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Durations of the photoperiod-sensitive and -insensitive phases of time to panicle initiation in sorghum

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Abstract

The development of sorghum [*Sorghum bicolor* (L.) Moench] is influenced by genes that control sensitivity to photoperiod, and their interaction with photoperiod and temperature. While temperature influences development throughout the life cycle of plants, photoperiod influences the vegetative stage (from seedling emergence to panicle initiation). In order to simulate plant development, it is essential to know when sorghum plants first become sensitive to photoperiod, and how long that photoperiod sensitivity persists. Ten cultivars with different levels of photoperiod sensitivity were grown in pots under natural climatic conditions both in short days (SD: 8 h day^{-1}) and long days (LD: 17 h d^{-1}). Plants were transferred at different times after seedling emergence from SD to LD and vice versa. The time to panicle initiation (PI) for each transfer treatment was determined. In cultivars that remained continuously in SD, the time to PI varied from 16 to 27 d, whereas, in continuous LD it varied from 22 to 37 d. The cultivars started reacting to photoperiod 4–9 d after seedling emergence. After sensing photoperiod stimuli, inductive effects among cultivars persisted for 4–14 d in SD, and for 15–33 d in LD depending on their intrinsic photoperiod sensitivity. The sensitivity ended 2–5 d before panicle initiation. This interval, between completion of the photoperiod-inductive phase and the actual observation of PI under the microscope, represents the time required for the photoperiod-inductive stimulus to promote sufficient cell division and growth at the shoot apex for the morphological change to become visible as a shiny globular structure. We conclude that photoperiod sensitivity in these sorghum cultivars ends shortly before or at the PI stage. Our results support the assumptions followed in several crop simulation models that sorghum remains photoperiod-sensitive until the completion of the vegetative stage.

Keywords: Photoperiod sensitivity; Juvenile period; Panicle initiation; Sorghum [*Sorghum bicolor* (L.) Moench]

1. Introduction

Cultivated sorghum [*Sorghum bicolor* (L.) Moench] was probably first domesticated in the Ethiopia–Sudan region of the northeastern quadrant of Africa around the equator some 5000 years ago (Doggett, 1965). However, it is now grown widely throughout tropical, subtropical, and temperate environments ranging from 40°S in Argentina (0.72 Mha) up to 50°N in the Ukraine (0.07 Mha) (FAO, 1993). Adaptation to such a wide range of growing conditions has been mainly facilitated by evolution of the photoperiod-response genes and their interaction with daylength and temperature so that the sorghum germplasm adjusts time to flowering to the growing

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season length (Quinby and Karper, 1945; Caddel and Weibel, 1971; Sorrells and Myers, 1982). The flowering stage is the most vulnerable stage to environmental stresses in development so that understanding the photothermal effects on time to flowering is the key to crop adaptation to variable environments.

The period to flowering in cereals consists of a vegetative phase (germination to panicle initiation) and a reproductive phase (panicle initiation to flowering). The basic concept of photoperiod response was proposed for rice by Vergara and Chang (1969). Following this concept, Major (1980) developed a system to describe photoperiod response that could be applied to many crop species. Subsequently, Vergara and Chang (1985) and Roberts and Summerfield (1987) divided the vegetative phase into an initial pre-inductive period, and a later photoperiod-sensitive inductive period. The pre-inductive (sometimes known as juvenile) period starts at germination; during this period, plants are not sensitive to photoperiod. In the photoperiod-sensitive inductive period that follows, plants can change from vegetative to reproductive development if exposed to appropriate inductive photoperiod. This basic understanding of plant development has led to major advances in the ability to predict plant development in simulation models.

