ₁ (d ² s ⁻¹)	SSs ₁ (d ² s ⁻¹)	Pb ₂ (h)	SRs ₂ (d ² s ⁻¹)	SSs ₂ (d ² s ⁻¹)	12 months		March–October	
										R ²	RMSD	R ²	RMSD	
(A) One latitude														
'IRAT 204'	Samanko	C	33.04	–	–	–	–	12.02	–0.056	–0.498	0.58	4.8	0.69	4.6
'CSM 63E'	Samanko	C	35.99	–	–	–0.2787	1.8779	12.12	–0.5603	–0.4638	0.70	11.2	0.29	10.0
'Sima'	Samanko	C	27.87	9.59	7.90	–0.097	0.5194	11.44	–0.653	0.2831	0.85	4.5	0.88	4.0
'IRAT 174'	Samanko	C	19.0	10.83	28.62	0.7825	2.3817	11.42	–0.215	0.5169	0.79	10.9	0.92	6.2
'Ouéni'	Samanko	C	46.0	11.92	46.27	–0.3063	1.0656	12.26	–1.160	0.3974	0.82	8.8	0.94	7.4
'Kaura D12'	Samanko	C	36.0	11.83	172.77	–0.2534	0.5210	12.34	–0.111	1.9927	0.86	18.1	0.99	5.5
'IS 15401'	Samanko	C	35.11	11.89	286.64	–0.1605	0.4183	12.22	4.8888	2.1078	0.98	8.7	1.00	10.6
'IBS 19'	Samanko	C	36.79	11.0	126.68	–3.0956	3.9852	–	–	–	0.85	29.0	0.98	7.7
(B) Two latitudes														
'CSM 335'	Samanko	C	38.35	11.92	110.37	–0.510	3.1132	12.35	–3.543	0.5383	0.66	7.6	0.95	5.8
	Montpellier	Val	–	–	–	–	–	–	–	–	0.82	10.4	–	–
'Sarioso 10'	Samanko	C	34.87	10.78	11.45	–0.164	0.5012	12.74	–0.753	1.1656	0.48	5.9	0.70	5.0
	Montpellier	Val	–	–	–	–	–	–	–	–	0.42	13.3	–	–
(C) Three latitudes														
'Souroukougou'	Samanko	C	42.17	12.3	915.14	–0.9634	0.5737	9.94	–1.286	–0.7193	0.93	13.8	0.94	11.9
	Cali	C	–	–	–	–	–	–	–	–	–	2.2	–	–
	Montpellier	Val	–	–	–	–	–	–	–	–	0.97	21.7	–	–

et al., 1997). Many experiments conducted in growth chambers on various species strongly supported this choice but observations reported in the current paper led to questions about both the photoperiod and the thermal time models. Thus, photoperiod-sensitive varieties sown simultaneously in May and June in Samanko and Montpellier repeatedly flowered at close dates despite the highly contrasting photoperiod and temperature at the two locations (Fig. 5). Indeed, May is a very hot month in Samanko (mean temperature = 31.5 °C), whereas germination and early growth can be difficult in Montpellier because of continued low temperatures (mean temperature = 16 °C) (Fig. 4C). Similarly, the duration to PI in days, limited to the BVP in the non-photoperiod-sensitive variety 'IRAT 204', was also insensitive to the temperature within a large range, 19.2–31.5 °C, in contradiction with the current photothermal models (Fig. 4D).

Sorghum plants appear to have the homeostatic ability to maintain the duration to PI at a rather stable number of days within a large range of mean temperatures. Kirby *et al.* (1985) previously hypothesized that in wheat and barley the phyllochron was set in response to daylength and temperature soon after seedling emergence. Birch *et al.* (1998) confirmed that maize plants also acclimated to the temperature and that their phyllochron increased by 1.7 °Cd per degree Celsius increase in mean temperature within a 12–25 °C mean temperature range, with small inter-variety variability. The simultaneous acclimation of the phyllochron and the duration to PI were observed in three sorghum varieties sown in May and June 2001 in Samanko and Montpellier (Hemberger, 2001) (Supplementary Data Table S4). This adaptation to the lower mean temperature at seedling emergence in May and June in Montpellier did not happen in 2006 because of exceptionally high temperatures at seedling emergence. Thus, in Montpellier

the durations to PI were much longer in 2006 than in 2001 and in usual cropping seasons.

