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Why tropical sorghum sown in winter months has delayed flowering and modified morphogenesis in spite of prevailing short days

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ABSTRACT

Sowing certain late photoperiod-sensitive tropical sorghum varieties under short-day conditions in November–January in the northern hemisphere can result in a pronounced delay in flowering and prostrate, high-tillering forms similar to the rosettes in winter small-grain cereals. The cause of this phenomenon in sorghum has long been questioned and is often attributed to the effects of low night temperatures during this period. Monthly sowings, from December to March, in greenhouse compartments with two contrasting night temperatures and under field conditions with contrasting soil conditions were conducted over two years near Bamako, Mali, with three contrasting sorghum varieties. Dates of panicle initiation, rates of leaf primordia initiation at the stem apex, and rates of leaf appearance were observed. In the greenhouse, colder night temperatures were found to have no effect on prolonging vegetative-phase duration when measured in thermal time and on plant development. Although a prolonged vegetative phase and prostrate forms were observed under field conditions, these were not observed in the greenhouse experiments despite having similar temperature conditions. Although the higher soil fertility of the potting soil increased the development rates slightly, and reduced the vegetative phase relative to natural soil conditions in the field, this difference between greenhouse and field growth remained when a comparison was made between plants grown in pots. Thus, it appears that the greenhouse glass had masked the UV component of sunlight, which would mediate the cue responsible for the delayed flowering and modified morphogenesis. This cue, which has strongly contrasting effects between October and November sowings, could be the daily changes in the sunrise and sunset hour that have negative values from November to July.

1. Introduction

Major delays in flowering of photoperiod-sensitive sorghum can be observed in tropical northern-hemisphere sowings during the November to January period relative to September–October or March sowings (Bezot, 1963; Miller et al., 1968; Vaksmann et al., 1997; Clerget et al., 2004; Dingkuhn et al., 2008). This lengthening of the vegetative phase for sowings done during short daylengths was not a simple effect of slower growth due to cooler ambient temperatures of this period, as flowering delays were still apparent when measured in thermal time (Vaksmann et al., 1997; Clerget et al., 2004; Dingkuhn et al., 2008). As short daylengths occur during this period, rapid progress to flowering, in thermal time, would normally be expected with this short-day species.

The prolonged vegetative period of these cool-season sown sorghum varieties is accompanied by a prostrate growth with high tillering (Bezot, 1963). All stems grow nearly horizontally in divergent orientations, constituting a rosette similar to that of small-grain winter cereals. Leaves of some varieties take on a red colour that can be very pronounced. Low night temperatures can drop below the minimum growth temperatures (10–11 °C) for sorghum during these months (Vaksmann et al., 1997; Clerget et al., 2004; Dingkuhn et al., 2008). Consequently, low night temperature has been envisaged as the reason for the delayed flowering of tropical sorghum sown in the field during November to January (Bezot, 1963; Miller et al., 1968; Vaksmann et al., 1997). However, temperatures never fall below 15 °C in Mayaguez, Puerto Rico, where Miller et al. (1968) had carried out their experiment and nevertheless found a large lengthening of the vegetative phase for winter sowings in spite of the very stable daily mean temperature year-round in the Caribbean islands. On the other hand, the prostrate rosette form had also been observed in growth chambers when a photoperiod-sensitive guinea variety from Burkina Faso, named

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Table 1
List of the treatments used each sowing month, with their sowing date.

Sowings		Field			Greenhouse	
Month and year	Day	Field soil	Buried pots	Potting soil	Warm	Cold
Dec 2001	10	•			•	
Jan 2002	11	•			•	•
Feb 2002	11	•				
	21		•			
Mar 2002	12	•				•
Dec 2002	2				•	•
	10	•	•			
Jan 2003	6				•	•
	10	•	•			
Feb 2003	10	•	•	•	•	•
Dec 2006	11	•	•	•		
Jan 2007	10	•	•	•		
Feb 2007	9	•	•	•		

Nazongala, had been grown under a 12/12 h light/dark and 27/23 °C alternation, and had not reached panicle initiation after 90 days because of the insufficiency of red radiation in the light spectrum (Clerget, 2004).

Photoperiod sensitivity and temperature interaction have been frequently examined in controlled environments in various day/night temperature combinations (Caddel and Weibel, 1971; Quinby et al., 1973; Ellis et al., 1997; Craufurd et al., 1998). All these authors have found that panicle initiation occurred earlier under short photoperiod of 10–12 h and an optimal mean temperature of 26–27 °C and was delayed by longer photoperiods and cooler or warmer temperatures. Based on similar results in pea, bean, and sorghum, Yan and Wallace (1996) proposed to model the duration of the vegetative phase through a U-shape function, product of the quadratic effects of both temperature and photoperiod. Additionally, in a study carried out on rice, Yin (2008) used 6 combinations of day/night temperatures under a unique photoperiod of 12 h on 3 rice varieties and showed that the temperature regime was able to nearly double the duration of the vegetative phase from 80 to 150 days. However, a weakness of all these studies was that the duration of the vegetative phase has never been expressed in thermal time, which is considered as the physiological time of plants, and their conclusions about the photoperiod × temperature interaction on the duration of the vegetative phase consequently remained debatable.

In the same studies, Quinby et al. (1973) and Craufurd et al. (1998) found that plants had produced a stable number of leaves under mean temperature from 18 to 31 °C, and more leaves at lower or higher mean temperatures. They also found that the plastochron, the number of days between the initiations of 2 consecutive leaves, had been stable between 18 and 31 °C mean temperature, but much longer at 14 °C or 33 °C. Although sorghum is traditionally sown during May–July in the northern hemisphere, its behaviour during November to January sowings was hypothesized to be one aspect of its photoperiod sensitivity, whose study could bring a more complete understanding of flowering responses. This study was thus initially conceived to assess the influence of low night temperatures on flowering and growing behaviour of sorghum varieties of contrasting photoperiod sensitivities and extended later to check the validity of the contrasting results between greenhouse and field environments.

2. Materials and methods

Three contrasting sorghum varieties were used in this study: CSM 335, a tall, traditional *guinea* landrace from Mali known to be highly photoperiod-sensitive; Sariaso 10, a less photoperiod-sensitive variety bred in Burkina Faso from a *guinea* × *caudatum* cross; and IRAT 174, a dwarf photoperiod-sensitive line bred in Burkina Faso from a *kafir* × *durra* cross. Seed of CSM 335 was provided by the ICRISAT-Samanko Sorghum Program, whereas seed of the other varieties came from the CIRAD Genetic Resources Unit in Montpellier, France.

Simultaneous or nearly simultaneous sowings were done in two adjacent compartments of a greenhouse and a field at the ICRISAT research station of Samanko, 15 km to the SW of Bamako, Mali (12°34′N, 8°04′W, 330 m a.s.l.), on 10 December 2001; 11 January, 11 and 21 February, 12 March, 2 and 10 December 2002; and 6 and 10 January and 10 February 2003 (Table 1).

