Does panicle initiation in tropical sorghum depend on day-to-day change in photoperiod?

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Abstract

Sorghum is known as a short day plant requiring short photoperiods (PP) to flower. However, in field experiments based on monthly plantings reported elsewhere, panicle initiation took place during long days as well as during short days even for highly photoperiod-sensitive varieties thought to be of the absolute type, or was particularly early for the sowings in September, well before days were shortest. In order to investigate these contradictory results, three tropical sorghum varieties of different photoperiod sensitivity were planted monthly in Mali and the dates of panicle initiation (PI) were recorded. The results indicate that the common concepts of a gradual (linear, or quantitative) response of photoperiod-induced phase (PIP) to PP at PI (PPi) (case of the variety Sariaso 10) or a threshold-type response (hyperbolic, or absolute; cases of CSM 335 and IRAT 174) could be reproduced for the sowing dates falling into the wet season (May–October), but did not describe adequately crop behaviour during the remaining months of the year. The same varieties were tested in controlled environments with four differential PP treatments composed of three different initial PP (12 h 15 min, 12 h 00 min and 11 h 45 min) and two opposite rates of day length change (±1 min/day). Thus after 15 days, two pairs of treatments with opposite day length changes reached the same average PP (12 h 07 min and 11 h 52 min) and after 30 d, another pair reached a similar average PP (12 h 00 min). In 2001, 2 varieties reached PI earlier under decreasing days and the same average PP, but no such additional effect of the rate of change of PP was observed in 2002. Modelling exercises showed that field variation in the duration to PI was better explained with rate of change of PP than with absolute PP observed during PIP, and best with a combination of both factors in an additive model. It is concluded that in tropical sorghum, floral induction is strongly associated with a negative rate of change of day length in the field, and under certain circumstances under controlled conditions, but more evidence is needed to ascertain the capability of sorghum to sense the rate of change of PP before a definite model can be formulated.
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1. Introduction

Sorghum is a short day plant that flowers only, or most rapidly, if illuminated during less than a certain number of hours per day (Thomas and Vince-Prue,

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1997). This photoperiodic behaviour is an adaptation to region-specific climatic patterns shown by many tropical species. It has been recently reported that sensitivity to photoperiod (PP) remains necessary, even for improved varieties, in the present grain production systems in the African savannas and the Sahel, to optimise natural resource use and minimise the risk of adverse climatic effects (Vaksmann et al., 1996).

The relations between day length and the duration of the vegetative phase, which ends with floral initiation, are complex and depend on temperature. Horie (1994) summarised the effects of day length as follows: the duration of the vegetative phase is increased by day length <8 h possibly due to trophic (nutritional, assimilation) constraints. It attains its minimum between 8 h and a first (''critical'') threshold. Between this first threshold and a second (''maximal'') threshold, the duration of the vegetative stage increases proportionally to photoperiod for quantitative response types, whereas for absolute types, floral initiation is fully inhibited beyond the maximal threshold and duration becomes theoretically infinite. Sorghum responds in the same manner. Major (1980) modelled the photoperiodism of two cultivars of sorghum as a linear response between a critical and maximal threshold in accordance with the concept of a quantitative response. The crop models DSSAT and APSIM use the same approach, assuming that daily progress towards panicle initiation (PI) is proportional to the ratio between the biological temperature ($T_{mean} - T_{base}$) and PP during the photoperiod-sensitive phase (PIP) (McCown et al., 1996; Jones et al., 1998). These models, however, are unable to predict the sometimes very long delay of flowering in guinea varieties when grown under short days in the tropics. Franquin (1976) and Vaksmann et al. (1996) proposed a hyperbolic response above the critical threshold, which essentially amounts to the concepts of a qualitative reaction. In this case it was proposed that PI occurred when PP dropped below a dynamic threshold PPt. PPt increases with time elapsed since sowing, thus making floral induction more probable as the plant ages (Vaksmann et al., 1998).

The possibility that plants might respond to change in PP, in addition to absolute day length, has received little attention (Thomas and Vince-Prue, 1997). Where this ''dynamic'' hypothesis (as opposed to quantitative or qualitative) was studied, evidence largely rested on time of sowing experiments with the inherent difficulty to distinguish among different PP effects (dynamic, quantitative or qualitative) and between PP and other environmental effects. Baker et al. (1980), working on winter wheat, found a strong, positive, linear relationship between the rate of day length change at emergence and the mean rate of leaf appearance during the life cycle. Kirby et al. (1982) found a similar relationship for barley and confirmed it later on various varieties of winter wheat (Kirby et al., 1985). However, the same author concluded 10 years later that a supplemental hypothesis on temperature acclimation gave a better-adjusted model than the hypothesis using day length dynamics (Kirby, 1995). One year earlier, Slafer et al. (1994a,b) had concluded that the rate of change in day length has no effect on the development rate and leaf number of wheat.

Curtis (1968) observed that the heading date of local varieties of sorghum in Nigeria was mainly a varietal characteristic nearly independent of latitude in Nigeria (between $7°30'N$ and $12°N$), when sown before July. Panicle initiation therefore occurred at different day lengths, giving rise to the hypothesis of a specific effect of the number of days of decreasing length following summer solstice (21 June), which is independent of latitude. Craufurd and Qi (2001) tested the ''dynamic'' hypothesis on data from an experiment in Nigeria in 1975, with a local *Sorghum* cv. sown weekly between 12 May and 21 July (Kassam and Andrew, 1975). The dynamic hypothesis was rejected because the relation between the mean day length and the duration of the vegetative growth phase was the same for sowing before or after summer solstice, and the CERES model using the quantitative hypothesis was able to simulate this data.

A study by Carberry et al. (2001) on pigeon pea in India in 1990–1991 gave very different patterns of vegetative phase duration between the first and second halves of the year, with one cultivar flowering after 50 days when sown on 28 January, and after 169 days when sown on 27 February. The authors explained this with a qualitative response to PP, assuming that during PIP for the February sowing, PP_{crit} had already been exceeded.

In four independent studies conducted in the northern hemisphere on sorghum using annual cycles of periodic sowing (Bezot, 1963; Miller et al., 1968;

Pandusastry and Krishna Murthy, 1984; Vaksmann et al., 1997), the longer vegetative phases generally occurred during the first half of the year (when PP increased) and the shorter durations in the second half of the year. A large number of cultivars showed maximal duration when sown in March (spring equinox) and minimal duration when sown in September (autumn equinox). The maximum observed in March is compatible with the threshold hypothesis as discussed above for pigeon pea, but neither the qualitative and quantitative hypotheses explain why the minimum was associated with sowing as early as September.

Franquin (1974) and Vaksmann et al. (1997) claimed that such discrepancies were the consequence of low night temperatures occurring in winter. In fact, they obtained better relationships between the average photoperiod and the thermal time to flowering based only on daily temperature minima, instead of means. (This approach is consistent with the fact that short day plants are actually long-night plants.) However, this explanation does not apply to Miller et al. (1968) experiments conducted under extremely constant thermal conditions in Puerto Rico. It therefore seems clear from the four field studies on sorghum cited above, that the classical, quantitative or qualitative models do not fit all cultivars when studied on a full annual cycle, and that in these cases the rate of change of PP at the time of sowing was highly predictive of thermal duration to flowering.

We considered there to be sufficient evidence to justify a re-evaluation of the dynamic hypothesis for photoperiodism in sorghum. The present study therefore aims at evaluating the effect of the rate of change in day length on the duration from germination to panicle initiation, based on three varieties with contrasting photoperiodic behaviour, grown in a sowing-date experiment in Mali and in controlled environments with PP changing daily.

