

Variability of Phyllochron, Plastochron and Rate of Increase in Height in Photoperiod-sensitive *Sorghum* Varieties

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• **Background and Aims** West African sorghum (*Sorghum bicolor*) varieties are generally highly photoperiod-sensitive, which is a necessary adaptation to the variable onset date of the rainy season and the variable dates of sowing in the savannah zone. Depending on sowing date, plants can produce from 12 to >40 leaves on the main culm, with height varying from 1 m to more than 5 m. The present study aimed to better understand the complex phenology of these variables.

• **Methods** A 2-year series of monthly sowings of three West African sorghum varieties was conducted near Bamako, Mali. Drought stress was avoided by supplemental irrigation. Rate of initiation of primordia at the stem apex was recorded, together with rate of leaf emergence and increase in plant height.

• **Key Results** Leaf initiation and appearance rates (plastochron⁻¹ and phyllochron⁻¹) were constant for a given sowing date in cases where less than 20 leaves were produced (generally observed with late sowing dates). In contrast, rates were bilinear for early sowing dates, for which plants produced more than 20 leaves. The secondary rates, which occurred from the 20th leaf onwards, were only half of the initial rate. Plastochron and phyllochron showed large variations among sowing dates, and were correlated with the rate of plant height increase. The initial plastochron and phyllochron were positively correlated with soil temperature and negatively correlated with both day length and day-to-day change of day length prevailing at plant emergence, but these factors explained only half of the variation observed.

• **Conclusions** Although they belong to different genetic groups and have different height and photoperiod sensitivity, the three varieties studied exhibited similar response patterns of development rates among phenological phases and seasons, with the local landrace showing the greatest variation due to its longer vegetative phase and longer stem internodes. The possible adaptive advantages in African savannah environments of bilinear development rates and the associated limitation in height increase are discussed.

Key words: *Sorghum bicolor*, phenology, plastochron, phyllochron, photoperiod, stem growth.

INTRODUCTION

The West African landraces of sorghum (*Sorghum bicolor*) cropped under rainfed field conditions during the summer monsoon, from May–June to September–October, are generally highly photoperiod-sensitive (Grenier *et al.*, 2001). This trait is an adaptation to environments where the rainy season is substantially longer than the basic growth cycle of the plant, i.e. the crop duration observed when flowering is not delayed by photoperiod. The effective crop duration expressed in thermal time, which is the time perceived by the plant, increases as latitude decreases. It has been observed that flowering of locally adapted landraces coincides with the end of the rainy season, which means that varieties adapted to the Sudan and Guinea savannah zones are late-maturing, with durations to flowering longer than 100 d, caused by photoperiod sensitivity (Curtis, 1968; Andrews, 1973). Due to this mechanism, maturing grains escape pest and disease pressures associated with the rainy season, such as moulds, insects and birds. On the other hand, farmers cannot sow their entire crop area at once due to labour limitation and the need for early weeding, and sowing dates are commonly spread

over 1 month following the onset of the rainy season. Farmers thus require varieties that flower at the end of the rainy season regardless of sowing date. The crop's life cycle can therefore vary greatly between sowing dates (Clerget *et al.*, 2004). Several studies have been published on the determination of the flowering date of West African landraces, but the consequences of the variable duration of the vegetative phase on plant development and height dynamics are still poorly documented. The only substantive research on this aspect of sorghum physiology is that of Goldsworthy (1970*a, b*), but is limited to a narrow range of sowing dates in May.

Wilhelm and McMaster (1995) defined phyllochron as the time elapsing between the visual appearance of two successive leaf tips, and the plastochron as the time elapsing between the production of two successive phytomers at the growing point. Rickman and Klepper (1995) reviewed available information on these processes in grasses. The concept of plastochron and phyllochron is based on the fact that the production rate of new phytomers is often found to be nearly constant from seedling stage to flag-leaf expansion when expressed in thermal time units (°Cd, degree-days) in wheat (Gallagher, 1979; Bauer *et al.*, 1984), barley (Kirby *et al.*, 1982; Ellis and Russell,

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1984), maize (Birch *et al.*, 1998), sorghum (Muchow and Carberry, 1990; Birch *et al.*, 1998; Craufurd *et al.*, 1998) and millet (Craufurd and Bidinger, 1988).

The corollary of the concept of a constant rate of leaf production is that the rate is not continuously affected by the environment. It depends, however, on the sowing date in wheat and barley (Baker *et al.*, 1980; Ellis and Russell, 1984; Kirby *et al.*, 1985; Miralles *et al.*, 2001), and is therefore set early in the life cycle, probably by environment factors at the time of seedling emergence. In sorghum, phyllochron has been described as being independent of sowing date by some authors (Muchow and Carberry, 1990; Craufurd and Qi, 2001), but Vaksman *et al.* (1998) observed phyllochrons from 45 to 57°Cd leaf⁻¹ for sowing dates between the end of June and the beginning of August for a sorghum variety of the *guinea* race, 'CSM 388', in Bamako, Mali.

Temperature has been suggested to be the major factor influencing the phyllochron. Studies conducted under constant temperature have shown that the phyllochron (expressed in °Cd leaf⁻¹) increases steadily with temperature from 7.5 to 25 °C in wheat (Cao and Moss, 1989) and from 12.5 to 27.5 °C in barley (Tamaki *et al.*, 2002), while in maize and sorghum the phyllochron remains stable at temperatures from 10–18 to 30 °C, but increases at higher temperature (Tollenaar *et al.*, 1979; Warrington and Kanemasu, 1983; Craufurd *et al.*, 1998). In maize, Birch *et al.* (1998) concluded from several field experiments that the phyllochron is correlated with the mean temperature from emergence to tassel initiation. However, various authors have shown that development rate is more closely associated with the soil temperature near the soil surface than with the air temperature during early stages of development (Bonhomme *et al.*, 1984; Jamieson *et al.*, 1995; Wilson *et al.*, 1995), and that the temperature of the apex, where new organs are developed, can significantly diverge from the air temperature measured at 2 m and is, in fact, similar to the soil temperature near the surface (Cellier *et al.*, 1993; Ben Haj Salah and Tardieu, 1996; Lafarge *et al.*, 1998). Consequently, the daily average soil temperature near the surface is similar to the average temperature of the apex, which in turn permits accurate estimation of plant development rate until the onset of the stem elongation. Thereafter, air temperature is an accurate predictor of development rate (Vinocur and Ritchie, 2001). These relationships hold true for plant development itself, i.e. the initiation of new leaves by the apex, but less reliably predict the rate of leaf appearance, which results from the dual process of apical development and leaf-blade elongation prior to tip appearance (McMaster *et al.*, 2003).

Apart from temperature, day length has been suggested to be responsible for different rates of leaf appearance observed for different sowing dates. Long photoperiods increase the rate of leaf appearance in wheat and barley (Masle *et al.*, 1989; Cao and Moss, 1991; Slafer *et al.*, 1994a) and maize (Warrington and Kanemasu, 1983). In contrast, long photoperiods decrease the rate of leaf appearance in quinoa (Bertero *et al.*, 2000). In other studies, a strong positive correlation between the rate of day-length change at crop emergence and the subsequently observed

rate of leaf appearance has been demonstrated for wheat and barley in southern England and Scotland (Kirby *et al.*, 1982; Ellis and Russell, 1984; Baker *et al.*, 1990). Leaf appearance rate was thus slow for autumnal sowings under decreasing days and accelerated for spring sowings. Slafer *et al.* (1994b), however, concluded from field experiments on wheat in southern Australia that phyllochron neither responded to the rate of day-length change nor to the average, absolute day length.

Lastly, radiation intensity in the field has been found to be negatively correlated with phyllochron in maize (Birch *et al.*, 1998) and to a lesser extent in wheat (Rawson, 1993). Bertero (2001) reported similar findings for quinoa varieties originating from temperate regions, whereas materials collected in the tropics were only responsive to photoperiod (but were insensitive to the rate of day-length change). In controlled environments under lower light intensities, Slafer (1995) found no effect of radiation on phyllochron in wheat.

An association between sorghum phenology and height increase has also been reported. Final plant height was observed to be strongly correlated with the duration of the vegetative phase for 22 contrasting varieties (Miller *et al.*, 1968). This relationship was related to the total number of internodes produced, as internodes of late-maturing varieties were found to be of constant final length (Bezot, 1963).

Renewed interest in local agro-biodiversity and current efforts of West African breeding programs to develop improved, photoperiod-sensitive sorghum varieties (Kouressy *et al.*, 1997) requires a better understanding of the interaction between photoperiod-dependent phenology (as affected by sowing date and latitude), crop morphology and yield components. This study sought to analyse the intra- and inter-annual variation of these phenological processes for three sorghum genotypes of contrasting phenology through field observations on crops sown on 26 successive monthly sowing dates.

MATERIALS AND METHODS

The three sorghum [*Sorghum bicolor* (L.) Moench] varieties used in this study were 'CSM 335' from Mali (Sorghum Collection of Mali), a tall, traditional, *guinea*-race landrace known to be highly photoperiod-sensitive; 'Sariaso 10', an improved *caudatum*, less photoperiod-sensitive line bred in Burkina Faso from a *guinea* × *caudatum* cross; and 'IRAT 174', a dwarf *kafir* × *durra*, photoperiod-sensitive line also bred in Burkina Faso. The ICRISAT Sorghum Breeding program in Bamako provided seeds of 'CSM 335', whereas the other seed came from the CIRAD Genetic Resources Unit in Montpellier, France.