The phenology subroutine of most crop simulation models operates on a similar set of assumptions about the pattern of crop development as explained earlier, and assumes that the photoperiod-sensitive phase ends at panicle initiation (PI) when the previously vegetative meristem becomes reproductive (Jones and Kiniry, 1986; Alagarswamy et al., 1989; Godwin et al., 1989; Rosenthal et al., 1989; Penning de Vries et al., 1989; Alocilja and Ritchie, 1991). However, Collinson et al. (1992, 1993) indicated recently that in rice and soybean, the photoperiod influence persists for some time after the completion of floral initiation. It is therefore critical to know when the photoperiod-insensitive and - sensitive stages begin and end in sorghum in order to correctly implement photoperiod relationships in simulating plant development.

The main objectives of this study involving diverse sorghum cultivars were: (i) to determine the duration of photoperiod-insensitive pre-inductive period (a_1), (ii) to determine the duration of photoperiod-sensitive inductive period in long day (I_L), and in short day (I_S), (iii) to determine when the photoperiod-inductive period is completed, and (iv) to establish the relationship between PI and time to flowering.

2. Material and methods

2.1. Experiment I

2.1.1. Plant husbandry and culture

Ten sorghum cultivars of differing maturity and zone of adaptation were used in this study. Based on the differential response to photoperiod ranging from 8 to 17 h day^{-1} (as determined by an other experiment), they were classified into three groups (Table 1). Plants were grown under natural climatic conditions in 10.5 cm diameter plastic pots containing a 4:1 mixture by volume of Vertisol and sand. Fertilizer, di-ammonium phosphate (8 g pot^{-1}) and urea (6 g pot^{-1}), was mixed in the soil. The soil mixture in the pots was soaked with water for 1 h before sowing. In each pot, 20 seeds were sown on August 1, 1992 and 1993. The seeds were covered with loose soil, and the pots were irrigated daily with tap water. The pots were thinned to 12 plants on the 6th day, and finally to 6 plants on the 15th day. Plants were protected periodically against shoot pests.

2.1.2. Environmental conditions

Plants were grown in long daylength (LD: 17 h d^{-1}) and short daylength (SD: 8 h d^{-1}) length conditions. For the LD treatment, the normal daylength (12.8 h d^{-1}) was extended using an incandescent bulb (40 W). For the SD treatment, galvanized steel framed black cotton cloth enclosures (12 m^3) were used. Each day, plants in SD treatment remained inside the enclosure only from 0600 to 0830 h and from 1630 to 1830 h. The maximum and minimum temperatures, solar radiation, and rainfall were measured daily at the experiment site using an automatic weather recorder. The weekly mean data during the 8-week experimental period is presented in Fig. 1. Temperatures inside and outside the cloth enclosure were also measured on a few occasions.

A split-plot completely randomized design with three replications was used, with daylength as main

Table 1
EEffect of short daylength (SD) and long daylength (LD) on time to panicle initiation (PI) and durations of the photoperiod insensitive pre-inductive phase (a_1), the photoperiod-sensitive inductive phase in SD (I_S) and in LD (I_L) in sorghum cultivars (SE in parentheses)

Group/ cultivar	Time to PI (d)		Photoperiod sensitivity coefficient (°Cd h^{-1})	Duration (d)			r^2 (%)
	SD	LD		a_1	I_S	I_L	
Weakly sensitive / insensitive (I)							
CSH 1	21	28	43(6.4)	4.7(0.65)	10.7(0.92)	16.9(1.10)	84
IRAT 204	16	22	I[b]	7.4(0.48)	8.1(0.75)	14.8(0.82)	92
IS 3693	21	27	20(6.5)	6.9(0.66)	9.8(1.17)	15.8(1.23)	92
Dorado	26	35	I[b]	8.9(0.92)	13.5(1.46)	22.6(1.57)	89
Moderately sensitive							
E 35-1	27	43	110(27.9)	8.9(0.67)	13.7(1.10)	29.6(1.5)	96
S 35	22	37	91(17.2)	7.8(0.53)	10.6(0.79)	25.3(1.0)	94
Highly sensitive							
Framida	17	31	221(82.9)	6.3(0.15)	4.2(0.23)	18.0(0.31)	98
IS 2284	15	30	152(19.8)	6.5(0.14)	3.7(0.20)	18.9(0.31)	97
Naga White	14	29	131(21.3)	4.4(0.15)	4.8(0.21)	20.3(0.32)	98
Seredo	20	50	194(47.0)	9.3(0.58)	8.0(0.76)	33.2(1.5)	96