2.1. Greenhouse experiments

The greenhouse (Cambridge Glasshouse Company, Comberton, Cambridge, UK) was glass covered and divided into compartments with glass walls. The light transmittance of the glass was measured under direct sunlight at 2 angles of incidence, 0 and 45°, with a radiospectrometer (FieldSpec® 3 JR (350–2500 nm), ASD Inc., Boulder, CO, USA) (Fig. 1). Canvas sheets were vertically installed against the northwestern walls of 2 compartments to mask possible contaminating sources of light from the offices and from a red light at the top of an antenna's mast. The "cold" compartment was cooled day and night, using an evaporative air cooler (RW4500, AdobeAir Inc., Phoenix, AZ, USA). The "warm" compartment was cooled from 0800 to 1800 with an identical air cooler and warmed during nights with an oil heater (KAI 20, Kongskilde Industries, Sorø, DK) to maintain the temperature above 23 °C. Each sowing date used 60 plastic 10-l pots filled with 8 kg of a mixture of 9 parts soil from the surface of a well-drained plot from the station (fine, loamy,

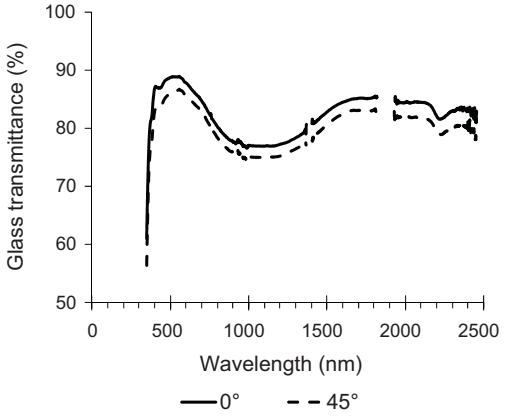

Fig. 1. Transmittance spectrum of greenhouse glass under 2 angles of light incidence, 0 and 45°.

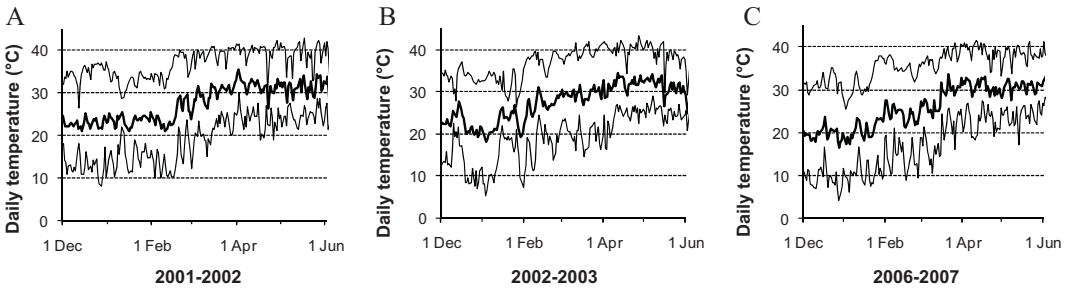

Fig. 2. Daily minimal, maximal, and average air temperatures at the Samanko station (A) from 1 December 2001 to 1 June 2002, (B) from 1 December 2002 to 1 June 2003, and (C) from 1 December 2006 to 1 June 2007.

mixed, isohyperthermic, Plinthic Paleustalfs, C:L:S ≈ 20:35:55, and $pH_{H_2O} = 5.0$) and 1 part compost of plant residues. Fertilizers were applied in each pot at sowing (2 g diammonium phosphate and 2 g KCL) and 1 month later (2 g urea). Each variety was sown in 20 pots, with 10 grains in a central hill, and 10 pots were placed in each compartment. Pots were thinned to 2 plants at 14 days after emergence and to 1 plant a month after emergence. Leaves of the main stem of each plant were labelled. Air temperature at 2 m and soil temperature at 10 cm below ground in 1 pot were continuously measured at 1-min intervals, averaged on an hourly basis, and stored in a data logger (21X, Campbell Scientific, Shepshed, UK) in each compartment of the greenhouse.

2.2. Field experiments

The field plot was a fine, loamy (C:L:S ≈ 25:50:25 and $pH_{H_2O} = 4.5$), Typic Haplaquets (USDA taxonomy) close to the Niger River. Fertilizers were applied at sowing (NPK at 36, 92, and 60 kg ha^{-1} as diammonium phosphate and KCl) and then every month (N at 46 kg ha^{-1} as urea). Soil moisture was never limiting due to gravity irrigation twice a week, keeping the soil near field capacity. Plots of 4 rows 5 m in length were sown with 10 grains hill^{-1} at 0.75 m × 0.20 m spacing, and thinned to 2 plants hill^{-1} 2 weeks after plant emergence and to 1 plant hill^{-1} at the onset of stem elongation. Leaves of the main stem of each plant of the 2 central rows were labelled and 10 consecutive plants in 1 row were used for weekly non-destructive measurements. Air temperature at 2 m and soil temperatures at 10 and 2 cm below ground were continuously measured at 1-min intervals, averaged on an hourly basis, and stored in a second data logger (Campbell, 21X).

Additionally, several series of pot sowings were conducted to test the possible effects of soil and root conditions on flowering responses under ambient field conditions. Three series involved sowing each variety in 10 pots prepared as previously described, simultaneously with the field plots of February 2002, December 2002, and January 2003, and the pots were buried in lines adjacent to directly sown plots. The following series of pot sowings consisted of 10 buried pots per variety as well as 10 holes, where field soil was removed and replaced by potting soil in a volume and shape equivalent to the pots and seeds sown in their centre on 10 February 2003, 13 December 2006, and 11 January and 14 February 2007 on the same dates as the directly sown field plots. Seeding, thinning, and leaf labelling were conducted as in previous experiments. Air temperature and soil temperature in soils and in pots were recorded hourly and stored in a data logger as was described above.

2.3. Data record and methods for assessing flowering time and phyllochron

The number of leaves emerged from the whorl, fully exserted (ligulated) and senesced (>50% of the leaf blade area dead), together with the number of live tillers were recorded weekly on the main stem of the same 10 consecutive plants. Two plants per variety were dissected every week from emergence to panicle initiation to count the number of leaves initiated on the apex and measure stem length in greenhouse and field experiments. Panicle initiation was recorded only when the first panicle branches could be observed and panicle initiation was certain. The additional plants per hill or pot were sampled before the last thinning at the onset of stem elongation.

Thermal time was calculated on an hourly basis using the shoot apex temperature estimated from soil at 2 cm temperature before the onset of stem elongation and from air temperature thereafter. Cardinal temperatures were assumed to be 11, 34, and 52 °C for base, optimum, and maximum temperatures, respectively, as justified in Clerget et al. (2008). Linearity of response was assumed between the cardinal temperatures, with thermal time equal to zero at temperatures below the base or above the maximum (broken-stick model).

Dynamics of leaf development were fitted to the better linear or bilinear segmented model, as detailed in Clerget et al. (2008). The observed leaf number (LN) (initiated or appeared) was regressed against the elapsed thermal time from plant emergence (TT) using the linear equation

$$LN = a + [b_1 * \min(TT, TL)]$$

or the bilinear equation

$$LN = a + [b_1 * \min(TT, TC)] + \{b_2 * \min[TL - TC, \max(0, TT - TC)]\}$$

where a is the number of leaves at emergence, b_1 and b_2 the initial and secondary rates of development, TL is the thermal time when the last leaf either initiated or appeared, and TC is the thermal time when the development rate changed in cases in which development exhibited bilinear growth. Parameters and their confidence intervals were iteratively estimated using the procedure NLIN of SAS (2008). The model that fit the data best with the least number of parameters was selected. Plastochrons and phyllochrons were calculated as the reverse of the developmental rates b_1 and b_2.

A visual estimation of the panicle initiation date was made while dissecting the apices to measure leaf initiation and a second estimation was obtained using the model of the leaf initiation dynamic, with panicle initiation determined to occur one plastochron after the initiation of the last leaf.