Acclimation of the duration to PI to the mean temperature has been observed previously. Thus, Yoshida (1981) reported a 1975 experiment in which four photoperiod-insensitive rice varieties with contrasting BVPs were grown in temperature-controlled glasshouses at 21, 24, 27 and 30 °C. From 24 °C upwards, the temperature had only a small effect on the duration to flowering, whereas this duration increased by 20–35 d when temperature decreased from 24 to 21 °C. Yoshida (1981) hypothesized that below a threshold between 21 and 24 °C plants could no longer ensure the homeostatic control of the duration to flowering that they maintained between 24 and 30 °C. Similarly, Roberts and Carpenter (1965) showed that the duration to flowering of one photoperiod-insensitive rice variety was also insensitive to the mean temperature between 30 and 35 °C. In another seven rice varieties, the duration to PI increased by 10–20 d between 30 and 35 °C. In beans, Wallace *et al.* (1991) reported stable durations to the first flower between 23 and 26 °C in ten varieties grown at various altitudes in Guatemala and nearly stable durations between 18 and 24 °C in a similar experiment with nine varieties in Colombia. These stable durations were accompanied by a nearly stable number of nodes below the first flower.

Thus, the continuous curvilinear response of the duration to flowering to the temperature often observed in growth chambers and used to support the photothermal model that currently predominates (Summerfield *et al.*, 1992) was not a unique relationship. Conversely, many data, including those presented in this paper, support the hypothesis of acclimation to temperature for the duration to flowering within a specific range of temperatures under natural lighting. Thus, plants actively create a

