EFFECT OF PHOTOPERIOD AND TEMPERATURE
ON THE MATURITY OF SORGHUM

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CHAPTER I

INTRODUCTION

Sorghum (Sorghum bicolor (L.) Moench) was probably domesticated about 3000 B C in the tropics of Africa (21, 22). It was brought to the United States about the middle of the 19th Century (53, 54, 123). The first sorghums grown in the U. S. were very tall and late types. The acceptance of this crop followed the selection of short, early maturity types which made it adaptable to wider growing areas and mechanical harvesting.

Several researchers have discussed the history of sorghum varieties in the U. S. (3, 53, 123). At one time about 400 varieties were grown in the U. S. Since the 1920's many varieties have appeared as the result of cross-breeding and selection, and new inbred lines continue to be developed to serve as parents for hybrids.

Actually, very little of the enormous germ plasm bank that exists in the world collection of sorghums, which includes over 10,000 entries, has been used. The main deterrent to the use of new gene sources is the fact that most of the tropical varieties are sensitive to photoperiods. During the summers in the temperate areas of the world, these varieties will not mature. One of the first things a breeder must accomplish while selecting among segregates from a cross involving a tropical parent is to select for early maturity. Since the maturity of a plant is the result of genetic and environmental factors, the breeder needs techniques to assist in the determination of the genotypes.

Control environment chambers may be a very useful tool for plant breeders, using new sources of germ plasm for the improvement of sorghum. With such facilities, breeders may learn more exactly what effects photoperiod and temperature have on plants. Then through the use of such facilities, plant breeders may produce certain environments under which effective selection procedures may be utilized.

The objectives of this study were (1) to determine the effects of several photoperiod and temperature regimes on the maturity of some sorghums; (2) to determine the age at which sorghums respond to photoperiod and temperature regimes; (3) to determine the age at which sorghum is most sensitive to changes in photoperiods; and (4) to develop the technique of growing and studying sorghums in control environment chambers.

CHAPTER II

LITERATURE REVIEW

The general effects of photoperiodism have been observed for a very long time (67), but in 1920 Garner and Allard (30) showed that such effects were not isolated curiosities. Since that time many scientists have reported observations related to the effects of photoperiodism on nearly all forms of plant and animal life (20, 33, 41, 62, 108). At this time papers reporting photoperiodic responses have become so numerous that it would be an insurmountable task to read all of them or even the review articles.

Shortly after it became obvious that photoperiodism was a very common phenomenon, researchers attempted to explain how it worked. It was obvious that some type of timing mechanism was involved. In 1960 Borthwick and Hendricks (6) showed that photoperiodic responses were closely related to several other light-related reactions in plants in that they were under the control of a plant pigment system called phytochrome. The timing mechanism they hypothesized, later known as the hour-glass concept (41, 90), involved the conversion of red light absorbing phytochrome (P_R) to far-red absorbing phytochrome (P_{FR}) by red light and the conversion of P_{FR} to P_R by the action of far-red light or darkness. They believed that P_{FR} (the enzymatically active form) changed in darkness to the inactive P_R form in the course of several hours, and the rate of the change and the rate of the enzymatic reactions were the essential factors in the plant's measurement of dark length.

This was a fairly straight-forward theory, as far as the chemical processes are concerned, but there is much evidence that much more is involved.

According to several writers (9, 35, 41, 88), Bünning (8) first proposed that endogenous rhythms participated in photoperiodic reactions in 1936. Now, most researchers are convinced that the endogenous rhythms are, in some way, involved with the photoperiodic response. In both long-day and short-day plants the flowering response depends upon the time at which the plants are exposed to light in relation to the ocillation of the rhythm. There seems to be a photophil (light requiring) phase and a scotophil (dark requiring) phase of the rhythm, and plants flower only if exposed to light during the proper phase.

Even though results have conclusively shown the existence of circadian patterns in relation to photoperiodic responses, a complete explanation as to how this makes plants flower has not been put forth.

There is much evidence reported throughout the literature which suggests the existence of a flowering harmone, but the search for the enzyme called florigen has been as fruitless as the search for the exact timing mechanism for photoperiodic reactions (40, 90).