2. Material and methods

2.1. The monthly planting experiment in Mali

The experiment was conducted at the ICRISAT research station in Samanko, Mali (12°34′N, 8°04′W, 330 masl). The climate is typical of the Sudan

Table 1
Monthly average maximal and minimal temperature and rainfall in Bamako, 1941–1980[a]

Month	Maximum temperature (°C)	Minimum temperature (°C)	Rainfall (mm)
January	33.5	16.9	0.0
February	36.2	19.4	1.6
March	37.5	22.8	0.2
April	38.6	23.7	8.4
May	38.0	25.2	63.0
June	35.1	23.4	173.9
July	34.2	22.1	257.4
August	30.5	21.7	336.6
September	31.7	21.6	229.6
October	33.1	21.3	97.4
November	34.8	18.5	10.1
December	33.0	16.8	1.7

[a] Data from ICRISAT No. 19, 1984, Bamako.

savannas, with three seasons: a hot and humid season from June to October during which crops are cultivated, a dry and cool season from November to February, and a dry and hot season from March to May (Table 1), astronomical day length varies from 11 h 15 min to 12 h 45 min and civil day length from 12 h 10 min to 13 h 38 min (Fig. 1). For hydrological reasons it was inevitable that wet and dry season crops were planted on different fields, in order to avoid water logging in the wet season and to enable irrigation in the dry season. The soil at the irrigated site (dry seasons), located close to the Niger River, was a fine, loamy Typic Haplaquet (USDA taxonomy) (C:L:S ≈ 25:50:25 and pH_{H_2O} = 4.5). The soil at the rainfed site (wet season) was a fine, loamy, mixed, isohyperthermic, Plinthic Paleustalf (C:L:S ≈ 20:35:55 and pH_{H_2O} = 5.0). Possible differences in soil fertility between fields were minimised with fertiliser application of 200, 100 and 200 kg ha^{-1} diamonium phosphate, KCl and urea, respectively. Soil moisture was never limiting due to irrigation in the dry seasons twice a week, keeping the soil near field capacity. The sites were 1000 m apart and weather was recorded at a weather station located not further than 800 m from either location. No visible differences with respect to plant health and nutritional status were observed between sites.

The three sorghum varieties used were CSM 335 from Mali (Sorghum Collection of Mali), a tall,
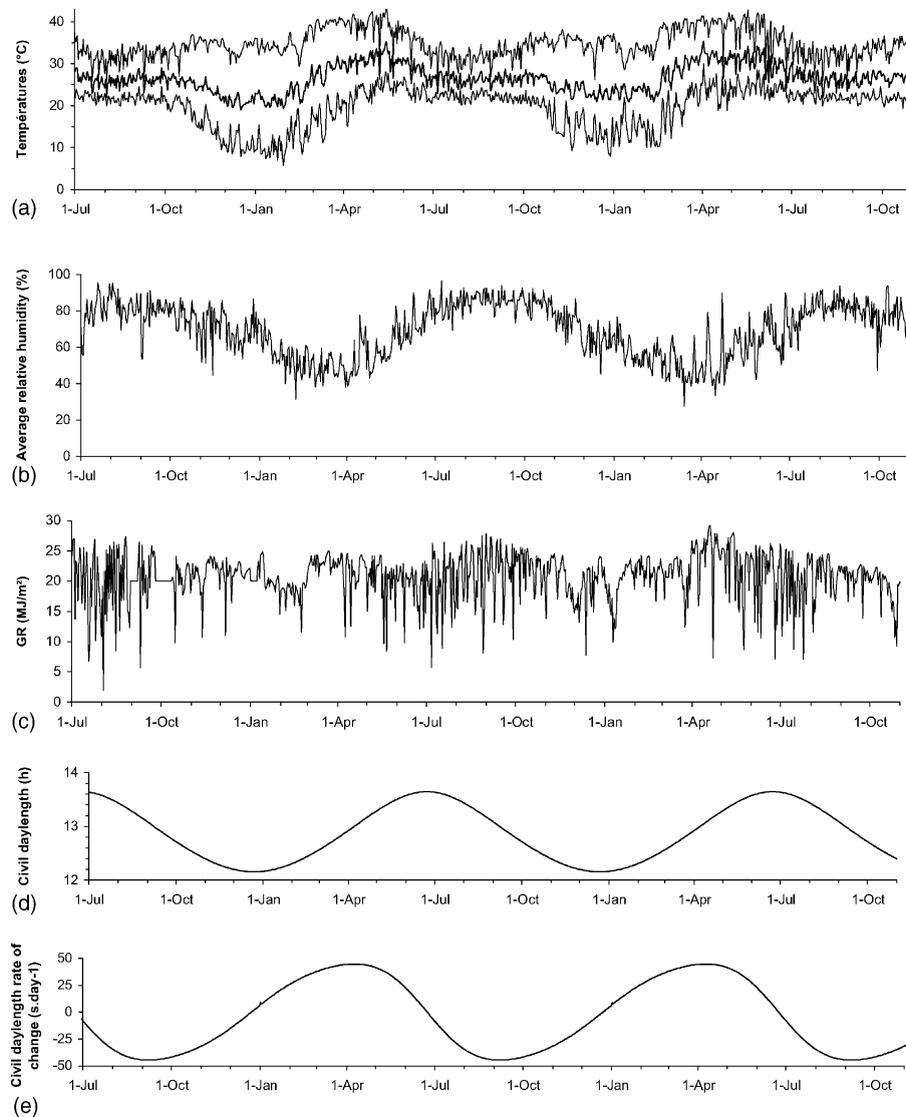
Fig. 1. Daily climatic conditions at the Samanko station from 1 July 2000 to 31 October 2003: (a) minimum, maximum and average temperatures; (b) average relative humidity; (c) global radiation; (d) day length and (e) day length rate of change.

traditional, guinea-type landrace known to be highly photoperiod-sensitive; Sariaso 10, an improved, less photoperiod-sensitive line from Burkina Faso having caudatum ancestry; and IRAT 174, a dwarf kafir × durra, photoperiod-sensitive line bred in Burkina Faso. A monthly planting schedule was initiated on 5 July 2000, followed by plantings on or about the 10th day of each succeeding month through August 2002. Plots had four lines 0.75 m apart and 5 m long, with 10 seed sown every 0.20 m and thinned to 1 plant/ hill 2 weeks after plant emergence. The ICRISAT Sorghum Breeding Program at Samanko furnished seed of CSM 335, and seed of Sariaso 10 and IRAT 174 came from the Genetic Resources Unit at CIRAD, Montpellier. Leaves of each plant of the two central rows were labelled for individual observations. Weeding was manual and insect control was chemical using local standards.
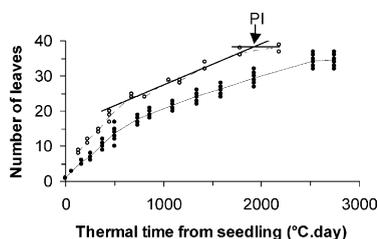
Fig. 2. Kinetics of leaf initiation by the apex (open circles) and their appearance out of the whorl (closed circles) recorded for the sowing of March 2001. The date of panicle initiation is estimated at the crosses between the linear regression and the final number of leaves when initiation was observed.

From emergence to panicle initiation, three plants per variety were sampled every week during the first 6 weeks and every 2–3 weeks later and dissected in order to count the number of leaves already initiated on the apex. Panicle initiation was recorded. The dates of panicle initiation (PI) were estimated using the equation of the linear regression of the initiated leaf number against time. PI was supposed to coincide with the time when the average total number of initiated leaves had been initiated (Fig. 2). Ten plants per plot (corresponding to sowing date) were labelled and the number of leaves appeared from the whorl, fully exerted and senesced were recorded weekly for each stem.