Monthly sowings were initiated on 5 July 2000, followed by sowing on or about the 10th day of each successive month through to August 2002 at the ICRISAT research station in Samanko, Mali (12°34'N, 8°04'W, 330 m a.s.l.). For sowings from September to May, which required irrigation, the soil was a fine, loamy, Typic Haplaquets (USDA taxonomy; C:L:S ≈ 25:50:25

and $\text{pH}_{\text{H}_2\text{O}} = 4.5$) located close to the Niger River, and for sowings in the wet season from June to August the soil was a well-drained, fine, loamy, mixed, isohyperthermic, Plinthic Paleustalfs (C:L:S \approx 20:35:55 and $\text{pH}_{\text{H}_2\text{O}} = 5.0$). Possible differences in soil fertility between fields were minimized with fertilizer application (NPK at 128, 92 and 60 kg ha⁻¹ as urea, diammonium phosphate and KCl). Soil moisture was never limiting due to irrigation twice a week in the dry season, keeping the soil near field capacity. Plots consisted of four rows 5 m long, and were sown with 10 grains hill⁻¹ at 0.75 × 0.20 m spacing, and thinned to 3 plants hill⁻¹ 2 weeks after plant emergence and to 1 plant hill⁻¹ at the onset of stem elongation. A randomized block design with three replications was used during the rainy seasons (July and August 2000, June to August 2001), and no replication for all other sowing dates. Plant dissections were done in the three replications during the first rainy season and in one replication during the following seasons, after it had been established that inter-plot variability was low. Weeding was done by hand and insecticide was applied when infestation required it. Leaves of each plant of the two central rows were labelled. From emergence to panicle initiation, three plants per variety were sampled every week and dissected in order to count the number of leaves initiated on the apex and to measure the stem length. Panicle initiation was recorded when having indisputably occurred, after the initiation of the first branches. The plant stand was little affected by this sampling, since there were several additional plants per hill before the onset of the stem elongation and later only the main culm was harvested, leaving the tillers in place to maintain a continuous plant canopy on the plot. All three varieties had tillers when their vegetative phase was long. Ten plants per variety and per sowing date were specifically labelled and the following were recorded weekly on the main culm: number of leaves already emerged from the whorl, number fully exerted (ligulated) and senesced (>50% of the leaf blade area dead), and plant height at the intersection of the two latest-emerged leaves or at the collar of the flag-leaf. Depending on sowing date, the number of observations used to calculate development rate by linear regression varied from 53 to 282 for leaf appearance rate and from 16 to 56 for leaf initiation rate.

Calculation of day length and thermal time

Daily civil day length (sun 6° below the horizon at beginning and end of day) was calculated according to Keisling (1982) based on latitude and calendar date (Fig. 1E). Thermal time was calculated on an hourly basis using the shoot apex temperature estimated from soil and air temperature (see below). Cardinal temperatures were assumed to be 11, 34 and 52 °C for base, optimal and maximum temperatures, respectively. Published values for cardinal temperatures derived from leaf appearance rates are not uniform, probably due to genetic variation between tropical and temperate varieties. According to Alagarwamy and Ritchie (1991) T_b , T_{opt} and T_{max} were 8, 34 and 52 °C, respectively; according to Hammer *et al.*

(1993) they were 11, 30 and 42 °C; and Lafarge *et al.* (1998) reported 11 °C for T_b . In a pre-study conducted on leaf elongation rates in controlled environments for the three tropical varieties utilized here, cardinal temperatures of 11, 34 and 52 °C were found (Clerget *et al.*, 2004) and applied to all calculations in this study. 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).

Modelling shoot apex temperature for thermal-time calculations

Because systematic errors can result from using wrong reference temperatures for calculations of thermal time, extensive measurements were conducted of soil temperature at 10 and 2 cm below ground under crop canopies, as well as air temperature at 2 m, during different seasons. Throughout the experiment, air temperature and relative humidity at 2 m (sensor HMP45C, Vaisala, Helsinki, Finland), soil temperature at 10 cm depth, solar radiation (sensor PY, Li-Cor, Lincoln, NE, USA) and rainfall (tipping bucket by Young, Traverse City, MI, USA) were continuously measured at 1-min intervals, and averaged or summed on an hourly basis and stored in a data logger (21 X, Campbell Scientific, Shepshed, UK) at a weather station located not further than 800 m from the experimental fields (Fig. 1A–D).

The temperatures of air at 2 m and soil at 10 cm depth were also recorded within a plant row using the same methods during specific periods, namely from 12 January to 14 May 2001, 26 June to 10 December 2001, 16 January to 16 April 2002, 13 June to 3 September 2002 and 4 February to 14 May 2003. During the 2003 measurements, the soil temperature at 2 cm depth was also recorded using copper–constantan thermocouples installed at plant emergence and remaining in place until the end of the recording period.

An additional set of 1-year observations on temperature dynamics of the air at 2 m and the soil at 2 and 10 cm depth under a crop canopy was conducted in 2006–2007 (two replications). Between 8 March 2006 and 7 March 2007, monthly sowings of sorghum were used to observe these temperatures from 15 to 45 d after emergence. After each observation period, the system was transferred to the next newly sown plot.

Apex temperature was assumed to be equal to the soil temperature at 2 cm depth under a crop canopy until jointing, because during that period the apex is located near the soil surface. Thereafter, apex temperature was assumed to be equal to air temperature because stem elongation rapidly lifts up the apex. A similar approach was used by Dingkuhn *et al.* (1995) to characterize the phenology of rice.

The observations used to estimate soil temperature at 2 cm depth are summarized in Fig. 2. Two distinct seasonal patterns were observed for the relationship between surface-soil and air temperature (Fig. 2A). From December to the end of April the daily average temperatures were lower for the soil than for the air, whereas the opposite was true from May to November. The underlying diurnal dynamics

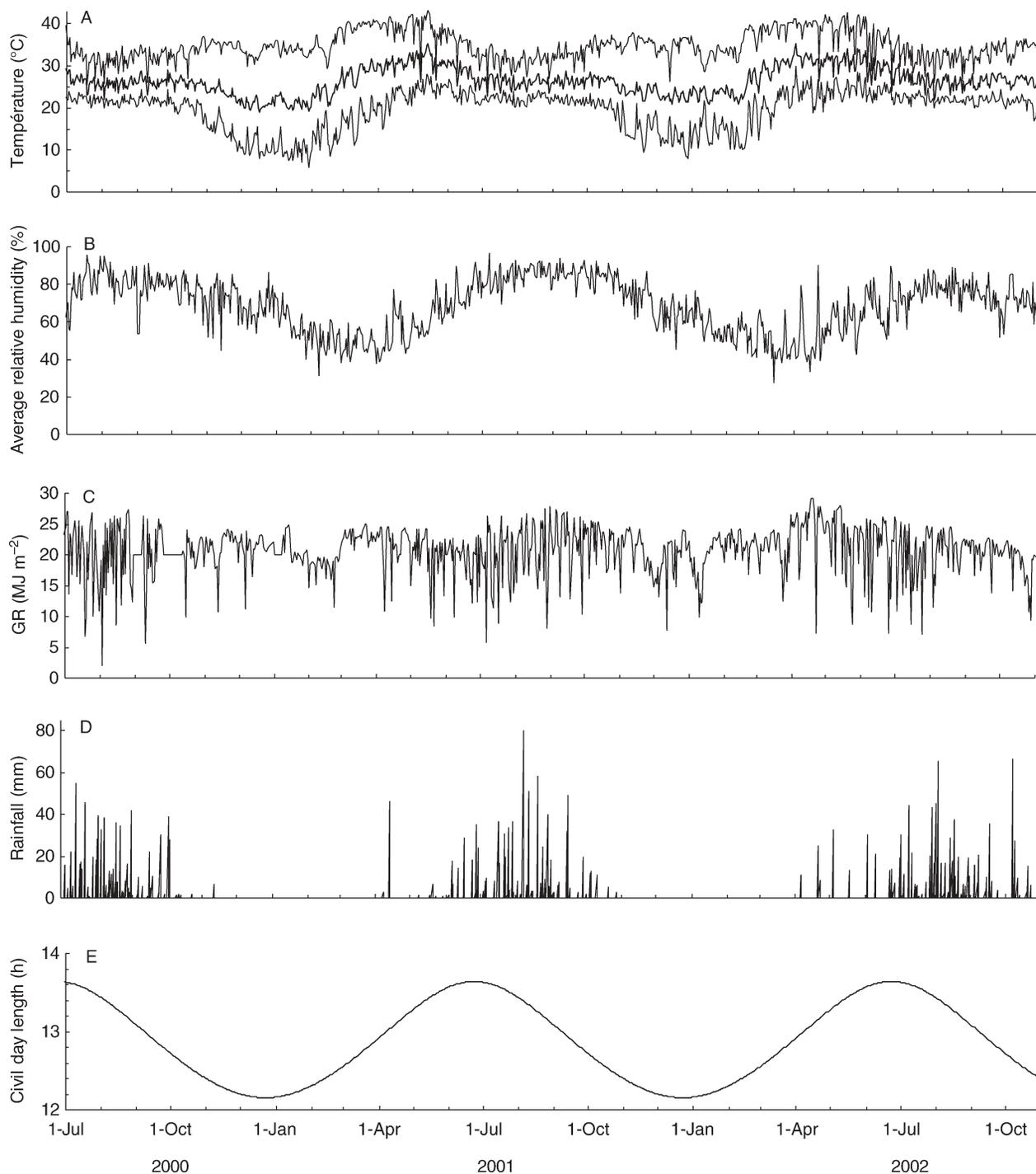


FIG. 1. Daily climatic conditions at the Samanko station from 1 July 2000 to 31 October 2002. (A) Minimal, maximal and average temperatures, (B) average relative humidity, (C) global radiation, (D) daily rainfall, and (E) civil day length.

are shown in Fig. 2(C, D) where a very dry and hot day in April (C) is compared with a humid and cool day in August (D). During the dry season, when plots were generally irrigated, soil temperature was cooler than air temperature, particularly in daytime, possibly due to the cooling effects of evaporation. Conversely, during the rainy season air temperature was lower than soil temperature throughout the

day and the night. The diurnal dynamics of the soil temperature at 2 cm and 10 cm depth were also different, but the difference between their daily averages was always smaller than 1 °C, with an annual average difference of only 0.01 °C.