[a]Degree days delay in time to flowering per hour delay in daylength above critical photoperiod. Results are from a separate experiment.
[b]Insensitive below 15.5 h d^{-1}.

plot and genotypes as subplots. Within each subplot, pots were completely randomized every week to minimize environmental influences. From each replication, one randomly selected pot was transferred after seedling emergence from LD to SD and vice versa daily in 1992, and on alternate days in 1993. Three pots in each replication were kept continuously in both LD and SD without reciprocal transfer, and were designated as control treatment plants. The plants from these pots were used to determine the time to PI in LD and SD. Individual plants were dissected for each transfer time and examined under a dissecting microscope to determine the time to PI. Eastin (1972) and Powers et al. (1980) provide illustrations of panicle development from inception through panicle initiation in sorghum and pearl millet. In our study, it was considered that the PI stage has occurred when the vegetative apical meristem elongated to 0.5 mm size as a glossy, globular structure just before the appearance of the primary panicle branch primordia on the floral apex. This corresponds to Figure 15-2 of Eastin (1972).

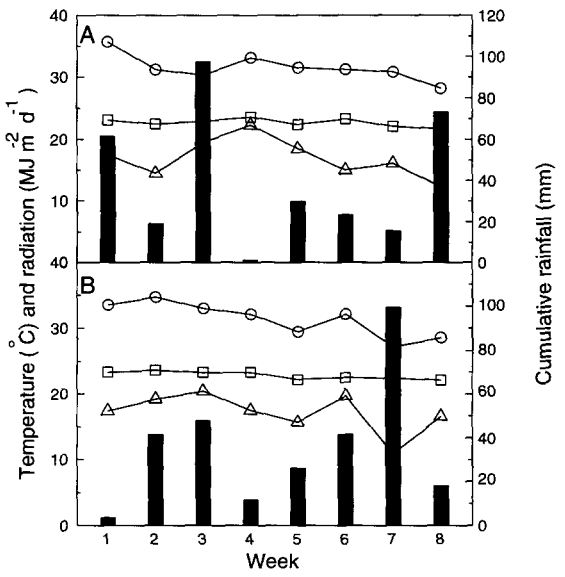

Fig. 1. Weekly mean maximum (○), minimum (□) temperatures, radiation (△), and cumulative rainfall (bars) for the 8-week period of the experiment during 1992 (A) and 1993 (B).

2.1.3. Analytical methods

A new nonlinear holistic statistical approach has been developed by Ellis et al. (1992) to objectively assess the duration of a_1, I_L and I_S from the observations of time to PI for plants reciprocally shifted (t_c) from LD to SD and vice versa. The time to PI

(f) for all reciprocal treatments can be defined as suggested by Ellis et al. (1992) using the following four equations.

For transfers from LD to SD:

$$f = a_1 + I_S \text{ when } t_c \leq a_1, \quad \text{(including SD control where } t_c = 0), \tag{1}$$

$$f = t_c + I_S - (t_c - a_1) I_S / I_L \times \text{when } a_1 < t_c < a_1 + I_L, \tag{2}$$

$$f = a_1 + I_L \text{ when } t_c \geq a_1 + I_L. \tag{3}$$

For transfers from SD to LD:

$$f = a_1 + I_L \text{ when } t_c \leq a_1, \quad \text{(including LD control where } t_c = 0),$$

$$f = t_c + I_L - (t_c - a_1) I_L / I_S \times \text{when } a_1 < t_c < a_1 + I_S, \tag{4}$$

$$f = a_1 + I_S \text{ when } t_c \geq a_1 + I_S$$

The detailed derivations for these equations are provided by Ellis et al. (1992). A GENSTAT program, specially written at Plant Environment Laboratory of University of Reading, UK, was used in this study to analyze the data obtained from these reciprocal-transfer experiments. This program uses the principals of FITNONLINEAR directives of GENSTAT V, Release 3 (GENSTAT 5 Committee, 1993). The FITNONLINEAR directive is an iterative procedure which requires initial estimates of a_1, I_L and I_S. The initial parameter values were estimated graphically from experimental data and used as input to the program. Since time to PI is a continuous variable, the data was log transformed and used in the iterative procedure.