It has been shown repeatedly that the timing mechanism for photoperiodic reactions are temperature independent (33, 90). However, since the general metabolism of plants is, at least indirectly, controlled by temperature, it is not surprising that temperature also controls the rate of maturity (107). Apparently the temperature effect is responsible for changing the rate of the transportation of inducers or inhibitors and the rate of enzymatic reactions following floral induction.

This literature review is divided into three sections according to crops. First, most of the literature related to maturity in sorghum will be discussed. In the next two sections, some of the literature on the other two important short-day cereals (corn and rice) will be reviewed. It appears reasonable to think that all three of these crops might behave similarly since their origin, evolution, domestication, and breeding are similar.

Sorghum

The literature reporting the results of experimentation related to sorghum's maturity is primarily devoted to the genetics involved, but several workers have reported the influence of temperature, and a few demonstrated sorghums photoperiodic response. Much of the literature dealing with maturity also includes generalized observations on plant characteristics such as height, leaf number, yield, etc.

In general sorghums are reported to be short-day plants, but the response to day lengths varies greatly. There has been at least one unconfirmed report that sorghum gave a long-day response (102), but Quinby (76) stated that it is highly doubtful that any sorghum is truly a long-day plant. Garner and Allard (31) were the first to report a photoperiodic reaction in sorghum. They showed that short days hasten maturity. Martin (61) stated that since sorghums were short-day plants the long days in the summer in the United States prevented tropical varieties from maturing. Winter plantings in Florida permitted the maturity of these types. He added that the commercial varieties could be matured under 16-hr days.

Quinby and Karper (79) reported the results of subjecting milos to normal (14-hr) day lengths and artificial short (10-hr) day lengths. Under 10-hr days five pure line milos, that differed in maturity genes bloomed at very similar dates. These varieties were much later and differed greatly in the number of days to anthesis under long days. They also showed that the number of days to floral initiation and number of leaves were controlled by photoperiods.

Later, Quinby and Karper (81) reported the results of subjecting many different types of sorghums to normal and short photoperiods. These results showed that the difference in day length caused a great range in response. Dwarf broomcorn exhibited no response to photoperiod in days to floral initiation or anthesis, whereas, Lemon Yellow initiated its head 43 days later and bloomed 55 days later under long-day conditions. Most of the other varieties exhibited some response to the day length. The short days shortened the interval from planting to initiation in all sensitive varieties. The interval from floral initiation to bloom was shortened in some varieties, lengthened in some varieties, while others exhibited no change in this interval.

Coleman and Belcher (17) compared five sorgo varieties grown in Mississippi in the spring and in southern Florida in the winter. Their results indicated that short days hastened anthesis, but the temperature was also very important.

Miller, Barns, and Cruzado (63) reported the effects of photoperiod on the maturity of 15 tropical sorghums, 7 temperate varieties, and 8 maturity genotype testers. They planted during each of 12 consecutive months in Puerto Rico. They suggested that tropical sorghums have a lower critical photoperiod than U. S. sorghums. All the types flowered at about the same time when planted from mid-September to mid-November. They divided the varieties into five general response classes on the basis of different photoperiod thresholds and the amount of response.

Sen Gupta and Saha (93) clearly demonstrated that *Sorghum roxburghii* var. *hians* (Jowar) (probably a shallu type) was a short-day plant by planting on monthly intervals and subjecting it to various day lengths. Ingle and Rogers (44) reported that the amount and duration of vegetative growth of *Sorghum halepense* (L.) Pers. was proportional to the day length. Their data showed that johnsongrass exhibited a quantitative short-day response, and that the photoperiodic response was dependent upon the temperature. At higher growth chamber temperatures they observed a greater response to photoperiod.