Finally, the data from the various series recorded at Samanko station being very coherent, an empirical model

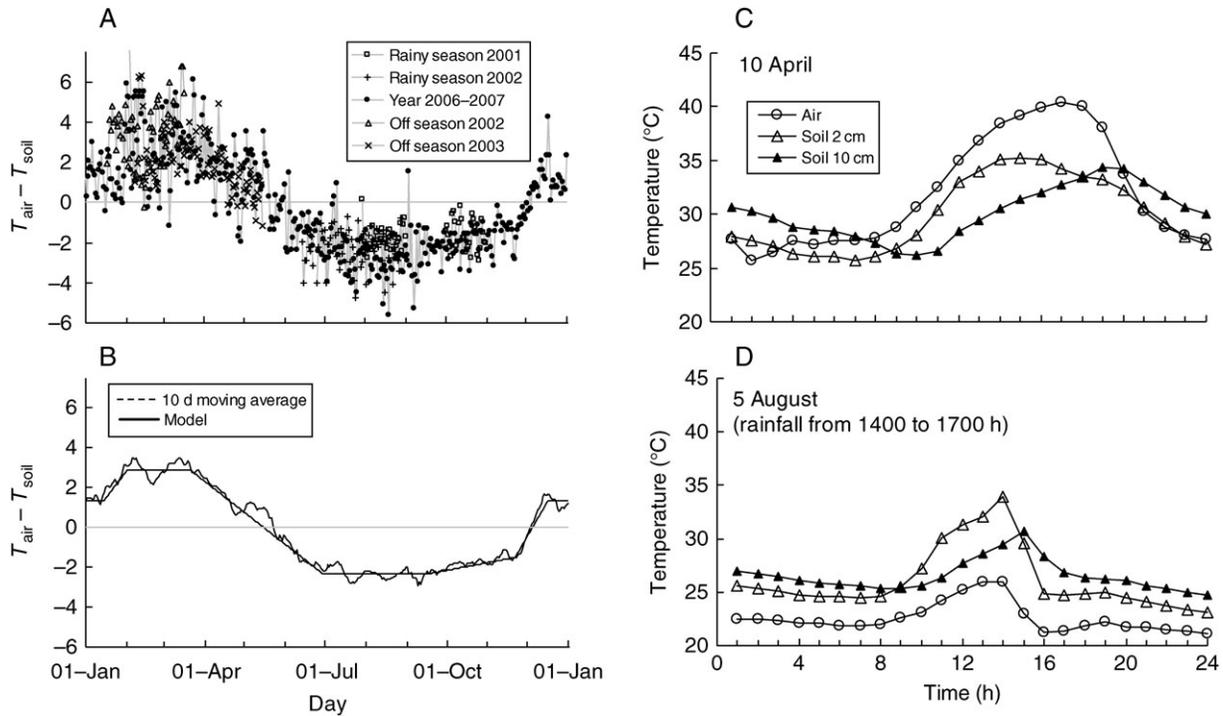


FIG. 2. (A, B) Differences between the daily air (2 m) and soil (10 cm depth) temperature during the year from data recorded in 2001, 2002, 2003 and 2006–2007 (A), and the 10-d common moving average, resulting in a model of the yearly dynamics (B). (C, D) Diurnal variation of air temperature, and soil temperature at 2 and 10 cm depth under a canopy of a 1-month-old sorghum crop for (C) a day in the dry and hot season (10 April 2006) and (D) a day in the rainy season (5 August 2006).

was established based on the 10-d moving average to predict the soil temperature from the air temperature when not recorded, by subtracting the simulated values Δ , (Fig 2B; jd = Julian day):

If $jd < 15$, then $\Delta = 1.37$

If $15 \leq jd \leq 32$, then $\Delta = 1.37 - [(2.87 - 1.37) / (32 - 15)] \times (jd - 15)$

If $32 \leq jd \leq 80$, then $\Delta = 2.87$

If $80 \leq jd \leq 180$, then $\Delta = 2.87 - [(2.87 + 2.35) / 100] \times (jd - 80)$

If $180 < jd \leq 258$, then $\Delta = -2.35$

If $258 < jd \leq 325$, then $\Delta = -2.35 + [(-1.5 + 2.35) / 63] \times (jd - 258)$

If $325 < jd \leq 350$, then $\Delta = -1.5 + [(1.37 + 1.5) / 25] \times (jd - 325)$

If $jd > 350$, then $\Delta = 1.37$

(1)

Figure 2B shows that the accuracy of the prediction of surface-soil temperature from air temperature was low when applied on a daily basis, but satisfactory on a monthly basis, which is the minimum duration of the vegetative phase observed for sorghum under field conditions.

For all calculations of thermal time, modelled soil temperature at 10 cm depth was used from crop establishment to onset of stem elongation, because the shoot apex is located at the level of the soil surface during these developmental stages. Thereafter, air temperature was used because the apex was located well above the soil surface. Figure 3 demonstrates for ‘CSM 335’ that this procedure resulted in slightly different dynamics of leaf appearance, as compared with the conventional method of using air temperature throughout. Importantly, the basic characteristics of phyllochron dynamics, namely their bilinearity (rapid leaf appearance rate before jointing and a slow one thereafter), were not affected by the choice of model.

Estimation of rates of development

Rate of development is defined here as the reciprocal of the thermal time elapsing between two development events, such as initiation, appearance or ligule emergence of two successive leaves on the main culm. This can also be expressed as the slope of leaf number vs. thermal time on linear portions of the relationship. As shown in the example in Fig. 4, dynamics of leaf appearance were generally linear, but sometimes showed an abrupt change in slope in mid-season. This was interpreted as a bilinear behaviour, consisting of an initial and a secondary, slower development rate.

Rates of leaf development were fitted to either linear or bilinear dynamics using a segmented model. Observed

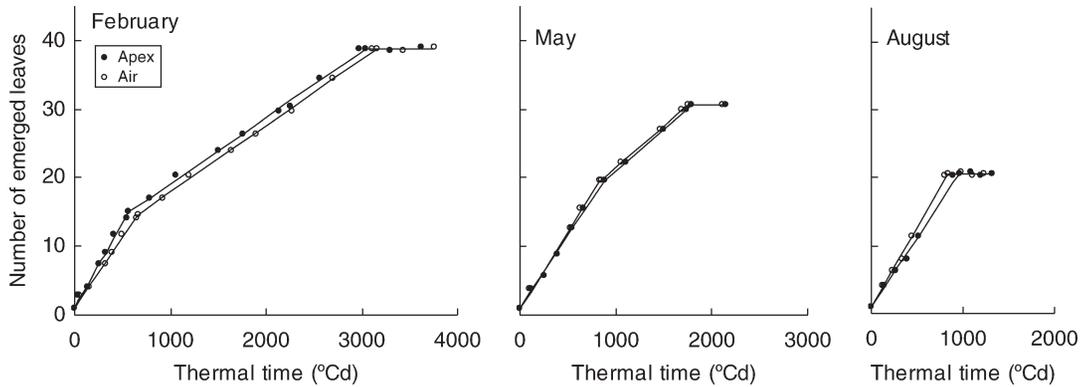


FIG. 3. Differences in the relationship between the number of leaves visible on the main stem and thermal time, depending on the calculation of thermal time. Thermal time was either calculated with the air temperature (2 m) or with the estimated apex temperature. Apex temperature was presumed to be equal to soil temperature before jointing and to air temperature during jointing. Data is presented for the variety ‘CSM 335’ and sowing dates with contrasting air–soil temperature differences in February (soil colder than air), May (similar) and August (soil warmer than air) 2001.

leaf number (LN; initiated, emerged, ligulated or senesced) was regressed against the elapsed thermal time from emergence (TFE) using one of the following equations:

$$LN = a + [b_1 \times \min(TFE, TS1)]$$

$$LN = a + [b_1 \times \min(TFE, TS1)] + \{b_2 \times \min[TS2 - TS1, \max(0, TFE - TS1)]\}$$

where a is the number of leaves at emergence, b_1 and b_2 are the initial and secondary rates of development, respectively, and $TS1$ and $TS2$ are the thermal time when either the change of rate occurred or the development terminated.