Air temperature and relative humidity at 2 m were measured every minute, averaged hourly and stored in a data logger (Campbell 21X). Daily temperature max, min and average and humidity average were calculated (Fig. 1) Thermal time was calculated on an hourly basis, using 11, 34 and 54 °C as base, optimal and maximum temperatures, respectively. The first value was calculated by Lafarge (1998) on the basis of leaf growth and appearance rates, and the two others by Alagarswamy and Ritchie (1991) for tropical sorghum varieties. These cardinal temperatures had been confirmed earlier using leaf elongation rates for the three varieties in a pre-study conducted in 2000 under controlled environments. Air temperature was increased hourly then decreased during daily periods in order to mimic natural conditions. Hysteresis due to a partial recovery of the lost elongation was observed after periods at very high temperature correlated with low humidity, but the three cardinal temperatures were equal to the 11, 34 and 54 °C within

an error range less than 1 °C. Linearity of response was assumed between the cardinal temperatures, with thermal time equal to zero at temperatures below the base or above the maximum. Daily summation of thermal time made use of daily averages calculated from the 24 hourly average temperatures, which were in turn calculated using the model described.

For calculations of the durations of phenological phases, it was assumed that the basic vegetative phase (BVP) is equal to the shortest thermal time elapsing from plant emergence to PI, and includes a juvenile phase that is either equal to or shorter than BVP. The photoperiod-sensitive or panicle induction phase (PIP) was calculated as the difference in thermal time between the end of BVP and PI.

Daily civil day length was calculated with the equations proposed by Keisling (1982) and the day length change of the day was calculated as the difference between the day length of the present and the previous day.

2.2. Experiments in controlled environments

This study used the same sorghum cultivars as the field experiment, and was carried out at CIRAD (Montpellier, France). A preliminary study on the duration of BVP was conducted in heated greenhouses. Ten plants of each variety CSM 335, Sariaso 10 and IRAT 174, were sown in 15 l pots on 10 November 2000 and 15 January 2001 (under very short days). Day/night temperature was approximately 30/20 °C and lighting was complemented during a period shorter than day length with HQL bulbs (Hg high pressure) giving an additional PAR of 300 μmol m^{-2} s^{-1} at plant tops (1 m from source). The minimal number of leaves initiated prior to PI were 10.5 (CSM 335), 11.8 (Sariaso 10) and 12.2 (IRAT 174), corresponding to a BVP of 165, 204 and 216 °C day (T_{base} 11 °C). These values, corresponding to 12–15 days, are in accordance with values published by Ellis et al. (1997) and Alagarswamy and Chandra (1998).

The main experiments were conducted in growth cabinets in 2001 and 2002. In 2001, four treatments differing in day length dynamics were implemented using fully light-insulated cabinets (1.20 m $\times$ 0.90 m $\times$ 1.95 m, W $\times$ D $\times$ H), open at the bottoms and tops, and built inside a larger room with controlled

temperature and air humidity. Illumination in the cabinets was provided with a combination of three HQI 150 W lamps and one incandescent 120 W lamp giving a PAR of 600 µmol m^{-2} s^{-1} at plant tops (1 m from source). Air temperature and relative humidity were maintained at 27 °C and 65% in the large room. A forced upward air flux in the cabinets using air circulated with the larger room minimised temperature differences (<1.5 °C among cabinets during the short periods when lighting was differential). The set up permitted programming of day-to-day photoperiod (PP) dynamics at a resolution of 1 min.

Drained pots contained 2 l of a growth medium consisting of field soil (silty sand from Lavalette experimental station, Montpellier, France), plant-based compost and crushed volcanic ashes mixed in a ratio 5:9:1 (v/v), soaked with de-ionised water prior to planting. On 26 June 2001, five seeds each were sown per pot, and 12 pots per cultivar were placed in each of the four cabinets on adjustable tables in order to maintain a distance of 1 m between plant tops and light sources. One week after emergence seedlings were thinned to one per pot. Pots were irrigated with de-ionised water during the first 3 weeks, then with a complete culture solution.

Initial PP was adjusted to 13 h (non-inductive) until 14 days after plant emergence (about 18 days after sowing, or 224 °C). This first phase was believed to fully cover the duration of BVP and consequently the juvenile phase, during which plants are not sensitive to PP. Thereafter, four differential PP treatments were initiated, composed of three different initial PP (12 h 15 min, 12 h 00 min and 11 h 45 min) and two opposite, constant rates of day length change (dPP) (±1 min/day). Thus two pairs of treatments reached the same average photoperiod after 4 weeks and another pair after 6 weeks. The values were chosen to be close to the PP conditions experienced by plants in the tropics at the two annual equinoxes. At these dates, astronomic day length is 12 h 00 min and dPP is ±40 s/day at Samanko.

Leaves were labelled on every plant and the dates of their appearance, full exertion and death were recorded weekly. Also at weekly intervals, three plants were harvested and dissected to count the number of leaves initiated and to record panicle initiation.

In 2002, two additional experiments were carried out under the same conditions except the following

changes. A second incandescent 120 W was added in each cabinet in order to improve the spatial light distribution and to decrease the red/far red energetic ratio of the light spectrum from 5.6 to 3.4, thus balancing the red spectrum. Short day plants are sensitive to this ratio because the PI is induced by far red (Thomas and Vince-Prue, 1997). The board carrying the pots was replaced with a grate and smaller 1 l pots were used, to increase the air flux inside the cabinets. Because of limited available space, plants were not grown in the isolated cabinets during the first 14 days after emergence, but in the common controlled room with light provided by four HRI-T 250 W bulbs. Only the variety Sariaso 10 was sown. After 14 days under the initial photoperiod of 13 h, two subsequent experiments were run, resulting in eight different treatments, four with constant photoperiod of 11 h 40 min, 12 h 00 min, 12 h 20 min and 12 h 40 min, and four with variable photoperiod with initial PP of 12 h 20 min, 12 h 00 min and 11 h 40 min and daily changes of PP of −1 min, ±1 min and −1 min, respectively. After the estimated end of the PIP (460 °C day, as recorded in September in Bamako, under average day lengths of 12 h 40 min), nine plants per treatment were weekly dissected to estimate the date of panicle initiation. The 0–4 scale defined by Lane (1963) was used to allow for interpolation, based on the assumption that 7 days elapsed from stages 0–4.

2.3. Modelling the field observations

Five models using two main ways of calculating the vegetative phase duration were tested with the data obtained from the field experiment. All models had in common the principle of a cumulating on a daily basis, starting at end of BVP, a variable dPI representing the rate of progress towards PI. The variable was a function, depending on the model, of current PP, incremental change in PP, or both. Temperature compensation of daily progress to PI was achieved with $dPI = dTT/PIP_d$, with dTT being the daily biological temperature (mean temperature less base temperature) and PIP_d the theoretical total thermal duration of PIP calculated on the basis of current photoperiod conditions. The models differed in the calculation of PIP_d.

All models were parameterised by optimisation against the measured data (26 sowing dates) through

the genetic algorithm of the Microsoft Evolutionary Solver. Although this type of optimisation procedure does not converge towards an absolute minimum of the sum of squares, it was preferred over other methods because parameter behaviour did not always allow using linear or quadratic optimisation procedures. It was verified that repeats resulted in similar estimations of parameter values, within reasonable, pre-set intervals. Then PIP was estimated with the optimised model using ModelMaker 4.0 for sowings on each day of year 2001, from 1 January to 31 December, using the corresponding meteorological data. PIP estimations were finally compared on scatter plots and by linear regression with the 26 values observed during 2 years. Model accuracy was assessed using R^2 derived from the regression of observed and predicted values, and the root mean square deviation (RMSD), calculated as $RMSD = [\sum (O - P)/n]^{0.5}$, where O and P are the paired observed and predicted values.

- *Model* 1 followed the concept of quantitative PP response described by Major (1980). The prolongation of the vegetative phase caused by PP was calculated under the assumptions of an empirical base photoperiod P_b (below which PI is instantaneous after BVP has ended), and an empirical slope coefficient describing photoperiod sensitivity (P_s, °C day h^{-1}). Model 1 was thus $PIP_d = P_s[PP - P_b]$, with PP being the photoperiod of the day, and parameters P_b and P_s estimated by optimisation. (For this and all other models, provision was made that the terms enclosed in brackets could not become negative.)
- *Model* 2 was the exact replication of Model 1 but using the daily rate of change of photoperiod (dPP) instead of the photoperiod itself. Model 2 was thus $PIP_d = dP_s{}^*[dPP - dP_b]$.