Lane (58) reported the results of some far reaching experiments dealing with physiological aspects of the photoperiodic response in milos. He showed that four milo genotypes required 19 days for floral initiation under 10-hr days, but they required from 35 to 70 days under 14-hr days. Floral development following initiation was retarded if the plants were subjected to long days. The critical photoperiods (lengths of day necessary to delay floral initiation) were 12 to 13 hours for these four genotypes. He also noted that floral primordia were observed even under continuous light. Light quality is very critical in photoperiodic studies (58). Light periods, 10-hr long, ending with incandescent light, hastened maturity more than those ending with florescent light. Short interruptions of a 14-hr dark period delayed floral initiation. The effectiveness of the interruption depended upon light intensity, source, and genotype. Further experiments indicated that red light inhibits floral initiation more than far-red and the reversal between red and far-red absorbing phytochrome could be carried out through several cycles. The hastening effect of far-red light applied to these milos at various times during dark periods depended upon the length of the dark period, the time and length of the far-red exposure, and the variety. From his measurements of phytochrome he concluded that all the varieties had the same basic phytochrome mechanism, and genetic differences worked through a dark-dependent step subsequent to phytochrome action in floral induction.

Vinall and Reed (122) stated that the optimum temperature for growth in sorghums is 92 or 93 F and that they could not thrive in regions of low temperature. They also pointed out that best yields are obtained if the soil is warm during germination and emergence, but moderate temperatures during flowering and fruiting enhance seed production. In summarizing the influence of temperature on sorghum production, Martin (61) concluded that the mean July temperature should be above 75 F, and from 120 to 160 frost-free days are required for high yields. Stoffer and Van Riper (103) reported results that confirm these generalizations. For good growth, they showed that the soil temperature must not go below 65 F. They also showed that as the temperature increased from 49 F to 70 F yield increased, carbohydrate content of the grain increased, plants grew faster, and reached the 8-leaf stage sooner.

Quinby and Karper (82) assumed that all varieties of sorghum were short-day plants because Hamner (34) stated that when photoperiodic sensitive types were found in a species all the other plants of that species should react similarly. For this reason they said that those sorghums which were not hastened by short days had a different thermal requirement. They stated that the thermal requirement must be met before a variety may react to a given photoperiod. Miller, Quinby, and Cruzado (64) attribute the variation in maturity of eight milo genotypes grown under winter Puerto Rican conditions to differential temperature responses. December planted sorghums in Puerto Rico were later than would be expected due to photoperiod alone (63). They concluded that the temperature was too low for maximum expression of the photoperiodic response. They also speculated that the U. S. sorghums, in their studies, did not respond to day length differences because a thermal requirement was not met.

Coleman and Belcher (17) showed that differences in spring plantings in Mississippi and fall plantings in Florida were due to a complex interaction of genotype, day length, and temperature. Hodo was the latest maturing in the summer but was early in the winter. Collier, on the other hand, was intermediate in the spring planting but was the latest maturing variety in the winter. Again, this indicated the thermal requirement must be met before a variety could respond to short days. The idea that the thermal requirement varies from variety to variety is illustrated by the fact that Honey and Hodo gave a large response to the short winter days even when the daily mean temperature was below 70 F.

Quinby (76) compared the number of days to anthesis for several varieties planted in the field at Kingston, Jamaica and summer plantings at Chillicothe and Plainview, Texas. Kingston had short cool days. Both Texas plantings had long warm days, but the night temperature was less at Plainview. His data show that some photoperiodic sensitive varieties may not respond under cool short days. However, some varieties showed no response to the temperature difference. Quinby (76, 77) reported that a difference of 2 C during the night is sufficient to cause a week or more difference in anthesis. Some varieties are hastened while others are delayed. This was demonstrated by planting on different times (both during relatively long days) and planting at different altitudes.

Pauli, Stickler, and Lawless (72) planted sorghums on May 1, May 20, June 10, and June 20. In general their results showed that earlier plantings delayed floral initiation, lengthened the interval from floral initiation to anthesis, and reduced the time from anthesis to physiologic maturity. The period from planting to physiologic maturity was shortest during the June 10 planting.