The intercept was set to $a = 1$ when modelling the number of emerged leaves, because the first leaf exerts immediately from the coleoptile at emergence under tropical conditions. When modelling the number of initiated leaves, it was set to $a = 5$, the number of leaves already

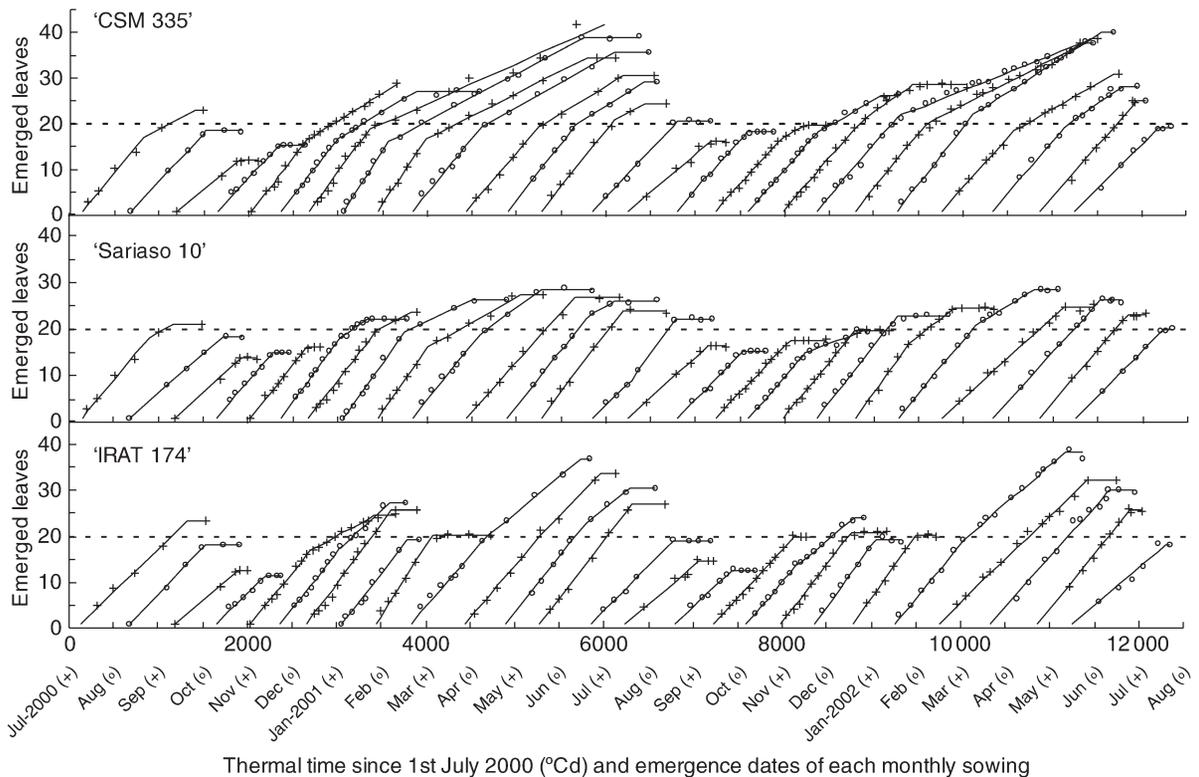


FIG. 4. Relationship between the number of leaves visible on the main stem and the thermal time for 26 sowing dates between July 2000 and August 2002, for three sorghum varieties (‘CSM 335’, ‘Sariaso 10’ and ‘IRAT 174’). Lines were fitted by regression analysis; the horizontal, dotted line marks the 20th. For clarity, different symbols are used for each monthly sowing date.

pre-formed in the embryo at emergence, as estimated for sorghum (Paulson, 1969; Muchow and Carberry, 1990). Parameters and their confidence intervals were iteratively estimated using the procedure NLIN of SAS (2004). The choice between the linear and bilinear models was made through a stepwise process. First, both models were applied to each sowing date. The linear model was selected either when the bilinear model did not converge due to non-determination of certain parameters, or when the reduction of the sum of squared errors (SSE) resulting from the use of the bilinear model was non-significant. This was tested with an F -value, calculated as

$$F_{\text{obs}} = [(SSE_{\text{lin}} - SSE_{\text{bilin}})/2]/[SSE_{\text{bilin}}/(n - p_{\text{bilin}})] \quad (2)$$

with SSE_{lin} and SSE_{bilin} being the SSE of the linear and bilinear regression models, respectively, n is the number of observations, and p_{lin} and p_{bilin} are the number of parameters of the linear and bilinear models (Seber and Wild, 1989).

The linear model was accepted when the probability of exceeding $F(n - p_{\text{bilin}}, n - p_{\text{lin}})$ was greater than 0.01.

This procedure was applied to the observations on initiated, emerged, ligulated and senesced leaves independently. Phyllochron and plastochron were calculated as the reciprocal of the slope coefficients for leaf initiation and appearance, respectively.

Correlations between the number of initiated and emerged leaves in the dissected samples, which were also bilinear, were calculated with the same procedure.

For comparisons of leaf production rates among varieties and among sowing dates, only the initial, linear portions of the dynamics (initial phyllochron or plastochron) were used, regardless of the linear or bilinear nature of the pattern. As the number of leaves at emergence is equal to 1, an intercept-less regression model was fitted on the number of leaves minus 1. Standard errors were estimated using the available replicates as independent subjects in a random slope model (Verbeke and Molenberghs, 1997). As the variance of the residuals was roughly proportional to the estimated number of leaves, a generalized linear mixed model was fitted, using SAS/STAT software (2004) and the Glimmix macro (Littell *et al.*, 1996). As this comparison was applicable only to the initial slopes, the secondary phyllochrons were compared using the standard errors estimated with the SAS NLIN procedure.

Lastly, in order to explain seasonal variations in initial phyllochron, this was regressed against the five environmental variables observed at plant emergence, using a stepwise multiple linear-regression model. The explanatory variables, whose daily values were averaged for a 10-d period to reduce noise, were daily temperature, relative humidity and global sun radiation averages, astronomical day length and its day-to-day rate of change. The underlying hypothesis was thus that the phyllochron is set by environmental conditions prevailing at crop establishment. The choice of the initial 10 d as a reference period also had a physiological basis, because it is the minimum duration to panicle initiation (Ellis *et al.*, 1997; Alagarwamy

and Chandra, 1998), meaning that after 10 d plants have perceived their environment and triggered their response.

Estimation of height increase rates

A similar comparison of models was performed to calculate the segmented regression of plant height (Ht) against thermal time (SumT), using two models in order to include two or three segments. The equations were:

$$Ht = [b_1 \times \min(\text{SumT}, ST_1)] + \{b_2 \times \min[ST_2 - ST_1, \max(\text{SumT} - ST_1, 0)]\} \quad (3)$$

$$Ht = [b_1 \times \min(\text{SumT}, ST_1)] + \{b_2 \times \min[ST_2 - ST_1, \max(\text{SumT} - ST_1, 0)]\} + \{b_3 \times \min[ST_3 - ST_2, \max(\text{SumT} - ST_2, 0)]\}$$

where b_1 , b_2 and b_3 are the slopes, and ST_1 , ST_2 and ST_3 are the values of SumT at the inflection or ending points.

Parameters were iteratively estimated with the procedure NLIN of SAS (2004) and one of the models was retained, based on an F -test at $P = 0.01$ as described above. Rate of height increase, thermal time at panicle initiation, and inflection points for leaf appearance and height increase were plotted against sowing dates. Linear-regression analyses of height increase rate vs. phyllochron were calculated using the procedure NLIN of SAS (2004).

RESULTS

Rates of leaf appearance, initiation and senescence

The total number of leaves produced per plant (mean \pm 5% C.I.) varied between a minimum of 12.0 (\pm 0.5), 14.1 (\pm 0.6) and 11.5 (\pm 0.4) and a maximum of 41.8 (\pm 2.0), 28.8 (\pm 1.5) and 38.8 (\pm 1.3) for 'CSM 335', 'Sarioso 10' and 'IRAT 174', respectively (Fig. 4). Rates of leaf appearance were constant for the initial 20 leaves, as indicated by the linear slopes when plotting leaf number vs. thermal time. However, rates decreased abruptly in 'CSM 335' and 'Sarioso 10' and sometimes in 'IRAT 174' after the appearance of about 20 leaves, suggesting a bilinear curve of leaf number vs. thermal time. We henceforth refer to an initial (short) and secondary (long) phyllochron, the latter apparently occurring only when a large number of leaves is produced. The initial phyllochron, exhibited until the appearance of the 20th leaf, varied among sowing dates but was nearly identical for all three varieties (means \pm 5% C.I.: 45.4 \pm 0.3, 46.9 \pm 0.4 and 46.6 \pm 0.4 for 'CSM 335', 'Sarioso 10' and 'IRAT 174', respectively] and averaged 46.3°Cd leaf⁻¹ across dates. The varieties did, however, exhibit differences for mean phyllochron values for leaves of rank greater than 20, with that of 'CSM 335' (89.0°Cd leaf⁻¹) twice that of its initial value, whereas 'Sarioso 10' (84.4°Cd leaf⁻¹) and 'IRAT 174' (63.2°Cd leaf⁻¹) exhibited smaller increases. Whenever a change of phyllochron occurred, it was between the estimated appearance of the 16th and 22th leaf for 'CSM

335', 15th and 21st for 'Sarioso 10', and 13th and 23rd for 'IRAT 174'. However, when the total number of leaves produced on the culm was below 25, the phyllochron remained constant until flag-leaf appearance.

Patterns of leaf initiation (Fig. 5) resembled those of leaf appearance. Where the rate of leaf appearance was constant throughout the life cycle, this was also true for the rate of leaf initiation, and where patterns were bilinear, this generally applied to both variables alike. The average value of the initial plastochron (before inflection) was the same for the three varieties ($38.6 \pm 1.3^\circ\text{Cd leaf}^{-1}$, 39.0 ± 1.4 and 38.2 ± 1.4 for 'CSM 335', 'Sarioso 10' and 'IRAT 174', respectively). Whenever a bilinear pattern of leaf initiation occurred, the plastochron roughly doubled, averaging 92.9 and $80.6^\circ\text{Cd leaf}^{-1}$ for 'CSM 335' and 'IRAT 174' across all dates. The secondary plastochron, where it occurred, was similar to the secondary phyllochron (Figs 6 and 7). Changes in the rate of leaf initiation (plastochron^{-1}) occurred between the initiation of the 20th and 25th leaf. When the total number of leaves did not exceed 25, the rate of leaf initiation stayed constant until flag-leaf appearance.

The rate of leaf senescence (example data shown for 'CSM 335' in Fig. 6) also exhibited either linear or bilinear kinetics. Similar to leaf initiation and appearance, leaf senescence kinetics depended on the sowing date and the total number of leaves produced, resulting in patterns

similar to Figs 1 and 2 (data not shown). The rate of leaf senescence was bilinear when more than about 20 leaves were produced, and the rate changed between the 10th and the 15th leaf to appear.