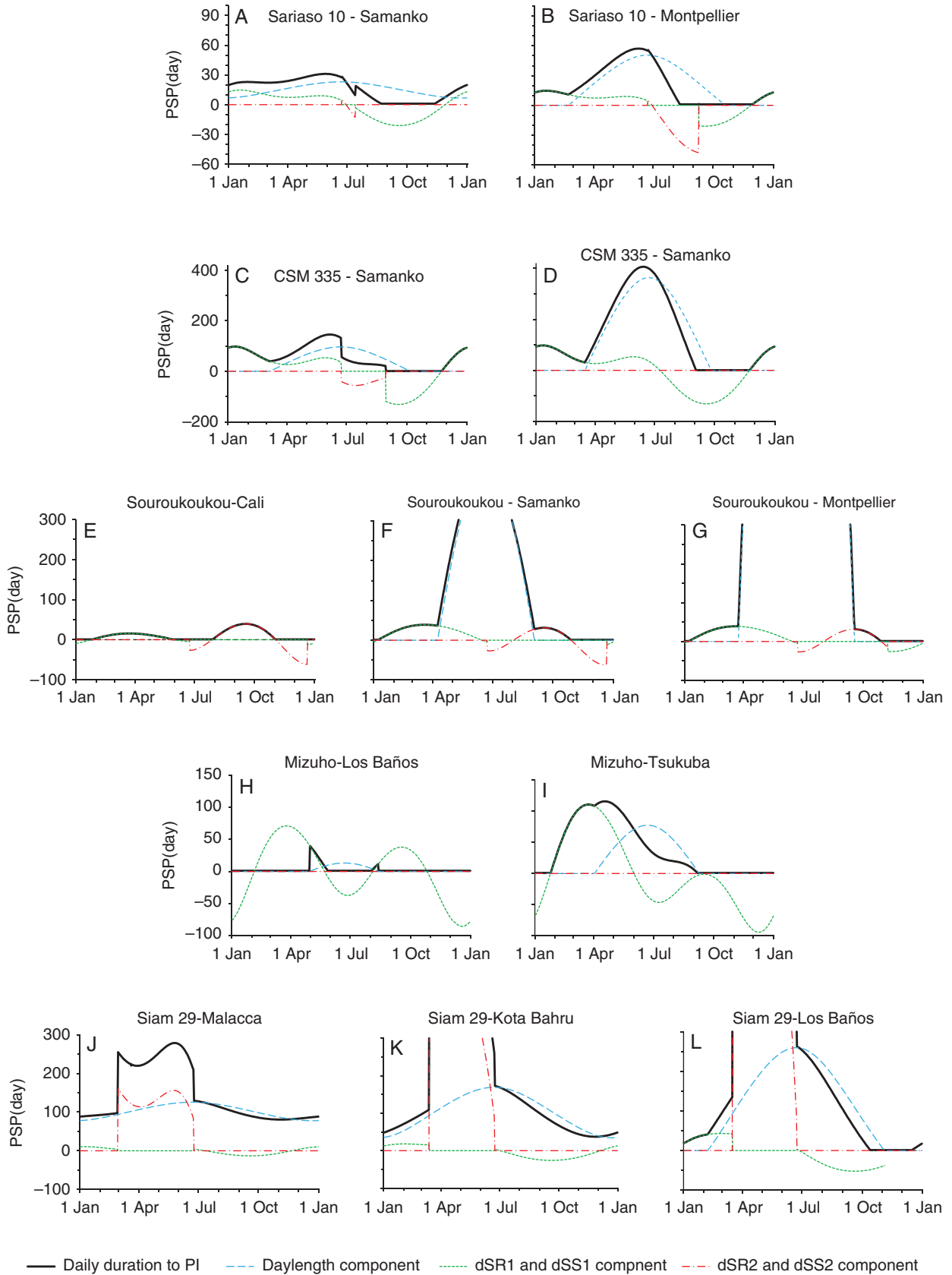


FIG. 6. Daily-predicted duration of the PPS [PSP(day), in days] resulting from the addition of the daylength component and of the daily change in sunset and sunrise time component 1 or 2 for Three sorghum varieties (Sariaso 10, CSM 335, and Souroukoku) and two rice varieties (Mizuho and Siam 29) grown at several latitudes.

TABLE 3. Parameters of crop photoperiodism model 2.0 and data fitting of (A) one rice variety grown in a greenhouse in Los Baños, (B) six rice varieties grown in greenhouses in Tsukuba and Los Baños, and (C) one late rice variety grown in Malacca, Kota Bahru and Los Baños. When data from several locations were available, they were used for either calibrating (C in Use column) or validating (Val) the model. Data fitting was computed either for all data from 12 sowing months or for data from only 8 sowing months, from March to October

Variety	Model type	Location	Use	Parameter										Data fitting			
				BVP		Pb ₁	Ps	SRs ₁	SSs ₁	Pb ₂	SRs ₂	SSs ₂	12 months		March–October		
				(d)	(h)	(h)	(d h ⁻¹)	(d ² s ⁻¹)	(d ² s ⁻¹)	(h)	(d ² s ⁻¹)	(d ² s ⁻¹)	R ²	RMSD	R ²	RMSD	
(A) One latitude 'IR 72'	Greenhouse	Los Baños	C	26	12.53	28.36	-0.0596	-0.0429	-	-	-	-	0.74	1.6	0.80	1.4	
(B) Two latitudes 'Akihikari'	Greenhouse	Tsukuba	C	20.17	9.97	0.94	0.0496	0.133	-	-	-	-	0.43	3.1	0.88	1.9	
	Greenhouse	Los Baños	Val	18	-	-	-	-	-	-	-	-	0.12	2.5	0.33	1.6	
	Greenhouse	Tsukuba	C	27.22	12.00	4.45	-0.0576	0.0425	-	-	-	-	0.69	3.4	0.82	3.1	
'Sasamishiki'	Greenhouse	Los Baños	Val	-	-	-	-	-	-	-	-	-	0.27	3.2	0.20	2.6	
'Koshihikari'	Greenhouse	Tsukuba	C	20	12.57	15.38	-0.0476	0.1612	-	-	-	-	0.66	7.1	0.69	6.9	
	Greenhouse	Los Baños	Val	17	-	-	-	-	-	-	-	-	0.29	2.3	0.39	2.2	
'Nipponbare'	Greenhouse	Tsukuba	C	21	12.77	28.21	-1.0667	-0.547	-	-	-	-	0.94	4.3	0.97	3.0	
	Greenhouse	Los Baños	Val	16	-	-	-	-	-	-	-	-	0	1.5	0	1.3	
'Mizutho'	Greenhouse	Tsukuba	C	24	12.57	38.64	-	-	-	-	-	-	0.98	8.0	1.00	2.7	
	Greenhouse	Los Baños	Val	16.9	-	-	-	-	-	-	-	-	-	5.5	-	6.6	
'Co 26'	Greenhouse	Los Baños	C	21.04	12.09	100.55	-1.4623	0.5274	12.09	-1.681	0.2238	0.99	3.0	0.99	2.8		
	Greenhouse	Tsukuba	Val	30.3	-	-	-	-	-	-	-	0.37	47.6	0.99	6.9		
(C) Three latitudes 'Stiam 29'	Field	Malacca	C	3156	11.56	196	-0.846	1.1243	12.04	-150	150	0.73	27.0	0.93	7.0		
	Field	Kota Bahru	C	-	-	-	-	-	-	-	-	0.91	25.9	0.97	12.0		
	Field	Los Baños	Val	-	-	-	-	-	-	-	-	0.99	10.2	0.97	8.9		

discontinuous interval in the relationships between temperature and either the rate of leaf appearance or the duration to flowering.