- *Model* 3 followed the concepts of quantitative or qualitative photoperiod response proposed for pigeon pea by Carberry et al. (2001). It uses the same calculation as Model 1 but imposes, in addition, a critical photoperiod P_c above which progress to PI either continues at ceiling rate (quantitative type) or is zero until PP falls again below P_c and immediately induces PI (qualitative type). Qualitative varieties are thus characterised by very different behaviour below and above P_c.
- *Models* 4 and 5 used basically the same concepts but instead of using a function of either PP or dPP, PIP_d was calculated as an additive function of PP and dPP (Model 4: $PIP_d = P_s{}^*[PP - P_b] + dP_s{}^*[dPP - dP_b]$). Finally, Model 5 combined the additive, double linear function of PP and dPP with a combination of the critical threshold P_c of the second model and a critical threshold of the rate of change of photoperiod, dP_c, with both critical conditions required together for arresting progress towards PI. This rule served to take into account the different behaviour observed for crops sown before or after summer equinox, under increasing (dPP > 0) or decreasing day length (dPP < 0).

3. Results

3.1. The monthly planting experiment in Mali

Variation among sowing dates of the duration from sowing to PI (VP, vegetative phase) and to flowering was much greater for the guinea variety CSM 335 than for Sariaso 10 and IRAT 174 (Fig. 3). In terms of calendar dates, the response of CSM 335 and IRAT 174 resembled the qualitative type: all plants sown
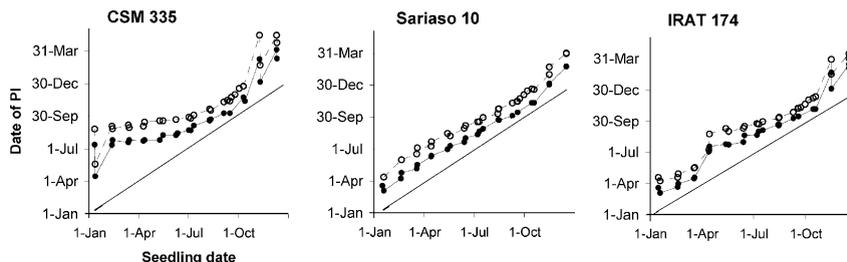
Fig. 3. Dates of panicle initiation (close circles) and flowering (open circles) in relation to seedling date. Lines join the monthly averages of the 2 years.
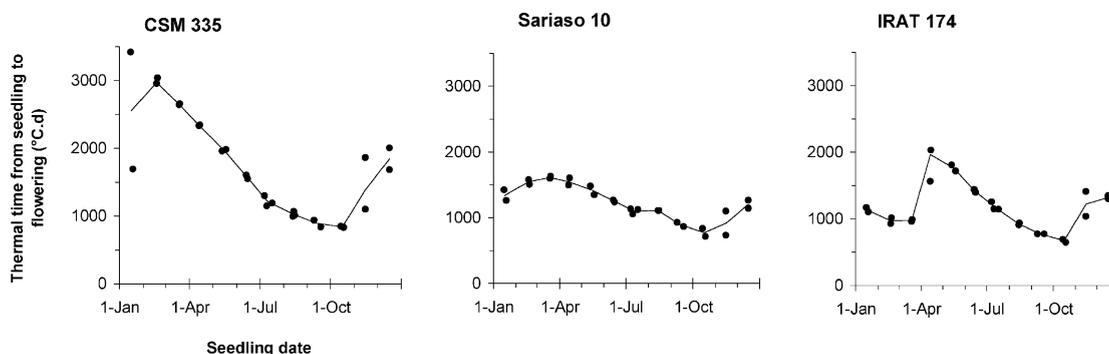
Fig. 4. Thermal time duration to flowering in relation to seedling date. Lines join the monthly averages of the 2 years.

between February (CSM 335) or April (IRAT 174) and early July flowered within 1 month, between late August and late September. According to stem dissections, PI for these flowering dates was between mid-July and mid-August, a period during which day length was close to its annual maximum but had started to decrease. In terms of thermal duration of VP, response curves of the three varieties differed markedly (Fig. 4). Duration was generally minimal for sowings in September and October, around the autumn equinox, whereas maximal duration was observed for sowing in January–February (CSM 335), March (Sariaso 10) and April (IRAT 174). Sowing dates gave nearly identical duration for the 2 years, except in January (CSM 335) and November (all cultivars).

Marked delays in PI, as indicated by sudden increases in the duration of VP and accompanied by increased inter-annual variability, were observed in January for CSM 335, in March/April for IRAT 174, and in October/November for all cultivars. The onset of these increases of VP is thought to be associated with threshold conditions, and the observed increase in variability with the system instability occurring near the threshold. On this basis, increases in VP in January and March can be interpreted as conventional PP thresholds encountered as day length increases. The second increase in VP in October was associated with decreasing minimum temperatures (Table 1), but it must be noted that ordinary effects of temperature on development rate are already taken care of in the thermal time term.

This experiment gave information on the duration of three sequential phases between seeding and flowering: the VP ending at PI, and the reproductive phase

divided between the time to the appearance of the flag leaf (PI-FL) and then the time to flowering (FL-FLO) (Fig. 5). The data confirmed that the variation of the duration from emergence to flowering was mainly caused by the variation of VP, which constituted 40–80% of the total duration to flowering. However, it also appeared that the second phase, IP-FL, was variable and its duration was slightly correlated with that of the previous phase ($r^2 = 0.31$, 0.25 and 0.19 and $P = 0.004$, 0.010 and 0.0271 for CSM 335, Sariaso 10 and IRAT 174, respectively). The phase PI-FL comprises the development of the ultimate leaf from its initiation until appearance outside the whorl. The main cause of this variation was a strong decrease of leaf appearance rates observed when more than 22–23 leaves were produced (Fig. 2). Finally, the third phase, FL-FLO, was constant and independent of the sowing date, equal in average to 211, 180 and 154 °C day for CSM 335, Sariaso 10 and IRAT 174, respectively.