2.2. Experiment II

Six sorghum cultivars (CSH 1, Seredo, E 35-1, IS 2284, Naga White, and Framida) were grown under three photoperiods: short daylength (SD: 10 h d^{-1}), normal daylength (ND: 12.8 h d^{-1}), and long daylength (LD: 17 h d^{-1}). Plant husbandry, culture, and experimental design (with four replications) were similar to Experiment I. Each day, plants in the SD treatment remained inside the cloth enclosure (as described in Experiment I) only from 0600 to 0730 h and from 1730 to 1830 h. Since both the experiments were located next to each other, daily weather conditions for this experiment was similar to Experiment I. The time to PI was determined as in Experiment I. After the attainment of PI in each of the three daylength treatments, three plants were retained in each pot and plants from all three treatments were grown subsequently under ND conditions until flowering stage. Time to 50% flowering was recorded in each plant when pollen grains were shed from anthers in the top half of the panicle.

3. Results

Daily weather conditions during the experimental period are presented in Fig. 1. There were 28 rainy days during 1992 and 21 d in 1993, and both maximum and minimum temperatures fluctuated marginally. The temperatures inside the cloth enclosure used in the SD treatment were generally higher by 1–2°C than outside, but only when the covers were applied at 1630 h. There was no differences in temperature inside and outside the enclosure when covers were applied in the morning hours. Since cloth covers were used as light-out shelter in SD treatments, it was assumed that there was free gas exchange inside and outside the cloth cover preventing likelihood of abnormal build up of CO_2 beyond the 350 μmol mol^{-1} inside the enclosure that might delay development of plants.

Plants in all cultivars studied reached PI stage in both continuous 8 and 17 h d^{-1} length treatments since most cultivated sorghum germplasm shows quantitative SD photoperiod response (Quinby and Karper, 1945). The LD treatment delayed PI compared with the SD treatment (Table 1). The delay was least in IRAT 204 (6 d) and greatest in Seredo (30 d). The delay in PI among cultivars between SD and LD was related to their intrinsic photoperiod sensitivity. In the weakly sensitive group, the delay ranged from 6 to 9 d while in the highly sensitive group it ranged from 14 to 30 d.

The nonlinear holistic model described the response of all cultivars (Figs. 2–4); the r^2 values ranged from 84 to 98% (Table 1). In this study, very short (8 h d^{-1}) and very long (17 h d^{-1}) photoperiods were used for the reciprocal treatments. The long