Precise information is lacking on the size and bounds of this range and on the level of homeostasis in the duration to flowering within this interval. However, in rice the range would extend at least from 24 to 30 °C (Roberts and Carpenter, 1965; Yoshida, 1981) and in sorghum at least from 19 to 31 °C (Fig. 4D); thus, they would cover the usual range of mean temperature for both tropical crops. Assuming that acclimation can nearly stabilize the duration to flowering, as shown by Yoshida (1981) and in Fig. 4D, using days instead of thermal time for modelling the duration to PI in tropical crops of rice and sorghum appeared to be a more accurate though open to improvement choice.

Crop photoperiodism model 2.0 perfectly fitted every variety pattern for the duration to PI

In sorghum, no previous model could consider the longer duration of the vegetative phase observed for November and December sowings in many varieties grown in Samanko (Dingkuhn et al., 2008) and other tropical locations (Bezot, 1963; Miller et al., 1968). Adding sensitivity to the changes in sunrise and sunset times to the effect of daylength fully resolved this failure of the models in every variety tested in Samanko without any temperature input. This was especially true for ‘CSM 63-E’, which had short and stable vegetative phases for May to October sowings and longer vegetative phases for November to April sowings (Fig. 2B). The combined effect of dSR and dSS successfully simulated the longer duration of the vegetative phase for sowings from July to October in the daylength-insensitive variety ‘IRAT 204’ (Fig. 2A).

The results of model 2.0 support the hypothesis that the prolonged durations to PI observed from November to February, independent of the level of photoperiod sensitivity, are the hidden side of photoperiod sensitivity. Flowering date is a major selective trait for sorghum adaptation to the mean dates of monsoon onset and end in each African location (Curtis, 1968; Clerget et al., 2004). Each sorghum variety used a specific combination of response to PP, dSR and dSS to precisely adjust the PI and flowering dates, and selection only acted on plants grown from the onset of the rainy season. Thus, the combination of the three responses at other sowing dates led to durations to PI that had no effect on plant adaptation but revealed that photoperiod sensitivity could not be reduced to daylength sensitivity.

To attain a good fit for the durations to PI recorded for rice in greenhouses, it was assumed that the glass of the greenhouses altered the sunlight effect on the duration to PI. Indeed, the absence of any response to the sowing month from November to February in the six varieties tested in greenhouses in Tsukuba and Los Baños (Fig. 3A–F) disagreed with previous observations made in the field in Ndiaye, Senegal (16° N) (Dingkuhn et al., 1995, 2015). In the 2015 paper, for instance, 16 varieties showed a longer duration to flowering for October and February sowings than for the September sowing. Nipponbare, the 17th variety, which was also present in the greenhouse series, showed a significant response to the sowing date from February to July (76–47 d to flowering) highly contrasted with the absence of

response to the sowing date in Los Baños (14° N) (Fig. 3E). It was previously observed that the duration to PI was much shorter in plants grown in a greenhouse than in plants sown in the field in three sorghum varieties sown in December (Clerget et al., 2012). The reason would be that UV is highly filtered by glass and thus no longer perceived by the dedicated receptors of plants grown in greenhouses whose photoperiod sensitivity is disrupted.

Thanks to knowledge obtained by Borchert et al. (2005) and Goymann et al. (2012), the adjunction of the additive effects of the daily change in sunrise and sunset times to the existing photoperiodism model greatly improved its efficiency in predicting the sorghum and rice responses to sowing date. An additional improvement of the model came from the hypothesis that plants could very differently combine the dSR and dSS cues either when $dSS > dSR$, before the summer solstice, or when $dSS < dSR$. Two sets of sensitivity parameters, SRs and SSs, were thus sought during the calibration. Such a change in photoperiod sensitivity at the summer solstice, when the daily change in daylength switches from positive to negative, was already suspected (Curtis, 1968; Clerget et al., 2004). However, evidence for the respective roles of dSR and dSS is needed.

For decades, the photoperiodic reaction has been classed as either quantitative or qualitative depending on its strength, with no definition of the limit between the two classes (Thomas and Vince-Prue, 1997). Quantitative varieties were modelled with a simple linear relationship between daylength and the duration to either flowering or PI (Major, 1980). Above a daylength threshold, PI was temporarily inhibited in models for qualitative varieties. The threshold could be either fixed (Carberry et al., 1992) or moving (Folliard et al., 2004; Dingkuhn et al., 2008). A unique linear relationship in crop photoperiodism model 2.0 regrouped all short-day plants into a continuum. The predicted duration to PI was sufficiently delayed by the very long duration of the daily-predicted duration of the PSP through high values of the sensitivity parameters (Fig. 6). Conversely, the concept of accrued daily progress towards PI (Summerfield et al., 1992) maintained its strength.

at the tropical latitude of the experiment used for its calibration, model 2.0 was more accurate than the previous models for some varieties even within the usual window for sowing the crop (Fig. 2A, J). As before, it will be feasible to estimate the eight parameters of model 2.0 from a sufficient number of observations of the PI dates after a series of sowing dates during the usual window for sowing. This will improve the prediction of the flowering date at tropical latitudes in some varieties, such as the sorghum varieties ‘IRAT 204’ and ‘CSM 335’.