3. Results

3.1. Temperature history

Daily minimum temperatures below 15 °C occurred nearly continuously from 1 December until 17 February in 2001–2002 but temperature below 10 °C occurred during only 3 nights during this period (Fig. 2). Minimum temperatures in the following year,

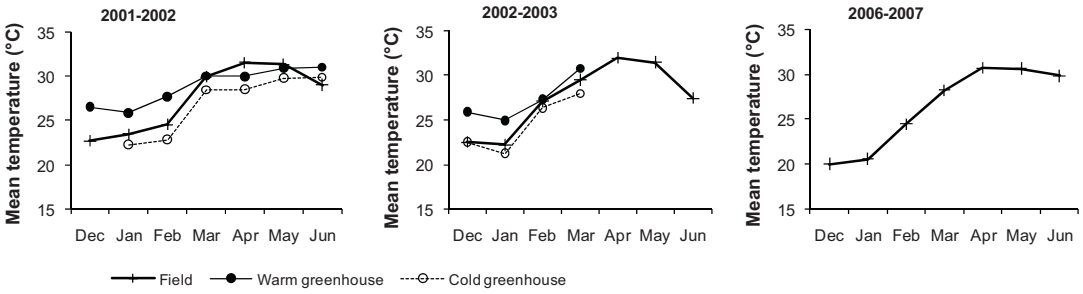

Fig. 3. Monthly average air temperatures in the field at the Samanko station and in the warm and cold compartments of the greenhouse from December to June in 2001–2002, 2002–2003, and 2006–2007.

however, dropped below 15 °C during three separate periods (24 November–9 December, 17 December–13 January with morning temperatures below 10 °C, and 28 January–9 February), with intervening periods that had minimum temperatures close to 20 °C. In 2006–2007, minimum temperatures remained below 12 °C on 55 days of 62, from 1 December to 31 January, and varied between 10 and 20 °C during the whole month of February. The mean monthly temperatures for December, 22.7 and 22.5 °C, and for January, 23.5 and 22.2 °C, varied between 2001–2002 and 2002–2003, respectively (Fig. 3). Temperatures began rising earlier in February 2003 than for 2002, resulting in higher mean temperatures for the month in 2003 than in 2002. Monthly mean temperatures were even lower in December 2006 and January 2007 than for the same months in 2001–2002 and 2002–2003, whereas the February 2007 mean temperature was intermediate between the means of that month in 2002 and 2003.

The heater in the heated glasshouse compartment successfully produced contrasting night temperatures when open-air temperatures descended below 20 °C. The hourly mean temperature profiles show that the heater significantly increased air temperatures from 2000 to 0800 during January 2003, but not in February and March, since night temperatures had already risen above 20 °C (Fig. 4A). However, the night temperatures in the cold compartment continued to be lower than in the warm compartment and in the field due to the continuous running of the cooling system. There was little difference between the field and greenhouse cold-compartment air temperatures during nights. Air coolers in both greenhouse compartments maintained day-time air and soil temperatures similar to those in the field through February, as indicated by hourly temperature profiles and monthly means. Soil (at 5 cm) temperatures remained cooler than air temperatures during days due to the cooling effect of evaporation, but both were close during nights. Thus, stem apices, whose temperature was close to soil temperature until the onset of stem elongation, experienced truly differential night temperatures in the two greenhouse compartments (Fig. 4B).

3.2. Responses to the temperature difference between the 2 compartments of the greenhouse

In the greenhouse, the mean durations in days until panicle initiation have been short in the 2 compartments, little variable between varieties and years, but longer in the cold compartment than in the warm compartment (Table 2). The differences in vegetative durations between compartments have been generally significant for varieties CSM 335 and IRAT 174 sown in December and January but rarely for Sariaso 10. There was no more difference for the February sowing, when temperature differences between compartments became weak.

When expressed in thermal time, the durations to panicle initiation appeared to have been very close and often not significantly different in the two greenhouse compartments, warm and cold (Fig. 5).

The aggregated data from sowings done from December to February in the 2 greenhouse compartments showed that the number of days from emergence to panicle initiation was linearly and

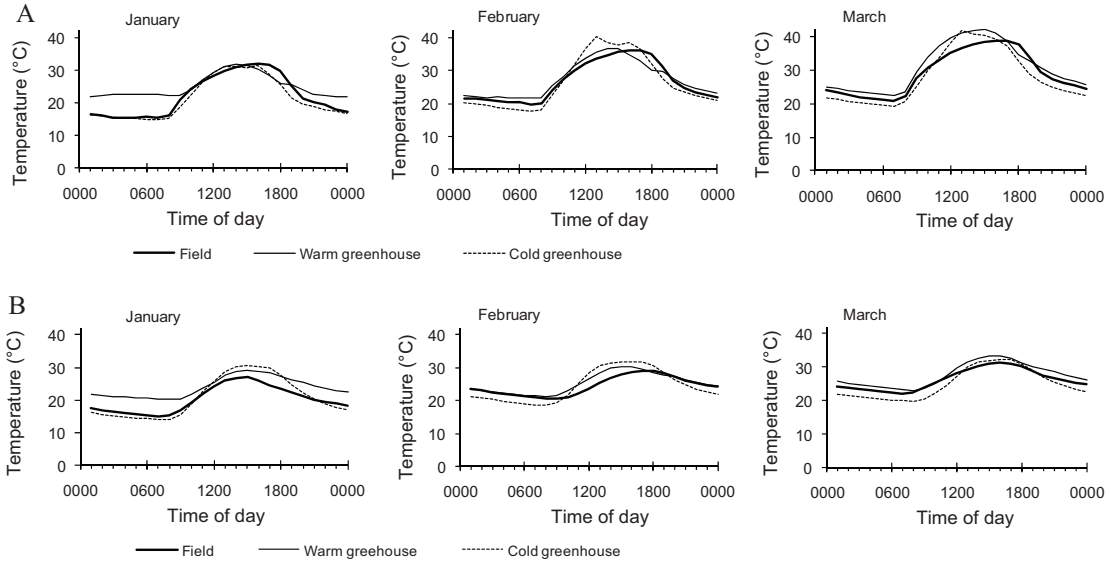

Fig. 4. Comparison of the hourly monthly averages of (A) air and (B) soil temperatures in the field and in the warm and cold compartments of the greenhouse in January, February, and March 2003.

Table 2
Estimations of durations in days from sowing to panicle initiation, by variety, sowing date, and treatment, with their confidence intervals and their means by factors × treatments.

Variety	Sowing month and year	Field soil	Warm greenhouse	Cold greenhouse	Buried pot	Potting soil
CSM 335	Dec 2001	86 ± 6	20 ± 1			
	Jan 2002	80 ± 11	22 ± 1	35 ± 3		
	Feb 2002	133 ± 25			43 ± 17	
	Mar 2002	120 ± 14			47 ± 12	
	Dec 2002	52 ± 11	24 ± 6	36 ± 4	38 ± 11	
	Jan 2003	44 ± 4	22 ± 3	33 ± 5	39 ± 5	
	Feb 2003	62 ± 17	23 ± 2	24 ± 3	42 ± 5	33 ± 6
	Dec 2006	78 ± 5			87 ± 4	88 ± 4
	Jan 2007	95 ± 5			78 ± 5	86 ± 3
	Feb 2007	152 ± 6			67 ± 3	60 ± 3
IRAT 174	Dec 2001	76 ± 6	18 ± 3			
	Jan 2002	50 ± 3	19 ± 1	35 ± 2		
	Feb 2002	36 ± 4			25 ± 2	
	Mar 2002	31 ± 2		44 ± 4		
	Dec 2002		20 ± 3	33 ± 6	39 ± 5	
	Jan 2003	39 ± 3	22 ± 2	30 ± 4	33 ± 2	
	Feb 2003		22 ± 3	23 ± 3	34 ± 4	25 ± 2
	Dec 2006	65 ± 4			53 ± 1	56 ± 8
	Jan 2007	65 ± 1			58 ± 2	61 ± 3
	Feb 2007	44 ± 1			39 ± 1	40 ± 1
Sariaso 10	Dec 2001	52 ± 10	22 ± 2			
	Jan 2002	50 ± 3	18 ± 2	29 ± 4		
	Feb 2002	46 ± 4			41 ± 9	
	Mar 2002	42 ± 5		37 ± 3		
	Dec 2002		26 ± 6	27 ± 4	39 ± 8	
	Jan 2003	42 ± 3	24 ± 3	27 ± 2	35 ± 2	
	Feb 2003		26 ± 3	24 ± 2	40 ± 3	29 ± 3
	Dec 2006	71 ± 4			49 1	56 ± 6
	Jan 2007	67 ± 4			51 6	62 ± 3
	Feb 2007	66 ± 3			48 4	53 ± 2
Means	Global	67	22	30	47	54
	2001–2002	68	20	33	36	
	2002–2003	48	23	29	38	29
	2006–2007	78			59	62
	Dec	69	22	32	51	67
	Jan	59	21	32	49	70
	Feb	77	24	24	42	40
	CSM 335	87	22	32	56	67
	IRAT 174	54	20	30	40	46
	Sariaso 10	56	23	27	43	50