Relationships among development rates

Three main patterns of relationship were observed among the dynamics of leaf-initiation, appearance, ligule exertion and leaf senescence over a year-round cycle of monthly sowings for 'CSM 335' (Fig. 6). The first pattern, represented by a February sowing, exhibited very large total leaf number (39) and bilinear development rates, whereby secondary rates were nearly identical for initiation, appearance, ligule exertion and senescence. The secondary phase spanned very contrasting climatic conditions, with April and May being hot and dry, June transitory, and July and August fully in the rainy season with lower temperatures and high humidity (Fig. 1). The inflections of these four dynamics occurred at about the same thermal time after sowing (approx. 600°Cd). At that time, an average of 21.9 leaves had been initiated, 15.9 had emerged and 6.0 senesced. (But leaf appearance rate sometimes changed later than leaf initiation rate on other sowing dates.) After inflection, the similar secondary rates for the four development variables resulted in a stable architecture of the whorl with six leaves growing inside the sheaths and three

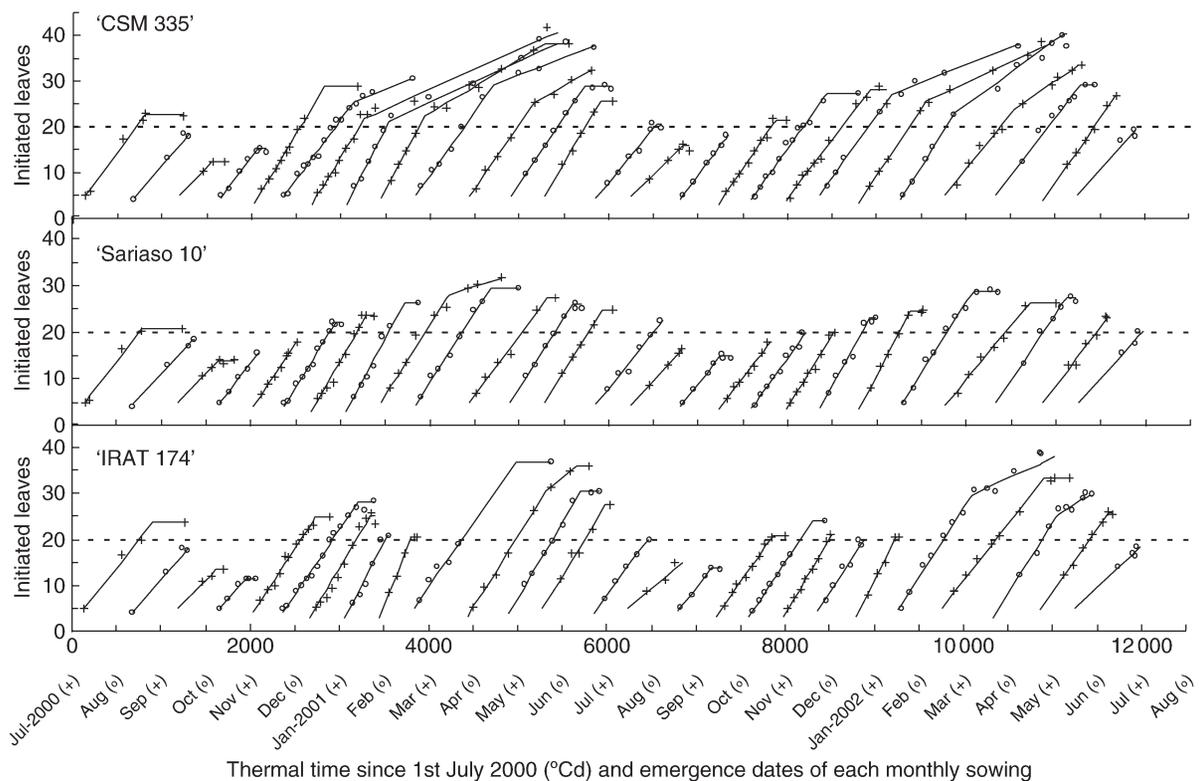


FIG. 5. Relationship between the cumulative number of leaves produced by the apical meristem and thermal time for 26 sowing dates between July 2000 and August 2002, for three sorghum varieties ('CSM 335', 'Sarioso 10' and 'IRAT 174'). Lines were fitted by regression analysis; the horizontal, dotted line marks the 20th. For clarity, different symbols are used for each monthly sowing date.

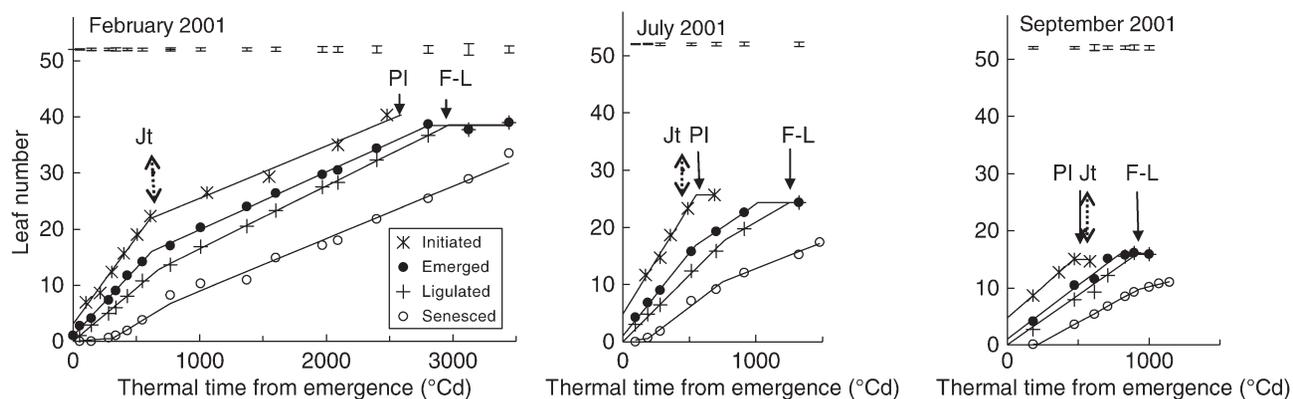


FIG. 6. Relationships between the cumulative number of leaves initiated, emerged, ligulated and senesced on the main stem and the thermal time from emergence for February, July and September 2001 sowings of 'CSM 335'. Time of the onset of jointing (Jt), panicle initiation (PI) and fully expanded flag-leaf stage (F-L) are indicated. Error bars indicate the 95% confidence interval of each mean value of the number of emerged leaves.

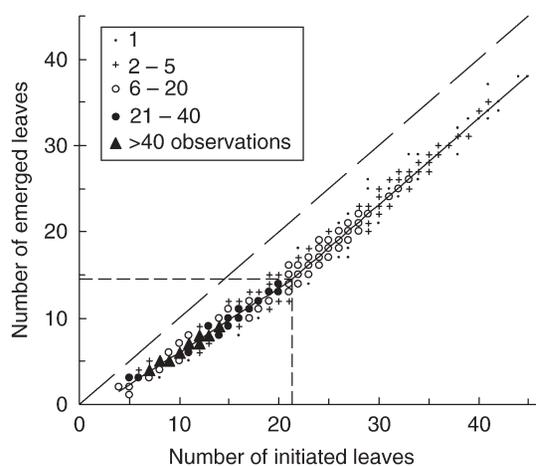


FIG. 7. Relationship between the number of initiated vs emerged leaves in the 1512 dissected samples (three varieties and 26 monthly sowing dates). The different symbols indicate different frequencies of similar observations. The 1:1 line and co-ordinates of the inflection point are plotted.

emerged, elongating leaves constituting the whorl. The internodes above the three leaves that had the most-recent fully expanded leaf sheaths elongated, causing the leaf sheaths to telescope out from one another. This architectural steady state was observed for a period up to 3 months, depending on sowing date. It was typical of all sowings between January and the beginning of June, all of which produced more than 25 leaves (Figs 4 and 5).

The second pattern, represented in Fig. 6 by the July sowing, was observed when the total leaf number was between 20 and 30. The plastochron showed no inflection and was thus constant until panicle initiation, whereas the dynamics of tip and ligule appearance were bilinear (mean inflection when 16.7 leaves had emerged). The dynamics of the senescent leaf number was also bilinear or curvilinear, but the inflection point could not be clearly identified.

The third pattern, represented by the September sowing, was observed when less than 20 leaves were produced on the main culm. In such cases, the dynamics of all

four development variables remained linear throughout the crop's life cycle. These three patterns were observed on 'CSM 335' and 'Sariaso 10', but less clearly on 'IRAT 174'.

The relationship between the number of initiated and emerged leaves was very tight and independent of variety and sowing date across all developmental stages (Fig. 7). This relationship was clearly bilinear:

$$\text{NFA} = -1 \cdot 44 + [0 \cdot 75 \times \min(\text{NFI}, 21 \cdot 35)] + [1 \cdot 00 \times \max(0, \text{NFI} - 21 \cdot 35)]$$

with NFI and NFA the numbers of leaves initiated and emerged, respectively.

Consequently, leaf appearance rate was lower than initiation rate until 21.4 leaves were initiated, resulting in a slope smaller than 1 (Fig. 7). During the second phase, both developmental rates were equal (slope = 1).

Effects of sowing date on development rates

Initial phyllochron varied between 40 and 65°Cd for all three varieties and showed distinct seasonal patterns (Fig. 8). The initial phyllochron had two annual minima (January and July) and two annual maxima (May and September). From the random slope model analysis, the effects of sowing date (differences among months) were significant ($P < 0.0001$, Table 1), but there was also an effect of the year ($P = 0.0008$). Slopes were not significantly affected by variety nor by the interactions of variety × sowing date and variety × year ($P > 0.05$).