Fryer, Pauli, and Stickler (27) reported the influence of temperature on anthesis date of six varieties of sorghum at eight Kansas locations during five years and four planting dates per year. They concluded that daytime temperatures above 70 F during the first 30 days of growth hastened maturity, as did 80 F temperatures after the first 30 days. Nighttime temperature in the 60's retarded maturity, but nighttime temperatures either below 60 F or above 70 F hastened maturity. Distinct differences among varieties were not observed and they could not predict the time of flowering with precision, using any of their summations. They did show that the total degree hours above 70 F during the first 20 days of growth were consistently and significantly related to the time of half bloom. This is probably important because it fixes the time of floral initiation.

Clegg and co-workers (15, 16) attempted to apply the concept of heat units to predict the maturity of several hybrid sorghums. They used several planting dates over two years, three base temperatures, and three different methods of calculation of heat units. The number of heat units required for each hybrid to reach 50% bloom was in close agreement during a year, but there was poor agreement between years. There was no consistency between planting dates or years for the number of heat units required for physiological maturity.

Hutchinson (43) implies that maturity of sorghums is a quantitative trait and is under the control of many genes. Quinby (76) states that the genes at only four loci control maturity, but these genes are not fully expressed under short days. Quinby and Karper (79) studied the inheritance of duration of growth and showed that the four milo phenotypes in their study resulted from the action of the genes at three loci. They said lateness was dominant to earliness, but Ma_2 and Ma_3 were not expressed except in the presence of dominant Ma_1. Also, the Ma_3 was not expressed in the presence of dominant Ma_2. The Ma_1 locus was found to be linked to Dw_2, a gene that influences length of internode. The Ma_3 gene was shown to be linked with R (later called Y), a gene that controls the presence or absence of a plant pigment. Under 10-hour days none of these genes were expressed, and all the milo inbreds, as well as the F_2 segregates, matured at the same time. They also stated that these three genes determined the time of floral initiation which, in turn, controlled the number of leaves, the duration of growth, and the ultimate plant size. Later Quinby and Karper (83) discovered that Ryer milo carries an allele (ma_3^R) at the third locus that differs from all the other milos. This locus causes extreme earliness even in the presence of dominant Ma_1. Lines carrying the ma_3^R allele have tall spindly seedlings and have a very surpressed tillering capacity. Further studies by Quinby (75) revealed a fourth maturity locus. This locus was dominant in all the milos, which had been studied so intensely. Both Hegari and Early Hegari were found to carry the recessive ma_4 gene. He noted that the fourth locus appears to be more sensitive to temperature than the other loci. At high temperatures recessive ma_4 acts like dominant Ma_4. When growing during higher night temperatures, lines carrying ma_4 are later than during cooler nights.

All the genetic data related to maturity was summarized by Quinby in 1967 (76). At that time he also presented more data which substantiated many previous assumptions. In that paper he suggested that there may be several, or perhaps many, alleles at each of the four known maturity loci. The combination of these four loci and multiple allelic series along with both photoperiod and temperature effects bring about the extreme variation in sorghum maturity, 38-100 days for anthesis (64, 76, 74).

Quinby and Karper (80) suggested that the heterozygous condition of the maturity genes was the primary reason for heterosis in sorghum hybrids. Later these same workers (82) produced hybrids from inbred isogenic lines that differed by only one allele that affects maturity. All the hybrids produced greater yields of grain and stover than their parents. Hybrids that differed in only one allele, in most cases, produced different yields of grain and stover. In one case, this difference was 37% in yield. This showed that one allele in sorghum can have a great influence on the combining ability of sorghum.

Quinby and Karper (81) also reported that the F_1 from photoperiod sensitive X insensitive were always sensitive, suggesting that sensitivity to day length was a completely dominant character. Hybrids that were relatively insensitive to short days always had two relatively nonsensitive parents. Miller, et al. (64) showed that all the milos studied that were recessive at ma_1 bloomed in about 50 days under short-day conditions and about 60 days under long days. When the dominant Ma_1 allele was present all the genotypes mature at different times under long days. During the Puerto Rican winters the days are short enough to hasten only those milos that carry both dominant Ma_1 and Ma_2 (63). The important difference in maturity of the milos in long and short days is the lack of influence of dominant Ma_1 to cause lateness in short days in the presence of dominants at the other maturity loci. F_2 populations, segregating for Ma_1 and ma_1, exhibit two distinct groups under long days but not under short days (64).