significantly related to the mean temperature of the stem apex during the vegetative phases for the 3 varieties ($P < 0.001$, 0.001, and 0.05 for CSM 335, IRAT 174, and Sariaso 10, respectively) (Fig. 6A). Correspondingly, the thermal times to panicle initiation showed no significant differences across the range of day-night temperatures tested for CSM 335 and Sariaso 10 but the negative relationship between temperature and thermal duration of the vegetative phase was significant for IRAT 174 ($P = 0.01$) (Fig. 6B). The mean thermal times to panicle initiation were 321, 299, and 304 °C d for CSM 335, IRAT 174, and Sariaso 10, respectively. In contrast, panicle initiation was largely delayed for the sowing done in March 2002 that experienced daylength above 12 h soon after seedling emergence (Fig. 5).

The mean initial phyllochrons, set up at plant emergence, have been larger in the warm compartment than in the cold greenhouse compartment, with a large inter-annual variation in the cold compartment (Table 3). In the cold greenhouse, mean phyllochrons were shorter in December and January than in February, when there was no more temperature difference between compartments and no more cool nights. In January 2002, phyllochrons were quite contrasting between the 2 compartments, but not in January 2003. From 13 to 28 January 2003, at the time of the emergence of plants sown on 6 January, minimum night temperatures remained above 20 °C (Fig. 2).

The average number of leaves produced by the main stems has been low in both compartments, in relation to the short duration of the vegetative phase, but slightly higher in the cold compartment (Table 4). These average numbers of leaves showed trends opposite to those of the initial phyllochron: in the cold compartment, plants produced leaves in 2001–2002 and for the December and January sowings, when phyllochrons were shorter.

The average number of emerged tillers was low in comparison with their number in the field, and nearly doubled in the cold compartment (Table 5). CSM 335 produced many more tillers than both other varieties and tiller production followed a decreasing gradient from December to February sowings, in both compartments. No prostrate form was ever observed in the greenhouse.

3.3. *Responses to soil fertility and container differences in field cropping conditions*

In the field, the average durations to panicle initiation of plants sown in field soil have more than doubled when compared with the greenhouse (Table 2). In the three types of cropping soil, these average durations have varied with year, being much longer in 2001–2002 and 2006–2007 than in 2002–2003; with month, decreasing from December to February sowings, with the strong exception of variety CSM 335 sown in field soil; and with variety CSM 335 being always later than both the other varieties. The increased soil fertility in buried pots or in potting soil reduced the duration of the vegetative phase. In February 2003, the vegetative phase also decreased for plants grown in buried pots, but this effect was not confirmed in the 3 sowings done in 2006–2007.

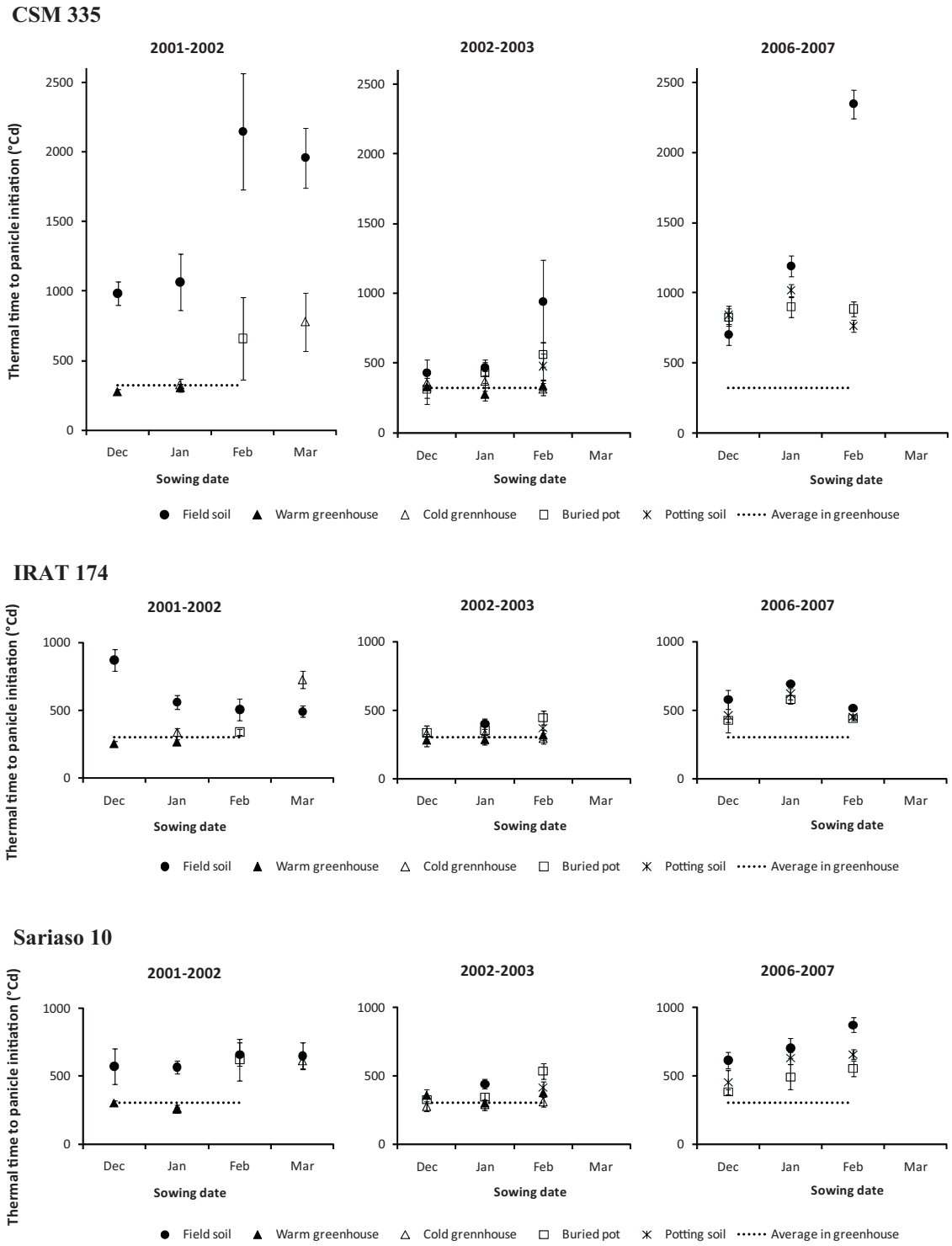

Fig. 5. Thermal duration of the vegetative phase of 3 sorghum varieties by sowing month. Error bars indicate the 95% confidence interval and dotted lines the variety average durations of the vegetative phase when grown in the greenhouse.

When expressed in thermal time, the longer duration of the vegetative phases of plants grown in the field and its inter-annual and inter-variety variations were confirmed, but not the decreasing trend from December to February (Fig. 5). In contrast, the thermal duration to panicle initiation tended to be stable or slightly longer from December to January and longer in February. The duration of this vegetative phase has been highly variable for variety CSM 335 and the February and March sowings, with a strong effect of soil type.

The average initial phyllochrons decreased markedly in the more fertile soils, without any effect of the container (Table 3). They have been little variable between years, months, and varieties.