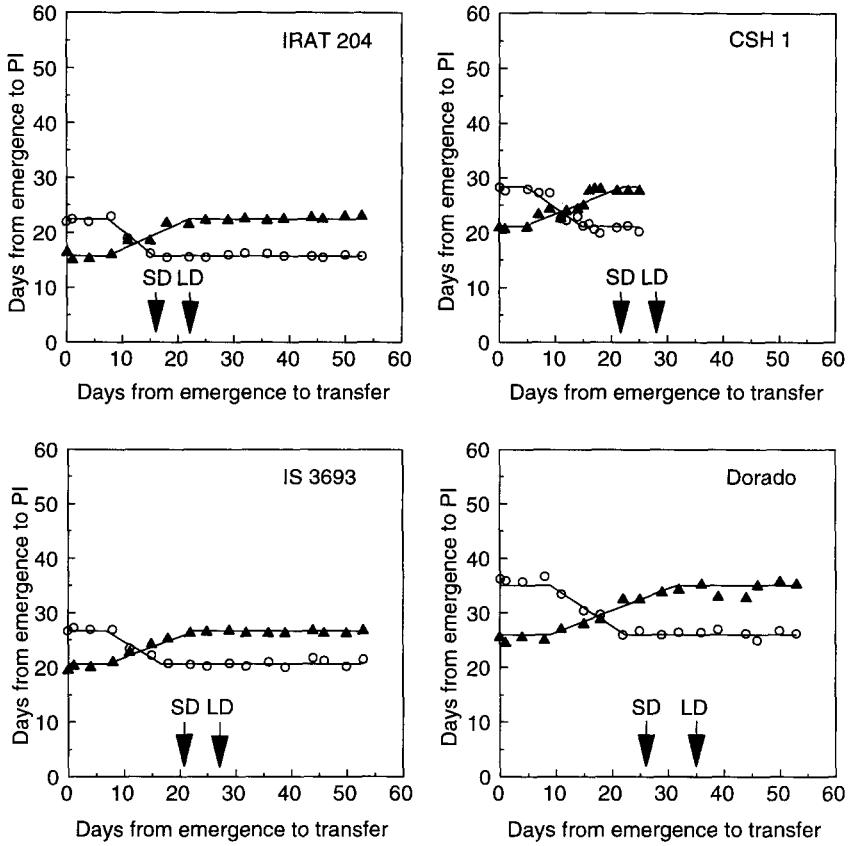

Fig. 2. Time from seedling emergence to panicle initiation (PI) for plants transferred from SD to LD (°) and from LD to SD (▲) at various times after seedling emergence in cultivars from the weakly sensitive/insensitive group. Solid lines are fitted lines from the nonlinear regression model. Arrow marks indicate the time to PI in continuous SD and LD.

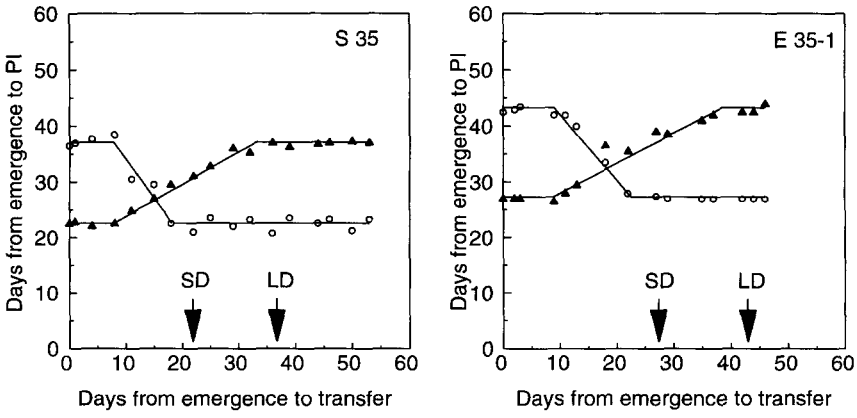

Fig. 3. Time from seedling emergence to panicle initiation (PI) for plants transferred from SD to LD (°) and from LD to SD (▲) at various times after seedling emergence in cultivars from the moderately sensitive group. Solid lines are fitted lines from the nonlinear regression model. Arrow marks indicate the time to PI in continuous SD and LD.