In the main stalk of a sorghum, the growing point (bud) produces leaves during embryo development and from germination to floral initiation. At the time of floral initiation the bud stops producing leaves and starts producing floral structures. If floral initiation is delayed, more leaves are produced. Hasketh, Chase, and Nanda (39) showed that as the temperature and day length increased, the leaf number and photosynthetic area increase.

Dalton (19) has shown under favorable growing conditions, there is a positive correlation between yield and days to maturity. For each additional day required for maturity there is from 150 to 250 kg/Ha increase in yield. With this type of relationship existing, it seems that it will be very difficult for plant breeders to attain high yield levels among early maturity hybrids. Some physical factors have been studied which provide insight into this problem. Clark (14) showed that the embryonic leaf number is very constantly four in grain sorghums. This implies that if more leaves are to be produced before germination, a wide search of the germ plasm is in order to find such a trait. Sieglinger (96) first pointed out the relationship between total leaf number and maturity. He observed that each additional leaf delayed heading by about three days, but some varieties produced leaves at different rates. Quinby and Clark (76, 78), using a different approach, came to the same conclusions. This shows that it may be genetically possible to achieve a greater rate of leaf production. Paulson (73) reported that all meristematic activity in a developing embryo had terminated by 25 days after pollination. Collier (18) concluded that maximum dry weight (physiologic maturity) occurred in about 30 days from anthesis. This is another part of the plant's life cycle that deserves special attention. It may be possible to decrease the time required for seed development without decreasing yield.

Rice

Rice (Oryza sativa L.) and sorghum are quite similar in several respects -- plant morphology, origin, adaptive range, etc. Many of the studies on rice photoperiodism indicate that there are also similarities between these two crops concerning the effects of day length and temperature on maturity. Photoperiodism in rice has been studied more extensively than the other short-day cereals. For these reasons a more detailed study of the rice literature will be more helpful in the interpretation of sorghum results than the other cereals. The literature reporting research work on rice photoperiodism has become voluminous, with an increased interest since 1960. Vergara, Chang and Lilis (113) have summarized much of this literature and attempted to interpret some of the contradictory findings.

Even though some varieties of rice are insensitive to photoperiods, most are sensitive and are generally considered short-day plants (110, 113). Some writers, however, do present evidence to show that short days delay the flowering in rice (29, 65, 66, 99). The delays in maturity attributed to short days are usually small and are probably the result of non-photoperiodic factors, such as light intensity, temperature, cultural practices, etc. (49, 113, 115, 117). Venkataraman (112), Roberts and Carpenter (85) and Yu and Yao (127) have shown photoperiodic response curves which indicate optimum day lengths for rice. Day lengths both longer and shorter delayed maturity. Critical studies of more than 100 varieties at the International Rice Research Institute have not detected any rice varieties with a long-day response (45, 46, 47, 48, 49, 50).

The reproductive phase, from floral initiation to anthesis, and the ripening phase, from flowering to full grain development are fairly constant in rice. They are often considered to require approximately 35 days each (114, 116, 117). Some workers found that temperature did affect these phases slightly. However, it is the duration of the vegetative growth phase that generally varies greatly and which largely determines the growth duration of a variety, especially in the tropics (113). The vegetative growth phase has been divided into the basic vegetative phase (bvp) and the photoperiod-sensitive phase (psp) by several workers. The bvp refers to the juvenile growth stage of the plant which is not affected by photoperiod. It is only after the bvp has been completed that the plant is responsive to photoperiodic stimulus for flowering -- this is the psp of the plants (111, 119, 120).

Vergara et al. (113) state that Suenaga (104) recognized the bvp as early as 1936. The range of bvp, reported in the literature, is from 14 to 63 days (91, 100, 111). Its length has been measured by the duration of the vegetative growth phase at the optimum day length. The bvp also has been measured by subtracting 35 days from the growth duration (sowing to flowering) of plants grown at the optimum photoperiod (119). They assumed that the period from panicle initiation to flowering was about 35 days. The length of the bvp has also been measured in terms of leaf numbers (113). The minimum may be less than five leaves. Some experiments showed that short-day treatments of young seedlings hastened heading (85, 100) or delayed it (66), which indicated a photoperiodic effect while the plants are very young and a very short bvp. The degree of photoperiodic sensitivity in rice plants increased with age (56, 111), but the accompanying increase in leaf area does not explain the observed change. Low sensitivity of young plants may be a matter of completing the bvp. If photoinductive cycles were given before the bvp had been completed, the effective cycles would have been less and the response smaller (113).