As the initial phyllochron for each sowing date remained constant until the appearance of the flag leaf or onset of the secondary phyllochron, environmental conditions at the time of plant emergence appeared to determine the initial phyllochron. Significant positive correlations were observed in the paired-correlations matrix between initial phyllochron and soil temperature and global radiation during the 10 d following emergence, but not with relative humidity, photoperiod or rate of change of day length. The same

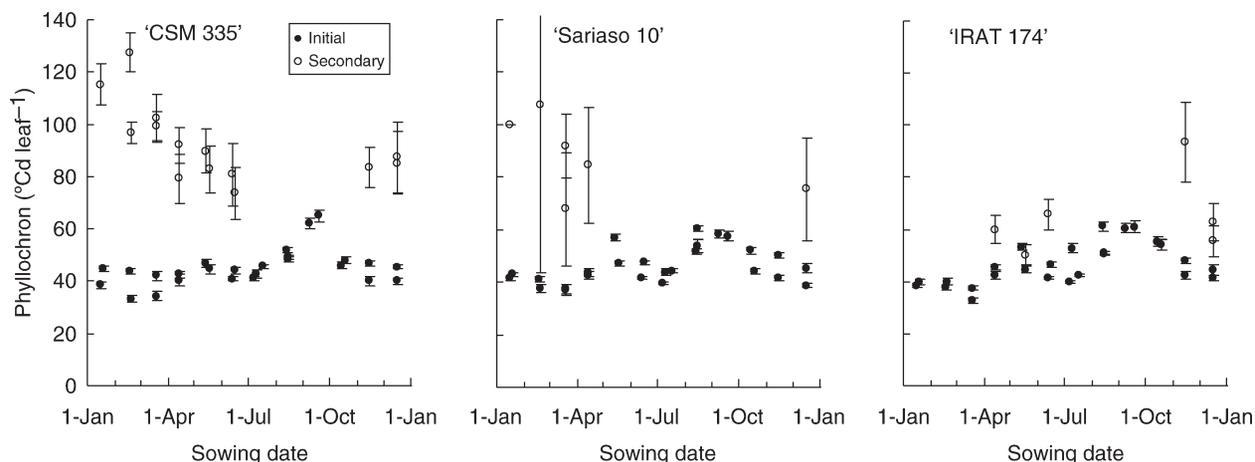


FIG. 8. Initial phyllochron values from emergence and secondary phyllochron values after rate change plotted against calendar date of sowing for observations between July 2000 and August 2002. Error bars indicate the asymptotic 95% confidence interval.

TABLE 1. Analysis of covariance on repeated measurements to test effects of variety, and month and year of sowing on the initial rates of leaf appearance (slope of regression in thermal time). Interactions between factors and thermal time indicate effects on slope, while single factors indicate effects on the intercept

Source	d.f.		F	P
	Num	Den		
Thermal time	1	24.9	33166	<0.0001
Thermal time × variety	2	24.9	2.0	ns
Thermal time × sowing month	11	24.8	48.9	<0.0001
Thermal time × year/sowing month	14	24.9	6.9	<0.0001
Thermal time × variety × sowing month	22	24.7	1.3	ns
Thermal time × variety × year/sowing month	28	24.8	2.2	ns

d.f.: degree of freedom, Num: numerator and Den: denominator.

analysis conducted for individual varieties identified the same predictor variables but at a lower level of probability (data not shown).

However, a stepwise multiple linear regression of the initial phyllochron against the same five mean environmental variables at emergence showed that a combination of three of them (soil temperature, photoperiod and daily change of the photoperiod) could explain 40–50% of the observed variability of the initial phyllochron of the three varieties, individually or together (Table 2). Photoperiod and its daily rate of change were both significantly correlated with soil temperature in the correlation matrix, but not with global radiation or relative humidity. The phyllochron was thus significantly increased by higher soil temperature at emergence and decreased by longer photoperiods or increasing day length.

The secondary phyllochron showed a strong response to sowing date for 'CSM 335' (Fig. 8A) but not for the other varieties, where large error terms and insufficient data points made a seasonal trend analysis impossible (Fig. 8B, C). In 'CSM 335', the secondary phyllochron

decreased from 120 to 60°Cd from the January to the July sowing date (Fig. 8A). It thus decreased as the duration of the vegetative phase and the total leaf number decreased (Fig. 4), and then disappeared from July sowings onwards when crop duration and total leaf number were small.

The ratio of the secondary over the initial phyllochron was between 1.6 and 2.5 for 'CSM 335' but the large scatter of the data did not allow a seasonal trend to be identified (data not shown). In addition for 'CSM 335', the phenological stage at which the phyllochron changed from its initial to its secondary rate varied among sowing dates, with the inflection point corresponding to the appearance of the 15th to 16th leaf for January–February sowings and increasing to the 18th to 19th leaf for the May–June sowings (data not shown).

Effects of sowing dates on increase in plant height

Final plant height varied two- to three-fold among sowing dates for 'CSM 335' (1.6–4.7 m), 'Sarioso 10' (1.1–2.4 m) and 'IRAT 174' (0.6–1.9 m; Fig. 9). The height of the whorl at which panicle initiation occurred varied from <25 cm up to 3 m (in the latter case, jointing was more than half completed). The rate of increase in plant height exhibited seasonal differences, with the highest rates observed for sowings in July and September for 'CSM 335' and 'Sarioso 10' (Fig. 10). Seasonal differences in rate of increase in height were greater in absolute and relative terms for 'CSM 335', a tall variety having a maximal internode length of 25 cm, than for 'Sarioso 10', a semi-dwarf (16 cm) and 'IRAT 174', a dwarf (8 cm). Although rates of increase in height were generally higher for sowing dates falling into the wet season (June–September) than the dry season, rates for 'CSM 335' and 'Sarioso 10' for August sowings were low in both years for unknown reasons.

There was a significant, negative relationship between the rate of increase in height and the plastochron or the phyllochron during jointing for 'CSM 335' ($R^2 = 0.39$ or 0.28 , $P < 0.001$ or 0.01) and 'Sarioso 10' ($R^2 = 0.37$ or 0.22 ,

TABLE 2. Multiple, linear-regression parameters and fits for the initial phyllochron vs three climatic parameters at emergence selected through the stepwise process, for the three varieties individually and combined (parameters global radiation and relative air humidity were rejected)

	Coefficients							Model	
	Intercept (°Cd) value	Top-soil temperature (°C)		Day length (h)		Change of day length (s d ⁻¹)			
		Value	Partial P	Value	Partial P	Value	Partial P	Adjusted R ²	P
'CSM 335'	114.9	2.15	2 × 10 ⁻⁵	-9.59	4 × 10 ⁻⁵	-0.11	9 × 10 ⁻⁴	0.51	3 × 10 ⁻⁴
'Sariaso 10'	99.7	2.23	1 × 10 ⁻⁴	-8.45	1 × 10 ⁻³	-0.13	1 × 10 ⁻³	0.40	2 × 10 ⁻³
'IRAT 174'	103.8	2.05	3 × 10 ⁻⁴	-8.42	9 × 10 ⁻⁴	-0.07	3 × 10 ⁻²	0.39	3 × 10 ⁻³
Combined	106.1	2.14	<1 × 10 ⁻⁸	-8.82	<1 × 10 ⁻⁸	-0.11	<1 × 10 ⁻⁸	0.45	<1 × 10 ⁻⁸

$P < 0.001$ or 0.05). The initiation of stem elongation, or jointing, approximately coincided with panicle initiation for the August-to-October sowing dates (Fig. 11). For January through to July sowing dates, a period that includes the normal dates when farmers sow sorghum (late-May to early July), the onset of jointing occurred earlier than panicle initiation and was associated with the phyllochron inflection point whenever it occurred ('CSM 335' and 'Sariaso 10' only).

DISCUSSION

Dynamics of leaf production and appearance

This study demonstrated the existence of bilinear dynamics for leaf initiation and appearance in highly photoperiod-sensitive sorghums from West Africa. Previous observations of the rates of leaf appearance in sorghum have not reported bilinear kinetics (Muchow and Carberry, 1990; Ritchie *et al.*, 1998; Craufurd *et al.*, 1999; Craufurd