The average total numbers of leaves have been much higher in the field than in the greenhouse and they decreased a little in more fertile soil (Table 4). Like for the duration of the vegetative phase, there were strong inter-annual and inter-variety variations in the numbers of leaves, but no clear effect of the sowing month. There was no difference in numbers of leaves between the buried pots and

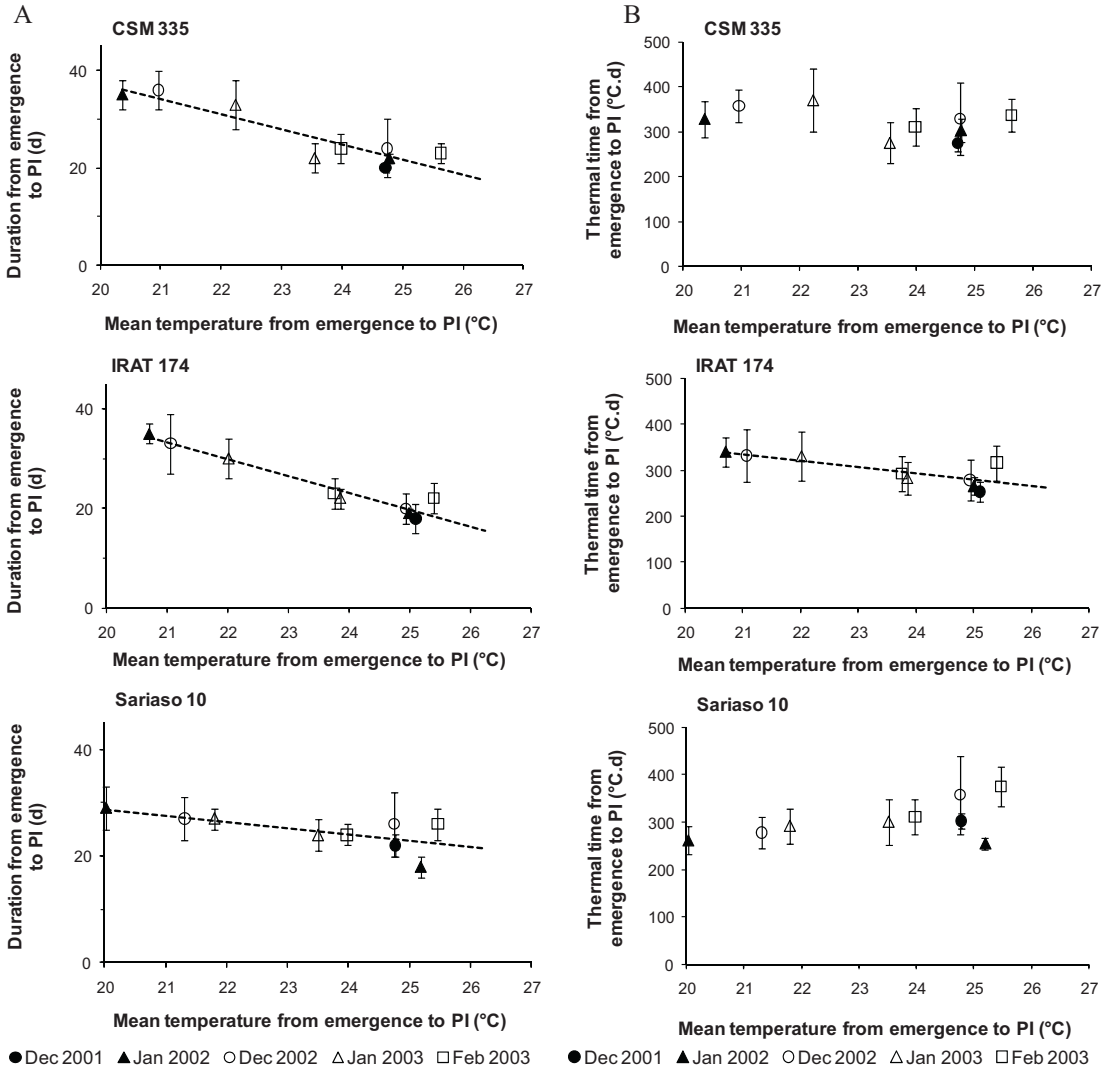

Fig. 6. Duration of the vegetative phase (A) in days and (B) in thermal time of 3 sorghum varieties grown in the greenhouse in relation to the average apex temperature from emergence to the date of panicle initiation. Monthly sowings were done simultaneously in 2 series from December 2001 to March 2002 (closed symbols) and from December 2002 to February 2003 (open symbols). Error bars indicate the asymptotic 95% confidence interval.

the potting soil in the 2 years of their common study, in 2002–2003 and 2006–2007.

Large average numbers of tillers were produced in field conditions by the 3 varieties, but CSM 335 produced more than the others (Table 5). Like for the duration of the vegetative phase, the number of tillers varied much with year. It also varied with month, decreasing regularly for sowings from December to February in field soils, and less regularly in more fertile soils. Prostrate forms were the rule for CSM 335 and IRAT 174 sown in the field in December and January in any of the 3 soils but were never encountered with Sariaso 10.

3.4. Comparative patterns of plants grown in pots in the field or in the greenhouse under similar temperatures

Since soil fertility has modified the development and growth of the plants grown in the field, the comparison between plants grown in the field or in the greenhouse under similar temperatures had to be established between plants in buried pots in the field and plants in pots in the cold compartment of the greenhouse. It was shown earlier that temperatures had been close between these 2 environments or even a little colder in the greenhouse. Since little variation in the recorded patterns was observed during the 2 years of experimentation in the greenhouse, opposite the situation registered in the field, it was assumed that means in the greenhouse were independent from year and could be extrapolated to 2006–2007.

The average durations to panicle initiation have been much longer in pots grown in the field than in the cold greenhouse compartment, with a larger difference in 2006–2007 because of the longer durations in the field in that year (Table 2). Since the durations in both days and thermal time were little variable in the cold compartment of the greenhouse, the variability of the differences between both treatments has been created by the variability in the field environment (Fig. 5).

The average phyllochrons have been a little longer in the cold compartment of the greenhouse than in the field, except in January 2002 (Table 3). They have varied more with sowing month and variety in the greenhouse than in the field.

The average numbers of leaves have been much higher in the field than in the cold greenhouse, in relation to the variation of the duration of the vegetative phase (Table 4). They have varied more in the field than in the cold greenhouse with year and sowing month.

The average numbers of tillers have been much higher in the field than in the cold greenhouse (Table 5). In both environments, the numbers of tillers were higher in 2001–2002 than in 2002–2003, decreased from December to February sowings, and

Table 3
Estimations of initial phyllochrons (°C d) (set up at plant emergence), by variety, sowing date, and treatment, with their confidence intervals and their means by factors × treatments.