Vergara, et al. (113) state that Best (4) gave the following possible explanation for the existence of the bvp:

1. The first leaves formed are completely insensitive to photoperiod.

2. The sensitivity of the first leaves formed is so low that they

do not reach an adequate level of induction to invoke floral initiation before the much more sensitive leaves at higher nodes have reached this stage.

3. The first leaves formed do not attain the induced state before the senescense of these leaves.

4. The total leaf area required before the plant can react by floral induction to the inductive photoperiod is so large that it is reached only at a relatively late state of plant development.

5. The growing point of the young plant is unable to react to the floral stimulus or the stimulus cannot reach the growing point.

The psp determines the degree of sensitivity in photoperiod-sensitive varieties. It lasts at least 31 days and often more than 200 days in photoperiod-sensitive types. Non-sensitive varieties may have a psp from 0 to 30 days (113). Vergara et al. (113) indicated that the response of a rice variety to photoperiod may be measured in terms of the length of the psp, which in turn is determined by both critical photoperiod and optimum photoperiod of the variety. Optimum photoperiod refers to the day length at which the duration from sowing to flowering is at a minimum. Several workers (85, 111, 112, 120, 125) reported 8-10 hours of light per day as the optimum for many day length sensitive varieties. Some workers reported that the less sensitive varieties have longer optimum photoperiods, but others have found no correlation between optimum photoperiod and photoperiod sensitivity of many varieties (126).

Critical photoperiod refers to the longest period at which the plant will flower or the photoperiod beyond which it cannot flower. The critical photoperiod for rice was reported to be about 12 to 14 hours (45, 50, 70, 125). Vergara et al. (113) cited work which indicated that the temperature affected the length of the critical photoperiod and it lengthened as the plants became older. Roberts and Carpenter (86) indicated that optimum photoperiods increased with the increase in temperature. Vergara et al. (113) indicated, in summarizing the photoperiod-sensitive phases, that the psp of a variety is probably a measure of the combined effects of the photoperiod on its optimum photoperiod and critical photoperiod. The shorter the critical photoperiod, the longer the psp. Short optimum photoperiod is also associated with long psp. A variety with a long optimum photoperiod or no critical photoperiod would have a wider adaptability, i.e. it could be planted at any latitude and any season provided it is not too sensitive to temperature.

A photoperiodic cycle which induces the initiation of flowers is called a photoinductive cycle. The minimum number of photoinductive cycles necessary to initiate the panicle primordium of a rice plant is reported to range from 5 to 24. It not only varies with varieties but with the photoperiod used. The minimum number of cycles increased proportionately with the photoperiod used in some experiments but not others (68, 120). The fact that a certain number of photoinductive cycles is required to induce flowering suggests that the stimulus produced by the treatment is cumulative, and that flower induction takes place when the stimulus has reached a certain threshold level (113). Noguchi, Nakajima and Yamaguchi (68) used a variety that requires 10 inductive cycles and interposed a long day in the middle of 10 photoinductive cycles. No flowering occurred. This showed that the long day eliminated the latent potentiality of floral induction previously produced by the five photoinductive cycles.

Floral initiation is a separate process from panicle emergence and sometimes floral initiation occurs with no subsequent head emergence (92). Plants subjected to insufficient photoinductive cycles sometimes form panicles that never emerge (111, 119). Photoperiods have very little effect on insensitive rice varieties (113). A reversal from a reproductive to a vegetative phase has resulted from incomplete stimulation by short-day treatments (68). Sometimes incomplete short-day treatments resulted in a change of a bract primordium into a leaf primordium. Other times true reversal did not occur, the terminal bud stopped growing and a shoot from below the panicle dominated (119).