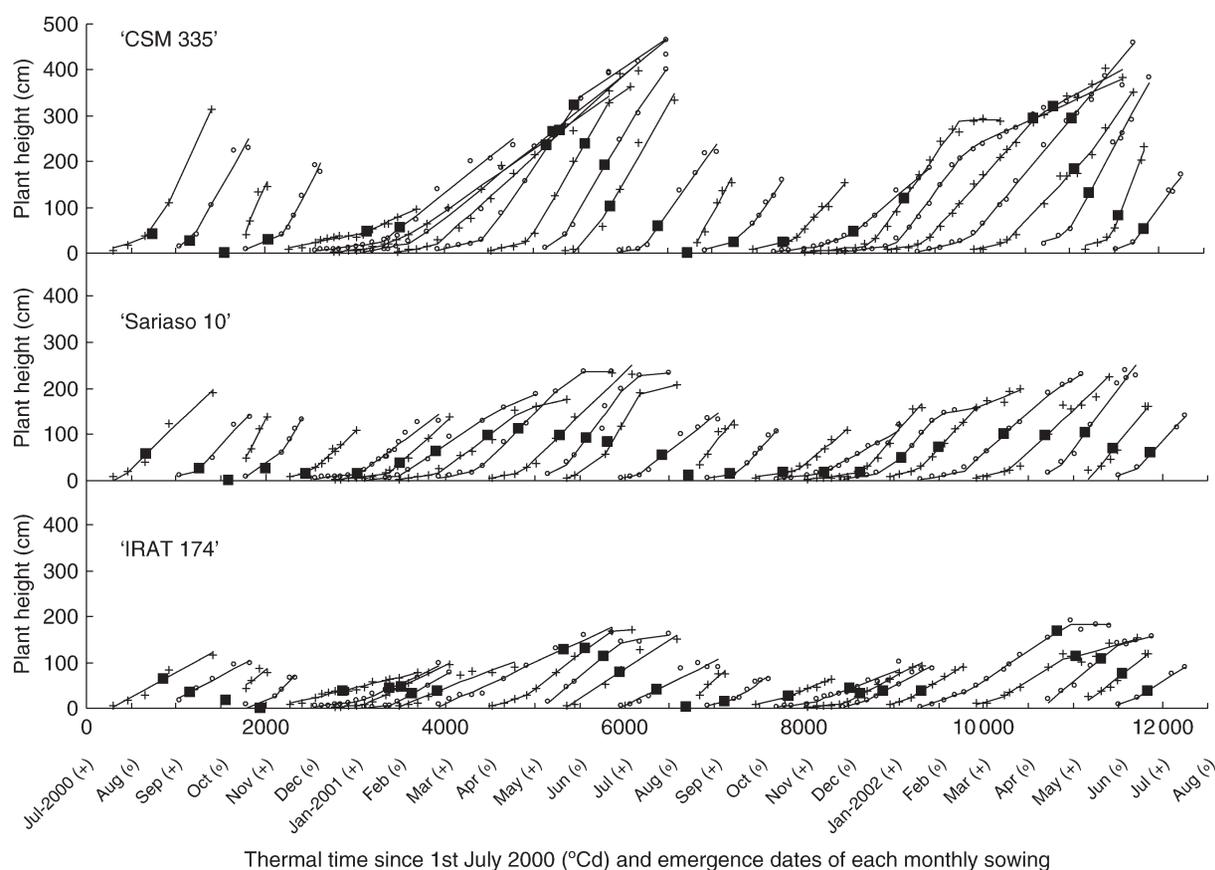


FIG. 9. Weekly observations of plant height plotted against thermal time from emergence, for 26 sowing dates of three varieties. Lines were fitted using a linear-segmented model, with plant height at panicle initiation indicated by a solid square. For clarity, different symbols are used for each monthly sowing date.

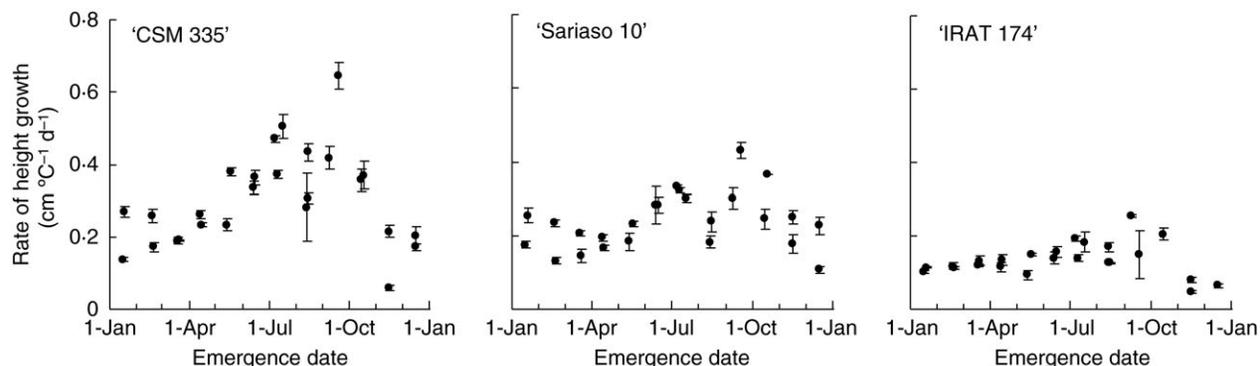


FIG. 10. Relationships between the rate of plant height growth during jointing and the calendar date of sowing. Error bars indicate the asymptotic 95% confidence interval.

and Qi, 2001). This may be due to prior work being conducted with less-photoperiod-sensitive germplasm or in environments in which total leaf number did not exceed 25, while as many as 38 and 41 leaves were produced by 'IRAT 174' and 'CSM 335', respectively, due to their strong photoperiod-sensitivity that extended pre-floral development to up to 8 months. Bilinear leaf appearance dynamics have been observed in wheat (Baker *et al.*, 1986; Hay and Delécolle, 1989; Cao and Moss, 1991; González *et al.*, 2002), barley (Miralles *et al.*, 2001; Abeledo *et al.*, 2004), rice (Tivet, 2000; Itoh *et al.*, 2001) and maize (Zur *et al.*, 1989; although not recognized by this author). The inflection point observed in photoperiod-sensitive sorghums in this study occurred at a much higher leaf rank (15–20) as compared with wheat and barley (5–7; Baker *et al.*, 1986; Hay and Delécolle, 1989; Cao and Moss, 1991; Calderini *et al.*, 1996; Miralles *et al.*, 2001; González *et al.*, 2002; Abeledo *et al.*, 2004).

The secondary phyllochron and plastochron in this study were 1.2–2.5 times longer than the initial phyllochron and plastochron, depending on the sowing date (Fig. 8A). A similar range of 1.2–2.1 times increase over initial phyllochron rates, depending on variety and sowing dates, was

observed in wheat and barley (Baker *et al.*, 1986; Hay and Delécolle, 1989; Cao and Moss, 1991; Calderini *et al.*, 1996; Miralles *et al.*, 2001; González *et al.*, 2002; Abeledo *et al.*, 2004).

The mean initial phyllochron observed in this study was $46^{\circ}\text{Cd leaf}^{-1}$, or about 3 d, and the mean initial plastochron was $36^{\circ}\text{Cd leaf}^{-1}$, or about 2 d, averaged over all three varieties and sowing dates. These values are similar to previously reported values for sorghum. Ritchie *et al.* (1998) observed the phyllochron to be $49^{\circ}\text{Cd leaf}^{-1}$. The phyllochrons (60.9 and $69.0^{\circ}\text{Cd leaf}^{-1}$) and plastochrons (46.9 and $40.3^{\circ}\text{Cd leaf}^{-1}$) reported by Birch *et al.* (1990) and Muchow and Carberry (1990), respectively, were higher; however, their calculations were used a base temperature of 8 and 7°C , compared to 11°C in this study, which was based on observations on West African sorghums (Lafarge and Tardieu, 2002). Re-estimation of the phyllochron and plastochron in this study using a base temperature of 7°C gave a phyllochron of $55^{\circ}\text{Cd leaf}^{-1}$ and a plastochron of $44^{\circ}\text{Cd leaf}^{-1}$, closer to the values reported by Birch *et al.* (1990) and Muchow and Carberry (1990).

A consequence of the initial plastochron always being shorter than the initial phyllochron is that the number of

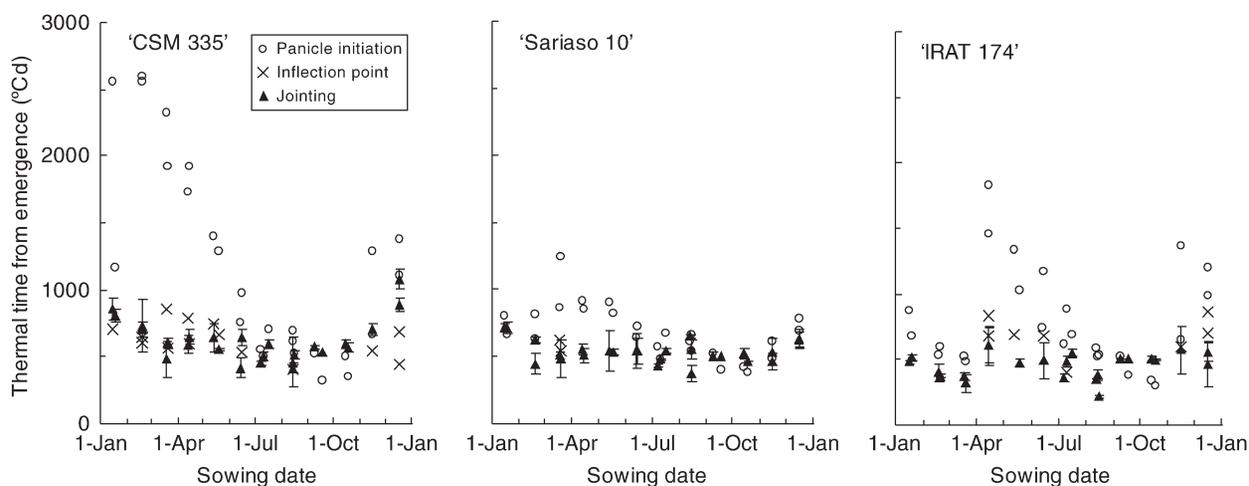


FIG. 11. Thermal time from sowing to the beginning of jointing, panicle initiation and the inflection point of the rate of leaf initiation, as a function of calendar date of sowing; for main culms on three sorghum varieties. Error bars indicate the asymptotic 95% confidence interval of the onset of jointing.

leaves growing inside the leaf sheaths increases from four at emergence to about six when the initiation and appearance rates changed (inflection point). This observation is common for cereals (Rickman and Klepper, 1995; Vaksman *et al.*, 1998), except for rice where the plastochron and phyllochron are equal (Nemoto *et al.*, 1995). It has been suggested that the phyllochron is necessarily longer than the plastochron because leaf appearance requires the tip of the elongating leaf to travel the length of the enclosing leaf sheath. If the elongation rate is supposed to be constant for subsequently developing leaves, the increasing distance (length of enclosing sheath) would lead to increasing delays in leaf-tip appearance (Skinner and Nelson, 1995; Fournier and Andrieu, 1998).