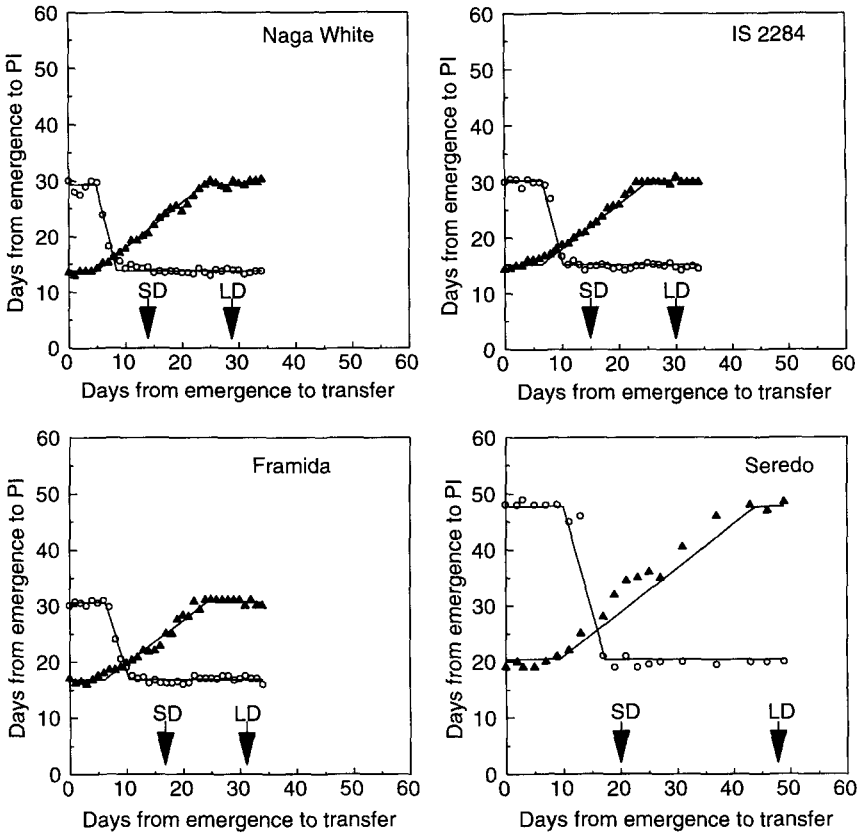

Fig. 4. Time from seedling emergence to panicle initiation (PI) for plants transferred from SD to LD (°) and from LD to SD (▲) at various times after seedling emergence in cultivars from the highly sensitive group. Solid lines are fitted lines from the nonlinear regression model. Arrow marks indicate the time to PI in continuous SD and LD.

photoperiod was beyond the critical or minimum threshold photoperiod, which ranged from 11 to 13 h, above which sorghum responds to changes in photoperiod (Alagarswamy and Ritchie, 1991). In view of this experimental condition, the response of cultivars, despite their intrinsic differences in photoperiod sensitivity, was remarkably similar to the reciprocal treatments. However, the magnitude of response to photoperiod was different among them.

The durations of a_1, I_L and I_S were determined using the holistic regression analysis (Table 1). The value of a_1 varied from 4 d in Naga White to 9 d in Seredo. The duration of a_1 as a proportion of time to PI varied from 22 to 47% in SD and 15 to 33% in LD. Under SD, the highly sensitive group required on an average only 5 inductive cycles (I_S) to promote PI, compared with 11 inductive cycles in the other two groups. In LD, the highly sensitive group required on an average 23 inductive cycles (I_L), compared with 17 inductive cycles required in the weakly sensitive group. In most of the cultivars examined, the photoperiod-sensitive period I_L and I_S ended 3–7 d before completion of PI (Figs. 2–4). In IRAT 204, the end of the photoperiod-inductive period almost coincided with the occurrence of PI.

4. Discussion

In understanding and modelling plant development in cereals, it is commonly assumed that: (i) the vegetative stage is most sensitive to photoperiod but temperature influences all developmental stages, and

(ii) the response to photoperiod is usually completed by the time the meristem becomes reproductive. The support for these assumptions originated from field studies in which crop development was determined from crops sown at different times (Hay, 1986; Martin et al., 1993) and from studies where plants were reciprocally transferred from SD to LD in growth chambers (Kiniry et al., 1983; Wilkerson et al., 1989). Delays in floral initiation due to maturity type or non-optimal daylength have been directly related to time to flowering in maize (Hunter et al., 1974; Kiniry et al., 1983), in soybean (Mayers et al., 1991), and in temperate cereals (Lopez-Castaneda and Richards, 1994). Results of this study also indicated the importance of the duration of the initial vegetative stage in determining the time to flowering in photoperiods ranging from 10 to 17 h d^{-1} (Fig. 5). This remarkable and consistent relation across crops is understandable because the duration of the vegetative phase determines the total number of leaf primordia to be initiated, and subsequently all leaves must emerge and expand to their full size before flowering can occur. It is important therefore to determine the duration of the vegetative phase in order to reliably predict time to flowering and total crop duration in crop simulation models.