For CSM 335, there was only a weak correlation between the photoperiod-induced phase (PIP), defined here from the end of BVP to PI, and the average photoperiod ($\overline{PP}$) occurring during the same period. (Fig. 6a). However, on the basis of plantings between May and October (wet season), an approximately linear relationship between PIP and photoperiod $\overline{PP}$ was observed, indicating a photoperiod threshold (critical PP) of about 12 h 40 min ($r^2 = 0.87$ for the model). For the same variety we could plot a hyperbolic relationship between PIP and PP at PI (PPi), similar to that modelled by Franquin (1976) for *sorghum* in Chad, but this relationship did not hold for crops sown in November and December (points
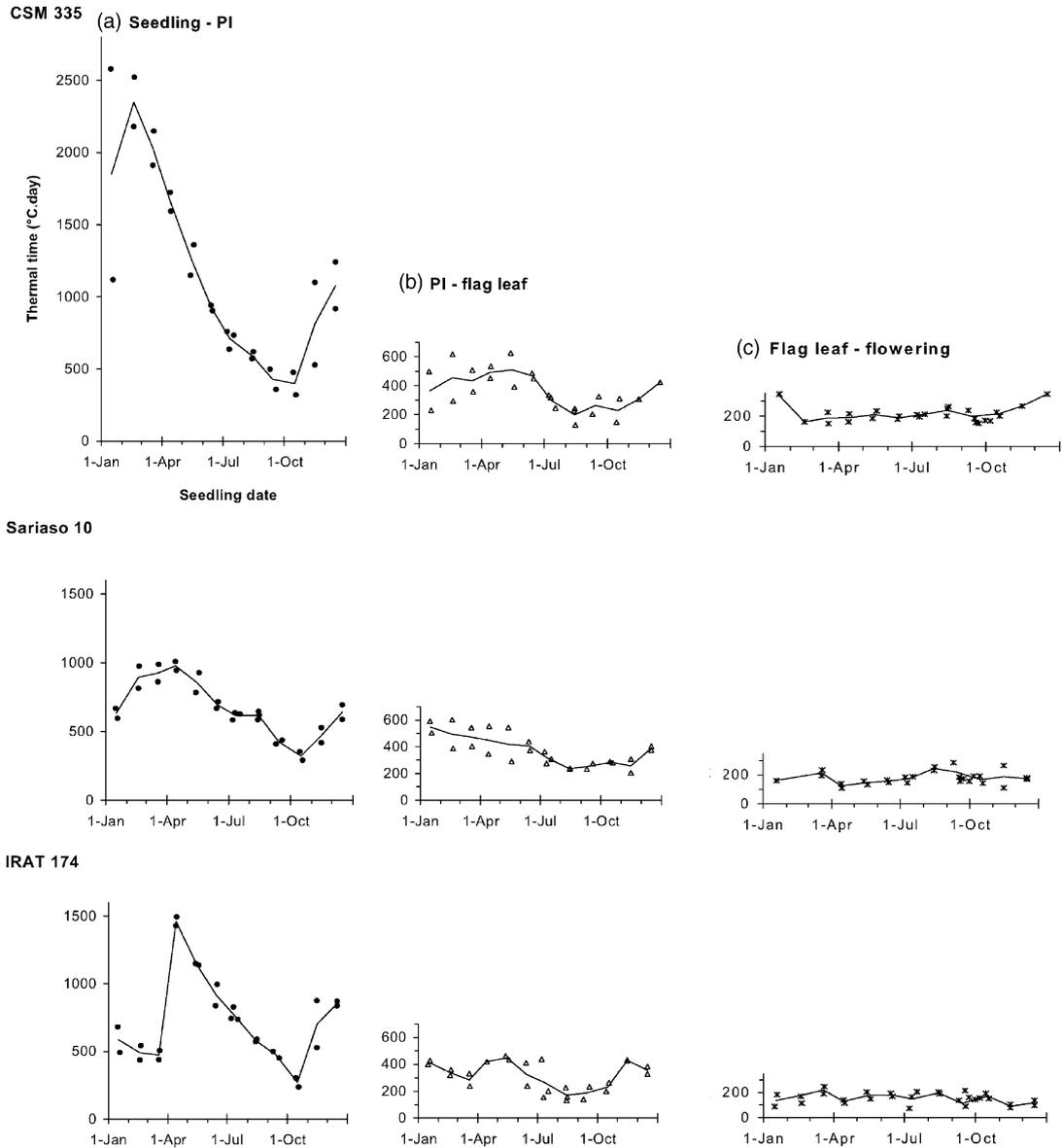
Fig. 5. Thermal duration of three consecutive phases (a) to PI, (b) from PI to flag-leaf appearance and (c) from flag-leaf to flowering in relation to seedling date. Lines join the monthly averages of the 2 years.

marked 11 and 12 in Fig 6d). However this last correlation appears to be of little explanatory value: for plants sown at the beginning of the year which first encountered short days, panicle initiation occurred after a long time under long day conditions, simultaneously with plants sown in May or June that were grown under long days throughout.

For Sariaso 10, there was a strong, positive, linear relationship between PIP and $\overline{PP}$ for May–October ($r^2 = 0.94, P = 0.002$) with a photoperiod threshold of about 12 h 20 min (Fig. 6b) but sowing on other months gave different results. Plotting PIP against PPi while using the same selection of sowing dates, showed the same level of correlation ($r^2 = 0.95, P = 0.002$)
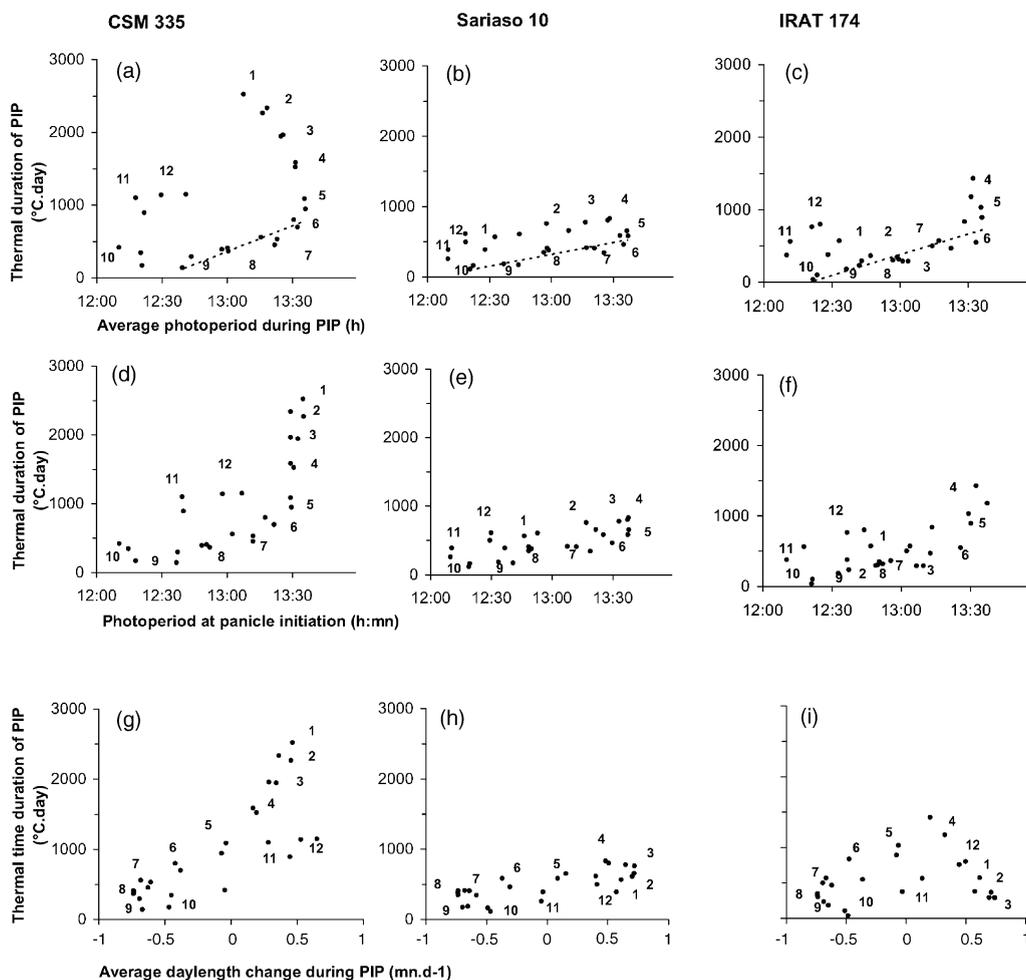
Fig. 6. Relationships between the thermal duration of PIP and the average photoperiod during PIP in (a)–(c), between the thermal duration of PIP and the photoperiod at panicle initiation in (d)–(f), and between the thermal duration of PIP and the average rate of day length change during PIP in (g)–(i). Each sowing is plotted with its occurring month. Linear relationships for summer plantings have been plotted with dashed lines.

(Fig. 6e). For IRAT 174, similar good linear relationships between PIP and $\overline{PP}$ was observed for May–October ($r^2 = 0.88$, $P = 0.006$) with a photoperiod threshold of about 12 h 20 min and between PIP and PPi ($r^2 = 0.89$, $P = 0.006$) (Fig. 6c and f).

The results show that the common concepts of a gradual (linear or quantitative) response of PIP to $\overline{PP}$ or PPi (case of Sariaso 10) or a threshold-type of response (hyperbolic, or absolute; case of CSM 335 and IRAT 174) could be reproduced for the sowing dates falling into the wet season (May–October), but did not fit crop behaviour during the remaining months

of the year. In fact, the PIP vs. PP scattergrams generally showed a strong hysteresis caused by delayed panicle initiation in the dry (off-) season, namely, between November and April. This hysteresis became smaller, but did not entirely disappear, in the case of CSM 335 and Sariaso 10 when PIP was plotted against the mean day-to-day change of PP ($\overline{dPP}$) (Fig. 6g–i).