A major phenological consequence of the variable phyllochron during stem elongation of photoperiod-sensitive sorghums (caused by facultative linear or bilinear dynamics and strong seasonal effects on the secondary phyllochron) is that the time elapsing from panicle initiation to flag-leaf appearance is highly variable. The photoperiod-sensitive variety 'CSM 335', when sown in May, exhibited a secondary phyllochron of $65^{\circ}\text{Cd leaf}^{-1}$, versus $42^{\circ}\text{Cd leaf}^{-1}$ for June sowing. In both cases, six leaves that had yet to appear were present at panicle initiation. The duration from panicle initiation to flag-leaf appearance of the May sowing was thus extended by 138°Cd [$= 6 \times (65 - 42)$] or about 9 d, assuming a daily average temperature of 26°C . This, together with the increased number of leaves elongating within the sheaths, can combine to prolong the period between panicle initiation and flag-leaf appearance from 200°Cd for an August sowing to 500°Cd for a June sowing (Clerget *et al.*, 2004).

Apparent co-ordination among growth and development processes

This study demonstrated that when leaf production rates change from the initial to the secondary rate (associated with situations where total leaf number is greater than 25), the rate of leaf appearance and leaf senescence change at about the same time. This synchronicity occurred across a wide range of sowing dates, although the phenological stage varied (18 and 25 leaves initiated). In fact, leaf initiation is a developmental process, whereas leaf appearance results from a combination of two processes, development and growth inside the enclosing sheath (McMaster *et al.*, 2003). The observation of nearly simultaneous changes of both initiation and appearance rates suggests that the rate of development (cell division and differentiation processes in the apex) and the rate of elongation (a process happening at some distance from the apex) were simultaneously altered at the inflection point. The height increase of the stem, driven by the simultaneous elongation of the internodes of the last three phytomers carrying fully expanded leaves, was also altered in plants showing a secondary phyllochron, as compared with plants that did not and produced less than 20 leaves.

It therefore seems that the change from primary (rapid) to secondary (slower) development rates is a co-ordinated and regulated event, involving different organs such as the apex,

the elongating leaves and the elongating internodes. Alternatively, competition among growth processes for resources such as assimilates, for example triggered by the onset of stem elongation, might also explain the observed synchronicity of rate changes. Whether development-related signalling processes, competition effects or both combined [for example, sugar-availability-based signals; Black *et al.* (1995); Roitsch *et al.* (2000)] are at work here could only be evaluated with specifically designed experiments.

The tight relationship observed between the number of leaves initiated and the number of leaves emerged for a given variety, across sowing dates and across varieties, agrees with previous observations on wheat (Kirby, 1990) and maize (Padilla and Otegui, 2005). In maize, with a maximal number of 25 leaves produced, the relationship was found to be linear and had a slope of 0.63, smaller than the initial slope of 0.75 calculated here for sorghum. Consequently, the difference between the number of leaves emerged and initiated increases more rapidly in maize than in sorghum. As indicated by the uniform behaviour of the three sorghum varieties studied here (Fig. 6), which belong to different genetic groups and represent different plant types, the relationship between leaf initiation and appearance dynamics is a characteristic of the species. It is therefore possible to predict leaf and panicle initiation dates from observations on leaf appearance.

The time at which cereals begin to joint has often been reported to coincide with panicle initiation (House, 1985; Alagarwamy and Ritchie, 1991; Ritchie *et al.*, 1998). However, stem elongation can begin before panicle initiation in late-maturing varieties of sorghum and pearl millet (Lane, 1963; Goldsworthy, 1970b; Lambert, 1983). Both cases were observed in this study, depending on the variety and sowing date. Panicle initiation and onset of jointing coincided for sowings between August and October for all genotypes. In contrast, earlier sowing dates generally resulted in panicle initiation occurring significantly later than onset of jointing (by up to 15 phyllochrons), indicating that initiation of flowering is not required for the initiation of stem elongation in sorghum. Whenever these two events did not coincide, stems began elongating at the time of the plastochron and phyllochron inflection points.

For wheat, a synchronization of the phyllochron inflection point with double-ridge formation, assumed to occur just prior to the appearance of the fifth leaf below the flag leaf, was suggested by Baker *et al.* (1986) and supported by Hay and Delécolle (1989) and Cao and Moss (1991). González *et al.* (2002), however, found no association between the change of phyllochron and any specific developmental stage. Likewise, Miralles *et al.* (2001) found no relationship between changes of the rate of leaf appearance and final leaf number or any particular development stage in barley. The phyllochron was observed to change after panicle initiation in rice by Katayama (1951, cited by Tivet, 2000) and Baker *et al.* (1990), whereas Nemoto and Yamazaki (1993, cited by Tivet, 2000) suggested that the change was associated with the beginning of internode elongation.

Environment effects on development rates

The significant variation of development rates among sowing dates, as observed in this study, contradicts reports by Muchow and Carberry (1990) and Craufurd and Qi (2001), but agrees with Vaksman *et al.* (1998). Various relationships of development rates with sowing dates were observed in wheat and barley (Baker *et al.*, 1980; Kirby *et al.*, 1985; Cao and Moss, 1991; Rickman and Klepper, 1995). Where the phyllochron was found to be affected by sowing date, the causal factor was not clearly identified, although correlations were found with temperature (Cao and Moss, 1989; Tamaki *et al.*, 2002), thermo-photoperiodic index (Cao and Moss, 1991), day length (Warrington and Kanemasu, 1983; Masle *et al.*, 1989; Cao and Moss, 1991; Slafer *et al.*, 1994b; Bertero *et al.*, 2000), the rate of change of day length at emergence (Kirby *et al.*, 1982; Ellis and Russell, 1984; Baker *et al.*, 1990) and radiation intensity (Rawson, 1993; Birch *et al.*, 1998; Bertero, 2001). The significant, positive correlation of the initial phyllochron with soil temperature at plant emergence found in this study (Table 2) is in agreement with some of the reports cited above. This is also true for the observed, negative correlation between the initial phyllochron and day length and day-to-day change in day length. On the other hand, the absence of a correlation of phyllochron with solar radiation as reported here contrasts with previous reports of negative correlations, mainly in maize and quinoa. However, the experimental conditions were different, the present work being based on high solar global-radiation levels ($18.0\text{--}24.6 \text{ MJ m}^{-2} \text{ d}^{-1}$), whereas studies indicating negative effects of solar radiation on phyllochron used lower ranges of light levels ($2.2\text{--}19.2 \text{ MJ m}^{-2} \text{ d}^{-1}$ in Birch *et al.*, 1998, and $8.6\text{--}18.6 \text{ MJ m}^{-2} \text{ d}^{-1}$ in Bertero, 2001). Although our study provides strong evidence for seasonal effects on the initial phyllochron, it cannot advance solid evidence on the environmental signals causing them. It is quite likely, however, that whatever environmental signal is responsible it sets the phyllochron at an early stage of plant development, because the initial phyllochron is remarkably constant. If standard climatic variables such as solar radiation, temperature or day length during seedling stage indeed constitute the signal, experiments under controlled conditions could probably provide better evidence than field experiments, in which these factors vary not only among seasons but also between and within days.

Environment effects on rate of increase in plant height

The rate of increase in plant height during jointing varied among sowing dates (Fig. 10) and was correlated with the plastochron and the phyllochron during jointing. This relationship is probably the result of physiological co-ordination between the dynamics of internode elongation and leaf appearance. It has been reported that the elongation of the *i*th internode is triggered by the emergence of the collar of the *i*th leaf from the previous leaf's sheath enclosing it, and growth of this *i*th leaf (blade and sheath) ends at the same time (Fournier and Andrieu,

2000). Therefore, a longer phyllochron delays the onset of elongation of each successive internode. Since these delays increase the time available for the growth of each internode but do not affect its final length (Bezot, 1963), it is probable that their elongation rate is reduced proportionally, and that elongation of the three internodes in the zone of elongation occurs continuously at this reduced rate.

Patterns of development rates vs. adaptation to environment

The high variability of crop duration in photoperiod-sensitive sorghums in response to sowing date has been described as an important adaptive mechanism that helps match growth duration with the period of moisture availability or, more specifically, synchronizes flowering with the probable end of the rainy season (Bunting and Curtis, 1968; Curtis, 1968; Andrews, 1973; Kassoum and Andrew 1975; Kouressy *et al.*, 1997; Vaksman *et al.*, 1998; Clerget *et al.*, 2004). This study shows that sowing a photoperiod-sensitive sorghum variety earlier in the year not only extends its growth cycle, but also reduces its rate of development and height increase during jointing. The consequences of these reduced rates of development and growth for plant architecture may indeed constitute adaptive advantages.

One consequence of reduced rates of leaf formation during jointing is that internode production is reduced to the same extent. In this study, this translated into reduced plant height because final internode length was fairly stable among environments (data not shown). The longer, secondary phyllochron, which was particularly long when the crop was sown early and thus had a long crop duration (Fig. 11), may thus serve to prevent excessive plant height under conditions of long crop duration. Even with these reduced, secondary development rates, photoperiod-sensitive sorghums commonly attain plant heights of 5 m or more when sown early (as for 'CSM 335'), which may approach the limits of mechanical stability for an annual cereal crop.

Furthermore, the stem of tall, tropical sorghum varieties is the heaviest organ of the plant (Goldsworthy, 1970b), exerting a high demand for photosynthates and mineral nutrients. Reduction of the rates of internode and leaf development probably results in a concomitant reduction in the demand for resources for vegetative growth under day-length conditions unfavourable to flowering, as compared with less photoperiod-sensitive varieties or species. Maize, for example, exhibits a single and comparatively high rate of development (Warrington and Kanemasu, 1983). Photoperiod-sensitive West African sorghums are considered as robust crops that are able to grow and produce under conditions of poor soil fertility (Giraudy *et al.*, 1997). This characteristic might in part be attributable to the phenological adaptations described here. The response to photoperiod expressed in this germplasm therefore covers an ensemble of phenological processes, including not only the well-known response of flowering date (considered as a mechanism for temporal escape), but also an intricate regulation of development and the growth processes associated with it. The latter may have

adaptive functions that have so far escaped ecophysiological research and that merit further study.

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