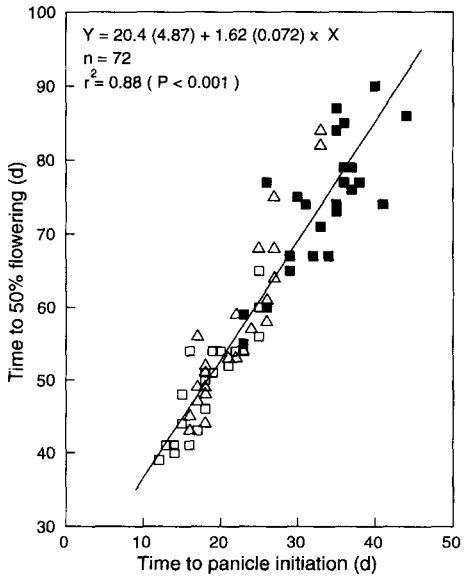

Fig. 5. Relation between the time to panicle initiation and the time to flowering in sorghum cultivars grown under 10 h (□), 12.8 h (△), and 17 h (■) daylengths. (Data are from Experiment II.)

4.1. Duration of the vegetative phase

The basic vegetative phase (BVP) is the minimum duration from seedling emergence to PI at very short photoperiod (Vergara and Chang, 1969). Major and Kiniry (1991) indicated that the BVP is the sum of the photoperiod-insensitive juvenile period and the photoperiod-inductive period (PIP). One of the main causes for low yields in several crops that show quantitative short daylength response is their precocious flowering behavior under the short daylength and warm temperatures that exist in and around the equator. Rapid development and the early cessation of the vegetative phase normally lead to smaller plants. Under such conditions, one way suggested to prevent precocious flowering is to utilize germplasms with a long juvenile period. Since the juvenile period is insensitive to photoperiod, such lines will flower late even under short days. Genetic variations for juvenile period have been shown in soybean (Wilkerson et al., 1989; Collinson et al., 1993). For successful low-latitude adaptation of soybean originating from higher latitudes, the use of cultivars with longer juvenile period has been suggested (Parvez and Gardner, 1987; Hinson, 1989; Kiihl and Garcia, 1989; Lawn, 1989; Neumaier and James, 1993). Results from several studies showed that sorghum genotypes differed in time to PI even when grown under a 10-h daylength (Caddel and Weibel, 1971; Quinby et al., 1973; Major et al., 1990). Since the daylength in these studies was < 10 h, any genetic differences in time to PI could likely be due to differences in duration of juvenile period. The duration of the juvenile period among the cultivars used in this study varied from 5 to 9 d. However, results from Alagarswamy and Ritchie (1991) indicated that the juvenile period among 25 sorghum lines ranged from 10 to 23 d. The existing information indicates the presence of genetic differences in juvenile period within sorghum germplasms. There are opportunities for utilizing a long juvenile period to breed early sorghum that is required in some agronomic niches near the equator. This approach might prevent sorghum from flowering too early in SD conditions. However, the use of the juvenile trait in improving

the adaptability of sorghum to SD conditions needs to be evaluated.

4.2. Duration of photoperiod-sensitive period

In the analysis of reciprocal experiments, the time from seedling emergence to PI was used to determine the durations of photoperiod-sensitive and -insensitive intervals. Previously, graphical (Kiniry et al., 1983) and segmental regression (Wilkerson et al., 1989) methods were generally used. Recently, a new nonlinear holistic statistical approach developed by Ellis et al. (1992) was successfully used in rice and soybean (Collinson et al., 1992, 1993). Results from the present study indicate that this holistic method also estimated the durations of a_1, I_L and I_S in sorghum.