Variety	Sowing month and year	Field soil	Warm greenhouse	Cold greenhouse	Buried pot	Potting soil
CSM 335	Dec 2001	46 ± 1	42 ± 1			
	Jan 2002	48 ± 2	43 ± 1	33 ± 1		
	Feb 2002	46 ± 1			38 ± 2	
	Mar 2002	42 ± 2		50 ± 4		
	Dec 2003	42 ± 1	44 ± 1	41 ± 1	30 ± 1	
	Jan 2003	46 ± 1	47 ± 2	51 ± 2	28 ± 1	
	Feb 2003	47 ± 2	47 ± 1	44 ± 1	42 ± 1	38 ± 2
	Dec 2006	33 ± 1			36 ± 1	31 ± 1
	Jan 2007	42 ± 2			35 ± 1	32 ± 1
	Feb 2007	43 ± 2			34 ± 1	34 ± 1
IRAT 174	Dec 2001	45 ± 3	46 ± 2			
	Jan 2002	42 ± 1	47 ± 1	32 ± 1		
	Feb 2002	41 ± 1			34 ± 2	
	Mar 2002	38 ± 1		56 ± 2		
	Dec 2003		49 ± 4	36 ± 2	32 ± 1	
	Jan 2003	44 ± 1	51 ± 2	42 ± 2	32 ± 1	
	Feb 2003		48 ± 1	46 ± 1	45 ± 1	38 ± 1
	Dec 2006	36 ± 1			32 ± 1	32 ± 1
	Jan 2007	45 ± 1			31 ± 1	33 ± 2
	Feb 2007	41 ± 1			33 ± 1	31 ± 1
Sariaso 10	Dec 2001	46 ± 3	44 ± 1			
	Jan 2002	46 ± 1	43 ± 1	28 ± 1		
	Feb 2002	43 ± 1			31 ± 3	
	Mar 2002	37 ± 2		51 ± 1		
	Dec 2003		46 ± 4	32 ± 1	37 ± 2	
	Jan 2003	43 ± 1	49 ± 2	45 ± 2	31 ± 1	
	Feb 2003		46 ± 2	43 ± 1	45 ± 1	37 ± 1
	Dec 2006	37 ± 1			35 ± 1	36 ± 1
	Jan 2007	41 ± 1			36 ± 1	44 ± 2
	Feb 2007	41 ± 2			33 ± 1	32 ± 1
Means	Global	43	46	39	35	35
	2001–2002	45	44	31	34	
	2002–2003	45	48	42	36	38
	2006–2007	40			34	34
	Dec	41	45	36	34	33
	Jan	44	47	39	32	36
	Feb	43	47	44	37	35
	CSM 335	44	45	42	35	34
	IRAT 174	42	49	39	34	33
	Sariaso 10	42	46	37	35	37

were higher for variety CSM 335 than for others. Rosettes developed in the field for varieties CSM 335 and IRAT 174 sown in December and January but never in the greenhouse and never for Sariaso 10.

4. Discussion

4.1. Flowering and growing responses to cold night temperatures in the greenhouse

The low night temperatures in the cold compartment of the greenhouse, where all factors were equal with the warm compartment except night temperature, did not cause any specific variation in the thermal time to panicle initiation of the 3 sorghum varieties in inductive short-day, cool-season conditions from December to February sowings (Fig. 5). These results contradict the hypothesis of Bezot (1963), Miller et al. (1968), and Vaksmann et al. (1997): cold night temperatures in inductive short days would only delay flowering proportionally to the mean temperature decrease that they induce, but they do not cause large increases in the thermal duration of the vegetative phase. They can appear contradictory to those of Caddel and Weibel (1971), Quinby et al. (1973), Yan and Wallace (1996), Ellis et al. (1997), and Yin (2008). However, the conclusions of these other studies would have changed if growth duration had been expressed in thermal time (Tbase = 11 °C). Fundamentally, these experiments in growth chambers have shown a conservative duration of the vegetative phase under inductive photoperiods within a range of mean temperatures that cover the natural conditions, from 12 to 27 °C. It is only under a higher temperature regime that stability was lost and thermal time to flowering increased linearly between 27 and 30 °C.

Thus, the stability of the vegetative phase observed in the greenhouse in short days within a range of mean temperatures of 21–27 °C has finally been in agreement with previous observations. Similarly, the stability of the vegetative phase for sowings done in the greenhouse from December to February also agreed with the observations previously reported from experiments in controlled environment: below a critical threshold, variations in the photoperiod do not affect the duration of the vegetative phase (Major, 1980). Plants sown in February initiated around 5 March when astronomical and civil daylength lasted 11 h and 54 min and 12 h and 38 min, respectively. The critical threshold for the 3 varieties is consequently above these values.

The phyllochrons have been much more variable between years in the cold than in the warm compartment of the greenhouse. In particular, they have been shorter in the cold compartment for the 3 varieties sown in January 2002 and for 2 varieties in December 2002. This acclimation of the phyllochron to the temperature has already been reported and was thus expected in the sowings of December and January (Kirby, 1995; Birch et al., 1998). Such acclimation did not happen in January 2003 because the minimum night temperature was above 20 °C from 13 to 28 January 2003 at emergence of the plants sown on 6 January. CSM 335 sown on 2 December 2002 reacted similarly to the warmer period between

Table 4
Estimations of total number of leaves on the main stem, by variety, sowing date, and treatment, with their confidence intervals and their means by factors × treatments.

Variety	Sowing month and year	Field soil	Warm greenhouse	Cold greenhouse	Buried pot	Potting soil
CSM 335	Dec 2001	26.4 ± 0.4	13.3 ± 0.3			
	Jan 2002	28.8 ± 2.4	13.7 ± 0.3	16.5 ± 1.0		
	Feb 2002	37.7 ± 1.9			23.3 ± 6.4	
	Mar 2002	38.4 ± 1.1		21.0 ± 2.6		
	Dec 2002	17.0 ± 2.4	13.3 ± 1.9	14.9 ± 0.6	17.3 ± 4.0	
	Jan 2003	16.9 ± 0.9	11.1 ± 0.7	12.9 ± 1.2	20.3 ± 0.6	
	Feb 2003	25.9 ± 3.1	12.8 ± 0.5	12.8 ± 0.7	21.3 ± 1.9	20.2 ± 2.2
	Dec 2006	27.0 ± 0.0			26.0 ±	29.0 ±
	Jan 2007	32.2 ± 2.7			28.0 ± 1.4	31.0 ± 1.0
	Feb 2007	46.7 ± 2.5			28.5 ± 1.2	26.4 ± 1.1
IRAT 174	Dec 2001	24.1 ± 0.5	12.3 ± 0.8			
	Jan 2002	21.0 ± 0.8	12.7 ± 0.3	17.4 ± 0.6		
	Feb 2002	19.8 ± 1.8			16.7 ± 0.4	
	Mar 2002	20.4 ± 0.7		20.7 ± 0.7		
	Dec 2002		10.8 ± 0.4	15.6 ± 1.3	17.5 ± 1.1	
	Jan 2003	15.3 ± 0.5	10.7 ± 0.4	13.8 ± 1.0	18.1 ± 0.8	
	Feb 2003		12.0 ± 0.5	11.8 ± 0.6	16.5 ± 0.8	16.2 ± 0.4
	Dec 2006	23.2 ± 1.9			20.8 ± 0.6	22.6 ± 0.9
	Jan 2007	23.3 ± 0.6			24.3 ± 1.2	25.4 ± 0.9
	Feb 2007	20.2 ± 0.5			20.9 ± 0.4	22.5 ± 0.5
Sariaso 10	Dec 2001	19.9 ± 2.7	13.7 ± 0.3			
	Jan 2002	19.9 ± 0.7	13.0 ± 0.4	15.6 ± 0.7		
	Feb 2002	23.1 ± 1.2			22.5 ± 2.0	
	Mar 2002	24.7 ± 1.5		19.4 ± 0.7		
	Dec 2002		13.6 ± 1.4	15.0 ± 0.8	15.0 ± 2.0	
	Jan 2003	16.9 ± 0.5	11.4 ± 0.7	12.0 ± 0.5	18.4 ± 0.3	
	Feb 2003		14.2 ± 0.4	12.9 ± 0.6	19.4 ± 0.9	18.1 ± 0.9
	Dec 2006	24.0 ± 1.7			18.2 ± 0.7	20.2 ± 1.2
	Jan 2007	25.0 ± 1.0			21.5 ± 1.2	22.3 ± 1.9
	Feb 2007	26.6 ± 1.8			23.7 ± 1.1	24.9 ± 1.0
Means	Global	24.4	12.6	14.3	20.9	23.2
	2001–2002	24.5	13.1	16.5	20.8	
	2002–2003	18.4	12.2	13.5	18.2	18.2
	2006–2007	27.6			23.5	24.9
	Dec	23.1	12.8	15.1	19.1	23.9
	Jan	22.1	12.1	14.7	21.8	26.2
	Feb	28.6	13.0	12.5	21.4	21.4
	CSM 335	29.7	12.8	15.6	23.5	26.7
	IRAT 174	20.9	11.7	15.8	19.3	21.7
	Sariaso 10	22.5	13.2	15.0	19.8	21.4

9 and 17 December. Due to this absence of acclimation, the daily appearance of the leaves of these non-acclimated plants decreased a lot when colder periods came back (data not shown). Such a reaction fully agreed with the concept of a stable phyllochron set up at emergence in response to the prevailing environment (Mc Master and Wilhelm, 1995).