Crop photoperiodism model 2.0 correctly fitted observations at other latitudes

In rice, once calibrated with data from lower latitudes, the observations conducted at a higher latitude were fitted well by the model (Fig. 3G, H). Conversely, in sorghum the durations to PI predicted in Montpellier for May to July sowings were close to the exceptionally late durations observed in 2006 for ‘Sariato 10’ and ‘CSM 335’ and too long for that of ‘Souroukoukou’ (Fig. 2I–K). The model was calibrated with Samanko data, where monthly mean temperatures were less variable than those in Montpellier (Fig. 4C). In Montpellier,

plants acclimated the duration to PI at exceptionally high temperatures during seedling emergence in 2006, whereas in most years plants acclimated in response to the cool May temperatures. In average years, June and July temperatures are much higher than the low temperature of acclimation; thus, plants would complete the short acclimated thermal time to PI in fewer days than the number predicted by the model.

The fortunate 2006 observations pointed out that similar durations to PI in Samanko and Montpellier resulted from the interaction of acclimation to the initial low temperature in Montpellier at seedling emergence with that to the subsequent high temperatures. As for the phyllochron, the thermal time duration to PI would be reduced by low temperatures at seedling emergence (Kirby *et al.*, 1985; Birch *et al.*, 1998). The relationships between the duration to PI and temperature were established under either artificially stable temperatures or quite stable tropical temperatures (Roberts and Carpenter, 1965; Yoshida, 1981). It will be useful to establish the relationship between variable combinations of temperature during seedling emergence and the vegetative phase and the duration to PI, in the absence of any other limiting factor, to confirm the hypothesis based on the results in Montpellier. Such information will help in determining the range of temperatures within which the number of days to PI is stable and especially the effect of the temperature outside of this range. If the hypothesis of the setting of the duration to PI in response to the temperature during seedling emergence is confirmed, the reduced duration to PI resulting from low temperatures during seedling emergence would play a crucial role in the adaptation of the flowering time of tropical species, such as sorghum, to the temperate climate.

Except for ‘Siam 29’, data are not yet sufficient to guarantee that the current variety parameters can be used at latitudes other than the latitude used for model calibration. It was disappointing to confirm that data on flowering time from greenhouse experiments could not be used for field crops, especially because monthly sowings over the entire year are not feasible at temperate latitudes. Such series were very helpful in the accurate parameterization of ‘Siam 29’. However, the results obtained for ‘Siam 29’ and from punctual comparisons in sorghum showed that crop photoperiodism model 2.0 could be parameterized to correctly predict the duration to PI at any latitude.

To definitively establish the multi-latitudinal validity of the current model and obtain reliable model parameters at every latitude, equatorial monthly sowing series would be valuable for sorghum and rice, particularly considering the unique case of the extreme photoperiod sensitivity of ‘Siam 29’. Attaining the eight parameters of crop photoperiodism model 2.0 for each tropical variety is a heavy task because the durations to PI of 12 consecutive monthly sowings in one tropical and one equatorial locations will likely be necessary. Dry areas with a reliable source of water are well adapted for such research because of the reduced risk of disease or pest damage.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Figure S1: location of the experiments. Figure S2: relationships between the duration to panicle initiation and the duration to flowering. Figure

S3: 2-year observations of the duration to panicle initiation. Figure S4: duration to panicle initiation estimated from the observed duration to flowering of six Nicaraguan varieties sown from June to late November at four contrasting latitudes. Figure S5: observations of the duration to panicle initiation on contrasting sowing dates. Table S1: list of experiments. Table S2: list of the 28 sorghum varieties sown monthly in Samanko, Mali. Table S3: list of the 16 sorghum varieties from the CIRAD Core Collection with duration to flowering >10 months when sown on 13 November 2007 in Samanko, Mali. Table S4: five developmental traits and ANOVA for three sorghum varieties simultaneously sown in Samanko, Mali, and in Montpellier, France, in May and June of 2001 and 2006. Table S5: parameters of the panicle initiation model and data fitting of 17 sorghum varieties sown monthly in Samanko. Table S6: parameters of the panicle initiation model and data fitting of three rice varieties grown in Ndiaye and one rice variety grown in Ndiaye and Los Baños.

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