The duration of the photoperiod-inductive period (PIP) is determined by the presence of photoperiod genes and their interaction with the prevailing photoperiod and temperature. The duration of PIP under short and optimal photoperiod (< 10 h d^{-1}) is said to be constant in soybean (Wilkerson et al., 1989). The duration of PIP in sorghum, unlike in soybean, ranged from 4 to 14 d in SD and from 15 to 33 d in LD (Table 1). The sorghum germplasm that originated around the equator is known to be very sensitive to even small changes (< 15 min) in daylength (Goldsworthy, 1984). The cultivars from the highly sensitive group of this study all originated from near the equator, and their relative photoperiod sensitivity ranged from 130 to 220°Cd for every hour increase in photoperiod beyond a critical threshold (Table 1). Strong photoperiod sensitivity is the characteristic of West African sorghum germplasm that enables it to flower nearly at the same time irrespective of sowing time (Kassam and Andrews, 1976). This germplasm has evolved a fine-tuned phenological survival mechanism that adjusts flowering and maturity to the most productive time relative to the availability of soil moisture.

4.3. End of the photoperiod-inductive period

In most crop simulation models, it is assumed that the end of PIP coincides with PI (Jones and Kiniry, 1986; Alagarswamy et al., 1989; Godwin et al., 1989; Rosenthal et al., 1989; Penning de Vries et al., 1989; Alocilja and Ritchie, 1991). From a reciprocal transfer study, Kiniry et al. (1983) indicated that the photoperiod-inductive period in maize plants began 4–8 d before the end of BVP and ended around the time of tassel initiation or soon thereafter. However, recently, Collinson et al. (1992) showed from a similar experiment on rice that PI occurred after 80% of PIP. This indicates that plants remain photoperiod-sensitive for a very short period after completion of PI. Results from the present study clearly showed that PIP in all 10 cultivars ended a few days before PI was observed under both SD and LD (Figs. 2–4). The reason for differences between rice and sorghum in the end of PIP in relation to the occurrence of PI needs further examination.

Sorghum plants reach the PI when an enlarged and glossy globular structure can be seen under the microscope at the tip of the vegetative meristem. This enlargement of the shoot apex in most cereals results from the contemporaneous expansion of leaf and panicle primordia. The interval between the completion of PIP and appearance of the globular structure under a microscope probably represents the time required for the photoperiod-inductive stimulus to promote cell division and expansion sufficient for the morphological change to become visible in the shoot apex. Further, in SD plants, the shoot apex needs an inductive photoperiod for a short time after receiving the photoperiod-inductive stimulus from the leaves for the formation of a normal panicle. If plants experience noninductive photoperiod immediately after receiving the inductive stimulus, reproductive primordia can revert back to vegetative state, producing leafy structures instead of a panicle (Pugsley, 1966; Ong and Everard, 1979).

Since development is a progression of responses to the environment, there are historic as well as current effects of environment on development (Slafer and Rawson, 1994). From experiments in which wheat plants were transferred between different photoperiod treatments, Slafer and Rawson (1995) supported their earlier proposal that both current photoperiod and a 'memory' of the past photoperiod affect development of wheat. Whether sorghum development beyond PI is influenced by current photoperiod or by 'memory' cannot be answered from the present study because the experiments were terminated when the plants were already committed to

PI. However, an earlier study in which plants remained in SD (9 h d^{-1}) conditions until PI was completed and were subsequently transferred to various photoperiods ranging from 9 to 18 h d^{-1} until flowering indicates no current or 'memory' effects of photoperiod on development beyond PI in sorghum (Alagarswamy, 1993). This finding, in conjunction with the results reported here, supports the assumption followed in the phenology subroutines of the CERES Sorghum crop simulation model that the photoperiod-sensitive phase ends at PI when the meristem turns from vegetative to reproductive.

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