Lastly, the study clearly showed that cold night temperatures in the greenhouse were not a sufficient factor to induce the rosette forms expressed in short-day cool-season field sowings.

4.2. Flowering and growing responses to soil fertility and container

Since experiments in the greenhouse had been carried out in 10-l pots filled with a soil–compost mixture in order to ensure good nutritional quality in spite of the reduced soil volume, it appeared that the possible effect of this factor had to be checked. The higher soil fertility of potting soils decreased vegetative phase duration, the phyllochron, and the number of leaves while the number of tillers was little affected. Soil fertility has previously been shown to affect plant phenology, with, for example, phosphorus deficiencies increasing plastochron, phyllochron, and vegetative phase duration in wheat (Rodriguez et al., 1998) and in maize (Plénet et al., 2000). The absence of an effect of higher fertility on tillering showed that it was mainly the phyllochron, set up at plant emergence, that was affected. As a consequence, the tillers of plants in low-fertility conditions started to emerge later but during a longer period, and reached a similar total number.

The lengthening of the vegetative phase in the less fertile soil of the field had a dramatic consequence for variety CSM 335 sown in February or March: if plants did not reach panicle initiation before about the end of April, the photoperiod was then beyond the threshold and flowering initiation was delayed until July or August (Clerget et al., 2004). This threshold effect explains the very large variability in the duration to panicle initiation of February sowing, between 62 and 152 days. However, no such soil fertility or agronomic environment variation could be responsible for the long vegetative-phase durations observed on sowings between November and January, since some varieties show a total absence of variation in the duration of the vegetative phase in response to these sowing dates (Dingkuhn et al., 2008).

4.3. Flowering and growing responses in the field vs. greenhouse

When grown in similar pots, plants of the 3 varieties had longer vegetative phases, in both days and thermal time, shorter phyllochrons, more leaves, and more tillers in the field than in the cold compartment of the greenhouse. The differences between the 2 environments have always been larger for the more photoperiod-sensitive variety CSM 335. This variety and IRAT 174 developed prostrate forms in the field but never in the greenhouse.

The differences in development and growth observed between plants grown either in the field or in the greenhouse imply that the greenhouse itself has been responsible for these modifications. One obvious difference between greenhouse- and field-sown plants is the glass and structure covering the greenhouse, which reduce the

Table 5
Estimations of number of tillers produced by plant by variety, sowing date, and treatment, with their confidence intervals and their means by factors × treatments.

Variety	Sowing month and year	Field soil	Warm greenhouse	Cold greenhouse	Buried pot	Potting soil
CSM 335	Dec 2001	5.8 ± 0.7	2.2 ± 0.4			
	Jan 2002	6.0 ± 0.6	2.9 ± 0.2	4.1 ± 0.4		
	Feb 2002	3.3 ± 0.6			2.6 ± 0.3	
	Mar 2002	3.7 ± 0.5		2.3 ± 0.5		
	Dec 2002	3.1 ± 0.9	3.7 ± 0.9	4.8 ± 0.9	7.0 ± 6.1	
	Jan 2003	3.0 ± 0.6	2.9 ± 1.0	2.2 ± 0.5	4.0 ± 0.4	
	Feb 2003	4.4 ± 0.5	0.6 ± 0.5	1.3 ± 0.6	4.9 ± 0.6	4.1 ± 0.6
	Dec 2006	6.5 ± 1.4			5.7 ± 6.4	5.4 ± 1.7
	Jan 2007	6.3 ± 0.7			7.7 ± 1.5	8.4 ± 1.2
	Feb 2007	4.5 ± 0.6			4.8 ± 0.6	5.2 ± 0.4
IRAT 174	Dec 2001	5.1 ± 0.4	0.2 ± 0.4			
	Jan 2002	3.9 ± 0.8	0.0 ± 0.0	2.5 ± 0.3		
	Feb 2002	1.3 ± 0.5			1.0 ±	
	Mar 2002	1.2 ± 0.7		0.2 ± 0.2		
	Dec 2002		1.2 ± 1.0	3.2 ± 0.7	3.5 ± 0.7	
	Jan 2003	0.2 ± 0.2	0.2 ± 0.3	1.8 ± 0.6	3.0 ± 0.4	
	Feb 2003		0.3 ± 0.3	0.2 ± 0.2	2.3 ± 0.7	1.7 ± 0.6
	Dec 2006	4.0 ± 1.7			4.0 ± 1.0	4.0 ± 1.3
	Jan 2007	4.2 ± 0.7			4.4 ± 0.9	4.2 ± 0.9
	Feb 2007	2.0 ± 0.5			2.4 ± 0.5	2.9 ± 0.5
Sariaso 10	Dec 2001	4.7 ± 0.9	0.8 ± 0.5			
	Jan 2002	4.1 ± 0.7	1.3 ± 0.4	2.9 ± 0.6		
	Feb 2002	1.4 ± 0.7			1.3 ± 1.0	
	Mar 2002	2.7 ± 0.3		0.5 ± 0.6		
	Dec 2002		2.3 ± 0.9	4.0 ± 0.8	3.3 ± 1.5	
	Jan 2003	0.8 ± 0.6	0.4 ± 0.5	1.2 ± 0.7	3.4 ± 0.8	
	Feb 2003		0.0 ± 0.0	0.5 ± 0.4	3.0 ± 0.7	1.8 ± 0.8
	Dec 2006	4.3 ± 0.9			4.2 1.2	4.4 ± 2.3
	Jan 2007	4.8 ± 2.6			4.2 1.0	5.7 ± 1.0
	Feb 2007	1.8 ± 0.8			3.2 0.4	3.9 ± 0.5
Means	Global	3.7	1.3	2.4	3.8	4.3
	2001–2002	4.0	1.2	3.2	1.6	
	2002–2003	2.3	1.3	2.1	3.8	2.5
	2006–2007	4.3			4.5	4.9
	Dec	4.8	1.7	4.0	4.6	4.6
	Jan	3.7	1.3	2.5	4.4	6.1
	Feb	2.7	0.3	0.7	2.8	3.3
	CSM 335	4.8	2.5	3.1	5.2	5.8
	IRAT 174	3.0	0.4	1.9	2.9	3.2
	Sariaso 10	3.1	1.0	2.2	3.2	3.9

visible light received by the plant canopy on average to about 70% (Warren Wilson et al., 1992). The fraction of transmitted light is further reduced in mornings and evenings due to the light angle, and this reduction in the quantity of light modifies the time of the light on and off perceived by plants at dawn and dusk. It can be estimated that the photoperiod reductions in mornings and evenings were both about 5 min in Samanko, assuming that transmittance was 50% at twilight and that the $\log_{10}$ of the light intensity decreased, from 3 to 0.2 mW m^{-2} nm^{-1}, proportionally with time during the twilight duration that lasted some 20 min (Salisbury and Ross, 1985). Consequently, the perceived photoperiod in the greenhouse was constantly about 10 min shorter than in the field. However, the vegetative phase of greenhouse plants sown from December to February was constant when measured in thermal time, whereas the external photoperiod at panicle initiation varied from 11 h and 30 min (25 January) to 11 h and 54 min (5 March). Thus, a 10-min difference in the perceived photoperiod between field and greenhouse plants would not likely induce the large differences observed for time to panicle initiation of CSM 335 and IRAT 174, when the 24-min difference between 25 January and 5 March panicle initiation in the greenhouse did not produce any at all.