A correlation matrix between PIP and nine factors that might influence it were calculated (Table 2). PIP was significantly correlated with $\overline{PP}$, dPP at the end of BVP (dPP_{BVP}), and PPi for each of the three varieties.

Table 2
Correlation matrix between PIP and nine environmental factors[a]

	PIP	$\overline{PP}$	$\overline{dPP}$	$\overline{T}$	$\overline{H}\,(\%)$	$\overline{SR}$	PP_{BVP}	dPP_{BVP}	PP_{PI}	dPP_{P}
CSM 335										
PIP	1.00									
$\overline{PP}$	0.40[*]	1.00								
$\overline{dPP}$	0.80[***]	−0.03	1.00							
$\overline{T}$	0.47[*]	0.84[***]	0.06	1.00						
$\overline{H}\,(\%)$	−0.61[***]	0.34	−0.93[***]	0.17	1.00					
$\overline{SR}$	0.23	−0.11	0.19	0.19	−0.19	1.00				
PP_{BVP}	−0.21	0.80[***]	−0.55[**]	0.54[**]	0.76[***]	−0.27	1.00			
dPP_{BVP}	0.87[***]	0.47[**]	0.84[***]	0.51[**]	−0.62[***]	0.08	−0.08	1.00		
PP_{PI}	0.74[***]	0.88[***]	0.41[**]	0.79[***]	−0.11	0.04	0.46[*]	0.75[***]	1.00	
dPP_{PI}	0.14	−0.63[***]	0.67[***]	−0.59[***]	−0.82[***]	0.12	−0.75[***]	0.22	−0.27	1.00
Sariaso 10										
PIP	1.00									
$\overline{PP}$	0.51[**]	1.00								
$\overline{dPP}$	0.70[***]	−0.06	1.00							
$\overline{T}$	0.51[**]	0.83[***]	0.12	1.00						
$\overline{H}\,(\%)$	−0.51[**]	0.32	−0.94[***]	0.08	1.00					
$\overline{SR}$	0.12	−0.04	0.27	0.27	−0.25	1.00				
PP_{BVP}	0.25	0.95[***]	−0.35	0.72[***]	0.58[**]	−0.14	1.00			
dPP_{BVP}	0.80[***]	0.22	0.96[***]	0.35	−0.82[***]	0.25	−0.08	1.00		
PP_{PI}	0.71[***]	0.95[***]	0.23	0.85[***]	0.04	0.06	0.81[***]	0.49[**]	1.00	
dPP_{PI}	0.53[**]	−0.32	0.96[***]	−0.11	−0.98[***]	0.25	−0.57[**]	0.84[***]	−0.03	1.00
IRAT 174										
PIP	1.00									
$\overline{PP}$	0.55[**]	1.00								
$\overline{dPP}$	0.23	−0.20	1.00							
$\overline{T}$	0.27	0.78[***]	0.00	1.00						
$\overline{H}\,(\%)$	−0.05	0.42[*]	−0.95[***]	0.15	1.00					
$\overline{SR}$	−0.29	−0.17	0.36	0.22	−0.38[*]	1.00				
PP_{BVP}	0.37	0.96[***]	−0.44[*]	0.71[***]	0.62[***]	−0.21	1.00			
dPP_{BVP}	0.48[*]	0.19	0.91[***]	0.31	−0.77[***]	0.26	−0.08	1.00		
PP_{PI}	0.67[***]	0.95[***]	0.08	0.78[***]	0.16	−0.09	0.83[***]	0.44[*]	1.00	
dPP_{PI}	−0.05	−0.50[**]	0.93[***]	−0.27	−0.96[***]	0.39	−0.67[***]	0.69[***]	−0.25	1.00

[a] PIP: thermal time duration of PIP; $\overline{PP}$: average photoperiod during PIP; $\overline{dPP}$: average rate of day length change during PIP; $\overline{T}$: average temperature during PIP; $\overline{H}\,(\%)$: average relative humidity during PIP; $\overline{SR}$: average solar radiation; PP_{BVP}: photoperiod at the end of BVP; dPP_{BVP}: rate of day length change at the end of BVP; PP_{PI}: photoperiod at PI; dPP_{PI}: rate of day length change at PI.

[*],[**] and [***]: significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$.

Many environmental factors were also inter-correlated, especially for CSM 335 and Sariaso 10, which had a more regular response to sowing dates, with longer PIP observed during the first 6 months of the year. This period, during which PP increases, is warmer and drier on average, resulting in significant correlations among $\overline{dPP}$, average temperature ($\overline{T}$) and average relative humidity ($\overline{H}$, %). Consequently, it is difficult to distinguish between causal and associated factors, although for the three varieties the factors showing the strongest correlation with PIP were always related to day length (rate of change for CSM 335 and Sariaso 10, or PPi for IRAT 174).

3.2. The experiment in controlled environments

The dynamics of leaf initiation during the 2001 experiment for the three varieties were initially identical and had a very small error, but then segregated and showed larger errors as PI occurred (Fig. 7). The large variation in leaf number in some treatments and varieties at the end of the experiment therefore indicate
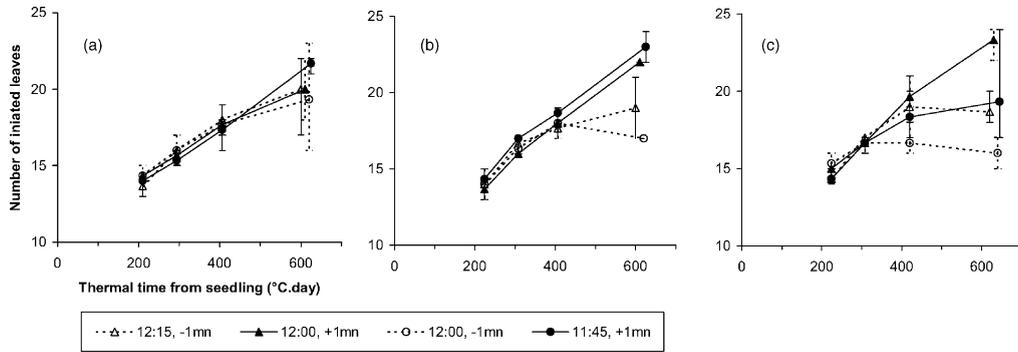
Fig. 7. Leaf initiation by the apex of (a) CSM 335, (b) Sariaso 10 and (c) IRAT 174 depending on day light duration in controlled environment in 2001. Three plants were dissected at each measurement, and the average data has been plotted together with the minimal and maximal values.
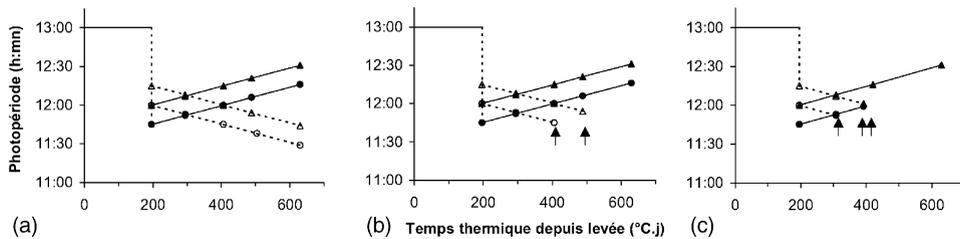
Fig. 8. Evolution towards the panicle initiation of (a) CSM 335, (b) Sariaso 10 and (c) IRAT 174 as depending of the dynamic of the day light duration in controlled environment in 2001. At the estimated date of PI, when occurred before the end of the experiment, line of the daily photoperiod is disrupted and marked with an arrow.

heterogeneity in PI among replications. Owing to this variability, 3 of the 4 treatments for CSM 335 and the 11 h 45 + 1 min for IRAT 174 are difficult to evaluate. For Sariaso 10, the treatment 12 h15 − 1 min showed large variation in final leaf number, but it can be safely assumed that PI had occurred in all replications because the number of initiated leaves was in all cases less than that of the two treatments that had remained vegetative. In the following, we use cessation of leaf initiation as indicator of PI, instead of the less reliable observation of the appearance of panicle primordia.