Various workers have found that the young fully expanded leaves were most receptive to photoperiod but the leaf sheaths, as well as, the culms are also receptive. The stimulus was not translocated from tiller to tiller (91, 114).

Takimoto and Ikeda (105) were unable to prevent the flowering of rice plants with light intensities less than 200 lux during the first or last three hours of a 12-hour dark period. Katayama (56) has shown that twilight in the morning can delay flowering while in the evening it may or may not delay flowering. Twilight ends when the light intensity is about 4 lux, as a general rule. Katayama attributes the greater effectiveness of the morning twilight to higher intensity. Takimoto et al. (105) concluded that twilight had no influence on rice plants' photoperiod.

Yu, Yao, and Wang (128) showed that light breaks during the dark period from a flash to 15 minutes long would delay heading. Their finding showed that the flowering response is determined by the longest dark period. Interruption of the light period with darkness did not accelerate heading.

For convenience, the interval of time from floral initiation to flowering is often considered to be about 35 days (110, 113, 120). However, Sen and Roy (92) found that the interval varies from 10 to 241 days. Vergara et al. (113) stated that 10 days is too short for full panicle development. Vergara and Lilis (117) showed that flowering may be delayed by long photoperiods after floral initiation unless the plants receive more than the minimum number of inductive cycles. Even with these apparent discrepancies, Vergara et al. (113) indicated that subtracting 35 days from the heading date is so much more practical than dissecting plants to determine the date of panicle initiation that it is preferred.

The effect of temperature on the rate of maturity of rice is even more complex than photoperiods. Yao (125) reported that temperatures affect both the photoperiod-sensitive and the photoperiod-insensitive varieties and high temperatures accelerate and low temperatures delay heading. Roberts and Carpenter (86) showed that high temperatures delayed flowering. Others (121) reported that the recently improved rice varieties with a wide adaptive range are sensitive to temperature, and the average minimum temperature gave the highest positive correlation with growth duration. The acceleration of the photoperiodic response by high temperatures has not been fully studied. The effect may be on the basic vegetative phase, photoinductive period, panicle differentiation and development, or critical photoperiod (113). Yu and Yao (126, 127) concluded that the optimum temperature for photoinduction may depend upon the photoperiod, and variety used. Many studies on rice involving photoperiod and temperature were conducted in the field by planting at different dates. Many of these studies may be misleading since so many factors are changed. Vergara et al. (113) pointed out that very small differences in weather conditions produce as much as 156 days difference in the growth duration of the same variety planted on the same day of different years in Malaysia. Using controlled conditions, Owen (71) showed that 15 C night prevented flowering with both 11-1/2 and 13 hour light periods. With these day lengths 23 C night temperature did not inhibit flowering. Nuttonson (69) studying temperate varieties of rice showed that a heat unit concept is far superior to calendar days in reporting growth duration.

Vergara et al. (113) summarized the diverse results of genetic studies of maturity with the following three postulates: (1) monogenic or digenic control of heading date with earliness dominant to lateness; (2) monogenic or digenic control of flowering date, with lateness dominant; and, (3) multiple-factor inheritance in which F_2 populations showed a continuous and often unimodal distribution and in which some populations might produce a bimodal distribution when grown in a different season. They added that most of the divergent interpretations arise from failure to recognize the two phases of vegetative growth, failure to control interactions between environmental factors and genetic factors and failure to relate the phenotypic expression with the prevailing environment.

Studies at the International Rice Research Institute (12, 48, 49, 50) have shown that it was possible to separate tillers from a single plant and study their reaction at various ages to different photoperiods. This enables them to determine the bvp (under 10 hour days) and psp (under 16 hour days) of the same plant. In this way they have studied the F_1 and F_2 progenies from crosses involving sensitive X insensitive. These studies indicated that strong photoperiod sensitivity was controlled by one (Se) or two (Se_1 and Se_2) dominant genes, producing F_2 ratios of 3:1 and 15:1. The F_2 variation in bvp can be attributed to two or more genes (Ef_1, Ef_2 . . .) of cumulative but unequal effects. The short bvp is dominant to the long one. The Se genes are epistatic to the Ef genes under a long photoperiod. An association between photoperiod sensitivity and a short bvp was indicated in some F_2 plants. Semi-dwarf varieties seemed to carry a recessive inhibitor for sensitivity (i-Se), producing an F_2 ratio of 9 sensitive to 7 insensitive. There appears to be a multiple allelic series at the Se_1 locus. Transgressive segregation for bvp was observed in most of the crosses at both ends of the F_2 distribution curves.