The greenhouse glass itself has also modified the light quality perceived by plants in a way that can change their photoperiodic reaction. It has been verified that the glass of the greenhouse used had a usual absorption spectrum with good transparency in the visible radiation from 400 to 800 nm and beyond (Fig. 1) but high filtering of a large part of UV-A (315–400 nm) and complete opacity to UV-B (280–315 nm).

In *Arabidopsis*, UV-A is absorbed by 8 of the 11 now described photoreceptors and this modified development and growth, including flowering time (Kami et al., 2010). The effects of UV-B on plant morphogenesis and flowering time have been shown by many authors on many species, with either a natural or increased dose (Deckmyn and Impens, 1995; Sampson and Cane, 1999; Meijkamp et al., 2001; Jansen, 2002; Hectors et al., 2007). The protein UVR8, which interacts with the cellular circadian rhythms (Fehér et al., 2011), has been recently recognized as a UV-B photoreceptor (Rizzini et al., 2011). The sum of evidence of the action of UV-A and UV-B on plant development has recently led to the use of a "UV-transmissible" glass to renew the cover of the Grand Pavilion at Berlin's Botanical Garden (DuPont, 2009). UVs will thus be responsible for the delayed flowering and prostrate forms observed in the field in Samanko. Moreover, they would mediate a cue different from the photoperiod, with a strong contrast between October, when the vegetative phase of photoperiod-sensitive varieties sown in the field was the shortest, and November, when this vegetative phase was longer, sometimes dramatically so (Clerget et al., 2004).

A first hypothesis could be that UV radiation caused a flowering delay and morphogenesis changes in the field when they interacted with cold night temperature, either through a morning effect (since temperature increases fast after sunrise) or through the longer life duration of leaves. In Bamako, daily minimum temperatures experienced by October and November sowings were effectively contrasting; indeed, minimum temperatures decrease regularly in November; thus, plants sown in October could not be affected by colder night temperature with panicle initiation before November

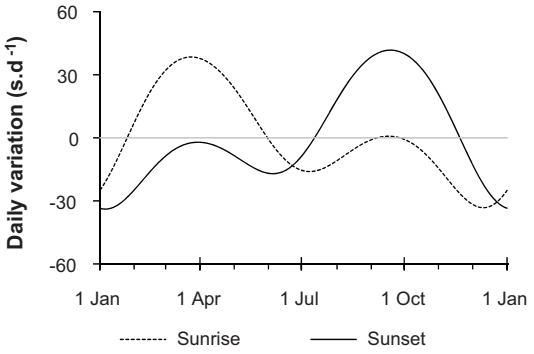

Fig. 7. Annual evolution of daily variations in sunrise and sunset hours in Samanko.

15. In contrast, sowings done in November and December were exposed to low minima of December and January. However, the fact that the lengthening of the vegetative phases observed in Puerto Rico (Miller et al., 1968), in the absence of really cold temperature, was as high as in Chad (Bezot, 1963) and in Bamako (Dingkuhn et al., 2008), that rosettes were observed under warm night temperature but inadequate light quality (Clerget, 2004), and that the duration of the flowering delay during winter sowings was linked to the rate of photoperiod-sensitivity during summer sowings tends to discard this hypothesis to the benefit of a second one, which is supported by many arguments.

The daily variation in the sunset hour clearly satisfies this required condition: it goes from positive to negative values on 19 November in Bamako, sufficiently late not to interact with the early panicle initiation of plants sown in October and only a few days after the emergence of plants sown in November (Fig. 7). The daily variations in sunrise and sunset hours have been presented as the possible cues for periodic flowering time of trees at the equator, where daylength is stable throughout the year (Borchert et al., 2005). These 2 daily variations have simultaneously low negative values (sunrise and sunset happen later from one day to the next) from 19 November to 25 January in Bamako, which is a unique situation in the year. A comparable seasonal effect, involving UV-B radiation, has previously been shown in *Rosmarinus officinalis* by Grammatikopoulos et al. (2001). Plants of this species produced more flowers in autumn than checks and fewer flowers in winter under a natural UV-B dose reduced by Plexiglas filters. In this experiment, the UV-B effect on the number of flowers on the stem reversed on 27 December, which would be compatible with a reversion of the signal controlling flower initiation occurring 21 days before, when daily variation in the sunset hour becomes negative in Patras, Greece.

Other knowledge recently acquired on the physiological pathways to the triggering of flowering also supports the hypothesis of a response to the variations in sunrise and sunset time: cells have rhythmic activities controlled by a circadian clock, which is a central component of the flowering pathway. This circadian clock is reset daily at dawn and dusk, which are perceived and mediated by the photoreceptors (Amasino, 2010). Consequently, the perception of daylength relies on adjustments of the phase angle of circadian rhythms relative to the light/dark cycle, rather than on the measurement of the absolute duration of light and darkness (Roden et al., 2002). Moreover, there is not only one clock, but two circadian oscillators in *Arabidopsis*, as previously reported in insects and mammals (Michael et al., 2003), and, in *Pharbitis*, a short-day dicotyledonous plant, it is a circadian rhythm set by dusk that promotes flowering (Hayama et al., 2007).

Based on these different observations and knowledge, including the conservation of the photoperiod responses within the plant kingdom, it is thus hypothesized that photoperiod-sensitive sorghum sown in winter months would flower late because the delayed sunrise and sunset hours from one day to the next inhibit the triggering of its flowering and modifies its morphogenesis. This effect of this variation in hours is effective only if the UV-A and/or UV-B components of sunlight can be received by plants since it could not be recorded within a greenhouse covered with conventional glass and probably under sandy winds. In fact, the near absence of any delay in flowering initiation in the field in 2002–2003 is highly questionable because, in contrast, low inter-annual variability of the sunlight cue is expected. Such a pattern would tend to argue in favor of a crossed effect between UV radiation and night temperatures, which were alternately warmer and colder at least for sowing done in December, whereas they remained more stably cold in December and January of the other seasons. However, another factor, sandy wind, was responsible for the warmer temperatures experienced in 2002–2003: in sub-Saharan countries, eastern sandy winds blow during the first part of the year, with year-to-year variable dates, strength, and sand load. Clear and calm nights are colder, whereas sandy aerosols block infra-red emissions and cause warmer nights when the wind continues to blow from the east as in December 2002 and January 2003. Dust aerosols also absorb and scatter the sunlight, at a much higher rate in mornings and evenings (Niu and Zhang, 2010), with scattering albedo coefficients between 0.65 and 0.95 for wavelengths from 300 to 800 nm (Lafon et al., 2006). The early sandy winds that occurred during the 2002–2003 experiments thus strongly filtered the morning and sunset light, including UVs, which would have disturbed the perception by plants of the exact sunrise and sunset times.

The conclusion of these experiments is that, apart from daylength, the flowering time and plant morphogenesis of photoperiod-sensitive sorghum varieties would also be influenced by the daily variation in sunrise and/or sunset hours. The variations in the duration of the vegetative phase of late photoperiod-sensitive varieties of tropical species that were monthly sown throughout the year could not be linearly correlated with daylength. To improve the relationships, a daylength threshold above which flowering was inhibited has been added as proposed by Carberry et al. (2001) on pigeon pea, and then it was proposed that this photoperiod threshold would increase with the age of the plant (Dingkuhn et al., 2008; Folliard et al., 2004) and lastly that the daily variation of the daylength was examined as a co-factor of daylength in sorghum (Clerget et al., 2004) and in yam (Ile et al., 2007). None of these models fitted the data perfectly. Daily variations in sunrise and sunset hours now need to be tested as possible co-factors of the daylength.

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