In Fig. 8 (2001 experiment) and Fig. 9 (2002), PI occurrence wherever certain is marked by an arrow on the PP by thermal time scattergram. In 2001, the first panicle initiations were observed 3 weeks or 300 °C day after plant emergence. When treatments were inductive, IRAT 174 reached PI most rapidly among the cultivars. On two particular dates in the experiment, pairs of treatments had equal $\overline{PP}$: at 410 and 620 °C day, corresponding to about 2 and 4 weeks after onset of differential treatments, or 4 and 6 weeks

after seedling emergence. In each of these cases, pairs of treatments had opposite rates of change of PP.

For CSM 335, no clear information could be obtained, since no treatment had clearly reached PI
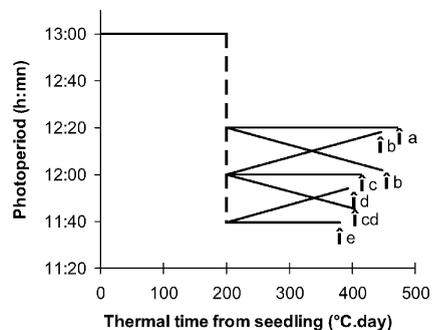
Fig. 9. Evolution towards the panicle initiation of Sariaso 10 as depending of the dynamic of the day light duration in controlled environment in 2002. At the estimated date of PI, line of the daily photoperiod is disrupted and marked with an arrow and the Newmann and Keuls group ($\alpha = 5\%$) of the date indicated with a letter.

before the end of the experiment. For Sariaso 10, on the contrary, one pair of treatments gave a well-contrasted result: at 410 °C day, PI was observed for the 12 h 00 − 1 min treatment, whereas the 11 h 45 + 1 min treatment was still vegetative despite identical $\overline{PP}$ (11 h 52 min). In fact, the latter treatment remained vegetative until the end of the experiment at 620 °C. Similarly, the 12 h 15 − 1 min treatment reached PI at about 490 °C day at $\overline{PP}$ = 12 h 07 min while the opposite treatment 12 h 00 + 1 min that had the same $\overline{PP}$ at that time remained vegetative. In these two contrasting pairs of treatments, those with decreasing photoperiod consistently reached PI before the opposite treatments.

For IRAT 174, the pair 12 h 00 − 1 min/11 h 45 + 1 min gave the same contrasting result as for Sariaso 10. At 310 °C day, at PP = 11 h 56 min and respective $\overline{PP}$ = 11 h 52 min (descending) and 11 h 49 min (ascending), the treatment 12 h 00 − 1 min had entirely initiated against only 1 out of 3 plants of the opposite treatment 11 h 45 + 1 min (same final number of leaves), indicating that the descending treatment was more inductive.

It must be noted that in three pairs of treatments where PI happened earlier under descending PP, the final PP just before PI happened was lower. In these cases, the rate of PP change is therefore not the only possible explanation for early PI. The only treatment× variety combination where PI happened earlier under descending PP despite higher or equal initial, mean and final PP, was the 12 h 00 − 1 min treatment for IRAT 174, as compared to its 11 h 45 + 1 min opposite. This case is compelling because all replications behaved identically. With a lesser level of certainty, the same observation can be made for Sariaso 10, some plants of which showed PI above 12 h 00 min in the treatment 12 h 15 − 1 min, while none did at a PP below 12 h 00 min in the treatment 11 h 45 + 1 min.

In summary, this rather complex experimental design reproduced on the one hand the well-known promotion of floral induction by short days, and in some treatments and varieties, an additional, apparent promotion by descending PP. At any given dynamics of PP (increasing or decreasing), plants exposed to the shorter day length progressed faster (Fig. 8). Conversely, wherever absolute PP was smaller or equal, and where PI was observed at all, PI happened earlier under decreasing PP.

In 2002, the second series of experiments conducted on Sariaso 10 only, did not confirm the first. The first PI were observed at 360 °C day (2001: 400 °C day) and all plants initiated before 510 °C day (2001: no PI observed at 630 °C day in two treatments), after having initiated between 13 and 15 leaves (2001: 16–18 leaves initiated at PI). In this experiment, the length of the PIP was been well correlated with the average PP ($P < 0.01$) and no relationships between PIP and dPP was observed (Fig. 9).

The different behaviour of plants in 2001 and 2002 experiments under controlled conditions were associated with a slight, but possibly important difference in light quality, a factor that is known to affect PIP (Thomas and Vince-Prue, 1997). In 2002, plants were raised until onset of differential PP in a room with different light sources, and were provided additional light from incandescent lamps rich in red (details in Section 2). Particularly, the latter change in lighting is likely to accelerate floral induction, but both 2001 and 2002 environments differ very strongly from field conditions and therefore are potentially prone to produce physiological artefacts.

3.3. Modelling the field observations

It was not possible to fit the field data with Models 1 and 3, even for the quantitative response type Sariaso 10 (Fig. 10 and Table 3) because the estimated PIP durations were not in phase with the observed, annual pattern of PP. Unlike the results on pigeon pea, the addition of P_c to the model did not enable fitting the data for the qualitative response type CSM 335, again because of a major phase shift between the physiological response and its supposed cause, photoperiod. This model provoked a discontinuous curve shape because PI is immediate when PP falls below P_c for crops that have reached end of BVP before this event. For IRAT 174, the use of P_c permitted to fit well the data observed in April and May. But the fit for the rest of the year, although improved, remained unsatisfactory.

Model 2, using only dPP despite the well established fact that absolute PP is positively known to be involved in floral induction, is presented for completeness. However, it appears that for CSM 335 this model fits much better the observations than Models 1
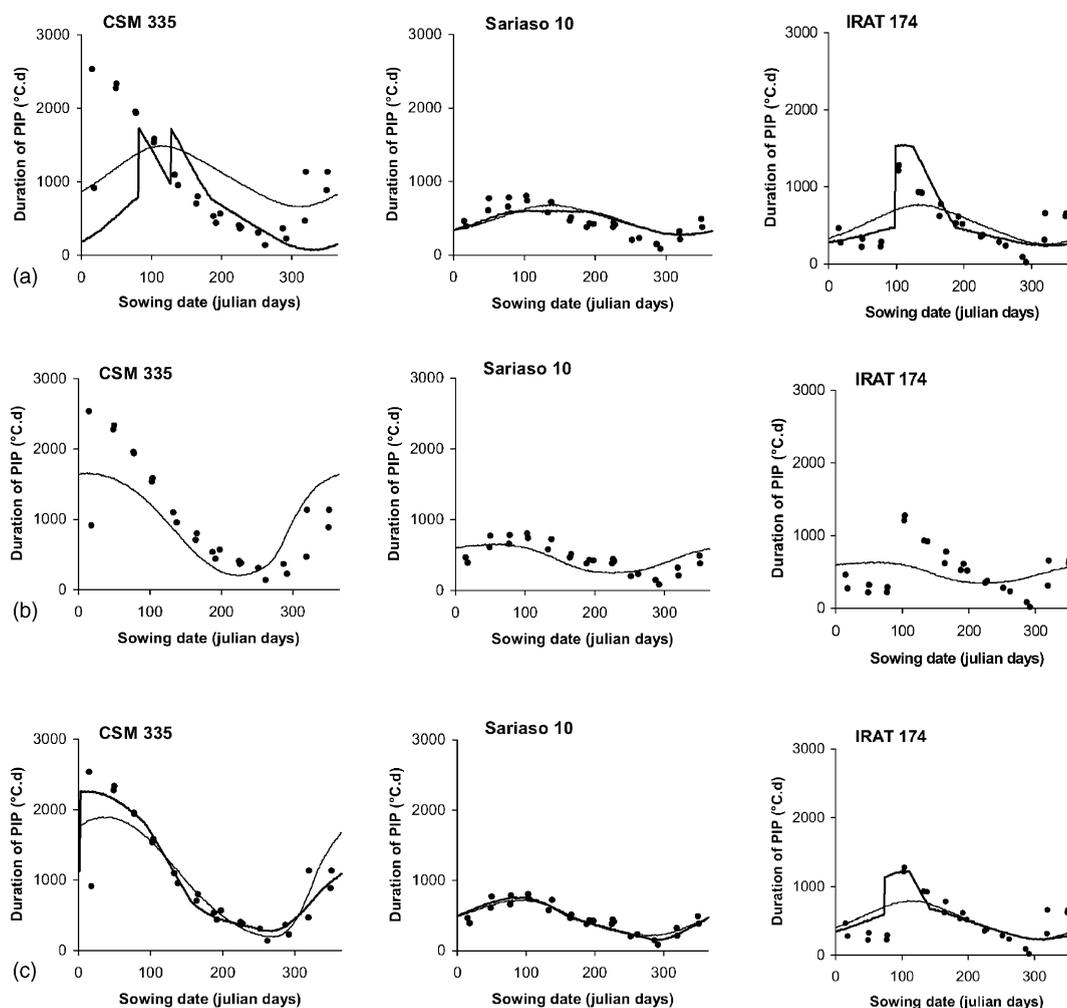
Fig. 10. Prediction of the duration of the vegetative phase depending on sowing dates in 2001 with (a) a model based on a linear relationship with the daily photoperiod (Model 1, regular lines) with the addition of a critical threshold P_c (Model 3, bold lines), (b) a model based on a linear relationship with the daily rate of day length change (Model 2, regular lines) and (c) a model combining linear relationships with the daily photoperiod and its rate of change (Model 4, regular lines) with the addition of a critical thresholds P_c and dP_c (Model 5, bold lines). Dots represent the observed data.

and 3 and above all gives estimations of PIP that are more in phase with the observed annual pattern. In fact, predictions using dPP are slightly advanced compared with observed patterns for CSM 335 and Sariaso 10, whereas predictions using PP are strongly behind, suggesting that a combined model might give a much better fit. The photoperiodic response of IRAT 174, in turn, appears to be different.

Indeed, Model 4 strongly improved the prediction of PIP for CSM 335 and Sariaso 10. It was able to

describe the increase of PIP at the end of the year without the need to introduce a specific effect of low temperatures as previously modelled by Franquin (1974) and Vaksmann et al. (1997). But for CMS 335, Model 4 was unable to predict the longer PIP duration observed for the first sowing dates of the year. The addition of a combined effect of two ceiling thresholds on the photoperiod P_c and its rate of change dP_c (Model 5) was necessary to adjust the model for these sowings.

Table 3
Parameters of the phenology models and estimations of model fit using r^2 for regressions of observed vs. predicted values and RMSD (see text)

Model	Variety	Pb (h)	Ps ($°C$ day h^{-1})	Pc (h)	dPb (min)	dPs ($°C$ day min^{-1})	dPc (min)	r^2	RMSD ($°C$ day)
Model 1									
PIP = Ps*(PP − Pb)	CSM 335	11.05	602					0.14	656
While PP > Pb	Sariaso 10	11.16	273					0.37	158
	IRAT 174	11.43	346					0.34	254
Model 2									
PIP = dPs*(dPP − dPb)	CSM 335				−0.93	1036		0.68	408
While Dpp > dPb	Sariaso 10				−1.63	271		0.46	147
	IRAT 174				−2.54	190		0.07	302
Model 3									
PIP = Ps*(PP − Pb)	CSM 335	11.03	428	13.5				0.13	700
While Pb < PP < Pc	Sariaso 10	11.31	316	13.17				0.40	154
	IRAT 174	10.94	192	13.5				0.72	243
Model 4									
PIP = Ps*(PP − Pb) + dPs*(dPP−dPb)	CSM 335	12.11	483		−0.54	1080		0.82	313
While dP < dPP < dPb	Sariaso 10	11.82	271		−0.46	303		0.89	67
	IRAT 174	11.47	359		1.47	1008		0.35	253
Model 5									
PIP = Ps*(PP − Pb) + dPs*(dPP − dPb)	CSM 335	11.45	235	13.11	−0.63	677	0.07	0.95	151
While Pb < PP < Pc and dPb < dPP < dPb	Sariaso 10	11.76	248	13.89	−0.44	333	0.16	0.88	69
	IRAT 174	11.72	307	13.36	−1.31	73	0.27	0.60	197

4. Discussion

The field experiment in Mali confirmed only partly the concept of a linear relationship between the duration of PIP and the mean PP observed during PIP as postulated by Major (1980) and used by numerous crop models. In fact, Major's model only fitted the behaviour of crops sown between May and October, corresponding to the rainy season. This model therefore, although useful to predict crop duration for the agronomically relevant range of sowing dates, does not satisfactorily reflect the physiological mechanisms at work. (In fact, some traditional sorghum production systems in West Africa using residual moisture after flood recession are based on sowing between November and January (Chantereau, 2002).) Although some of the hysteresis of PIP annual patterns might be due to errors in the assumed cardinal temperatures or to specific effects of very high or low temperatures, it seems certain that the classical model is inaccurate or incomplete.

Applying the critical photoperiod threshold P_c proposed by Carberry et al. (2001) failed to improve predictions mainly because it did not remove the major problem constituted by phase shift between the annual patterns of PP and PIP. On the other hand, the hypothesis of an influence of the rate of day length change, either quantitative for Sariaso 10 or qualitative for CSM 335, as evidenced by the superior fit with field data and the results of the 2001 experiment in controlled environments, gave a large improvement of the model (Models 3 and 4). Model 5, that is quite complex with 2 input variables, 2 critical and 2 ceiling thresholds, extends the model proposed by Carberry et al. (2001) on pigeon pea by adding an additional sensitivity to dPP. This model was able to explain the somewhat odd behaviour of IRAT 174, but the use of a large number of variables and rules reduces its credibility, or likelihood of having generic value. Essentially, the introduction of dPP in Models 3–5 enabled predictions for both the first and second half of the year, under increasing or decreasing day

lengths, which was not possible with absolute PP alone.

These results support the hypothesis that in sorghum the photoperiod sensitivity would be proportional to both PP and dPP, possibly in an additive fashion. On the other hand, this may not be the only possible explanation, and a mathematical artefact could be suspected since PP and dPP are inter-dependent, with a constant $\pi/2$ phase shift between them. Unfortunately, the results obtained in controlled environments did not conclusively support the hypothesis of dPP directly affecting PIP. In fact, they demonstrated that profoundly different effects of day length might be generated with different light quality, thus raising the question how meaningful experiments under artificial lighting are if the complex dynamics of field situations cannot be mimicked. For instance, it is obvious than natural dawn and dusk are very different from an abrupt switching on and off of the light source, both in terms of light quality and quantity. For example, plants are sensitive to dynamics of both light intensity and its shifting red/far red ratio associated with dawn and dusk (Salisbury and Ross, 1985). Moreover, the inability to fit the more complex PIP pattern for IRAT 174 with a reasonably simple model shows that the hypotheses remain incomplete and that other, unknown factors must have influenced the panicle initiation of this variety.

Finally, it appears impossible to conclude definitively in favour of the hypothesis of an effect of the rate of day length change on the duration of PIP. Indirect evidence has been presented here, the strongest of which might be this model's ability to predict accurately the behaviour of both the quantitative variety Sariaso 10 and the qualitative variety CSM 335 on a yearly cycle. But results presented for IRAT 174 and the failure to reproduce in 2002 the observations made under controlled environment in 2001 leaves this question open. Consequently, this study provided a model that significantly improves the simulation of sorghum phenology in the field, but not necessarily on the basis of established physiological knowledge.

Acknowledgements

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