Tsai and Oka (109) compared a well adapted late variety with two early isogenic lines, produced by backcrossing to the late variety seven and ten times, to estimate the effects of the early (E) gene block. The line with three extra backcrosses lacked some of the effects of the E-gene block. The primary effect of the E-gene block seemed to promote flower initiation and development. It also increased sensitivity of the plants to temperatures in the floral initiation period. The E-gene block did not seem to affect the seasonal and regional adaptabilities of the original genotype.

Corn

The literature reporting the photoperiodic reaction of maize (_Zea Mays_ L.) is somewhat contradictory. Some writers have assumed that it is day neutral (28, 87), but most report maize as a short-day crop (2, 13, 31, 57, 84, 106). Francis and co-workers (24, 25, 26) have recently reported that maize genotypes range from extremely sensitive to day lengths to day neutral.

Garner and Allard (31) were the first workers to report a photoperiodic reaction in maize. They showed that two tropical varieties reached anthesis about 1 month earlier in artificially shortened 13-hr days than in normal summer Maryland days. McClelland (62) reported similar results. Kiesselbach (57) used maize varieties adapted to Nebraska, Texas, Oklahoma, and Louisiana in trials in these four areas. Nebraska Krug grown in southern states produced silks 13 days earlier than when grown in Nebraska. The southern varieties silked about 18 days later in Nebraska than when grown in the southern areas. Thomas (106) found that artificially shortened days (11-12 hr) hastened both tropical and temperate varieties of maize in Iowa. The most difference in maturity was produced by subjecting the plants to 4 weeks of short days beginning at 4 weeks of age. Galinat and Naylor (28) found that the critical photoperiod for the sweet corn variety C 31 id was 13 hr and that the critical photoperiod decreased with age. Ragland, Hatfield, and Benoit (84) artificially lengthened the spring days and reported a delay of 10 to 14 days in the time required for silking.

Francis, Grogan, and Spearling (24) evaluated 40 maize inbreds and two hybrids for photoperiod sensitivity. These lines represented early and late maturing types, as well as, tropical and temperate varieties. They used 10- and 16-hr days with 30 C days and 25 C nights in growth chambers. Under these conditions they demonstrated a wide range in sensitivity to photoperiod. The most sensitive line underwent initiation more than 16 days sooner under the short-day condition than under the long-day regime. Since they selected several genotypes with a wide adaptative range, most of the differences in maturity between the two photoperiods were not significant. One genotype gave a long-day reaction. Early maturing inbreds often showed little sensitivity.

Francis, Sarria, Harpstead, and Cassalett (25, 26) developed a technique to screen maize genotypes for photoperiod sensitivity under Colombian field conditions. They extended the day-lengths to 17 hours and also produced a light intensity gradient from about 20 ft-c to less than 1 ft-c. Of the 48 genotypes tested, 25 were classified as sensitive to photoperiod. Two Carribean genotypes and a hybrid from Minnesota exhibited very little delay in floral initiation under the long days. Among the sensitive genotypes, the time from emergence to floral initiation was 20 to 26 days longer under the longer days in their spring planting. The results from the fall planting differed somewhat. The average difference due to day lengths among the sensitive group was 22.5 days in the spring, compared to 16.8 days in the fall. Several of those genotypes which appeared to be intermediate in sensitivity in the spring became more sensitive in the fall. In the group classified as insensitive in the fall the difference due to day length was also less than in the spring. The fall planted insensitive group included one which was previously classified intermediate and one which was classified as sensitive in the spring.

Francis et al. (26) reported differences in photoperiodic reaction due to light intensity. In general the light was more effective as the intensity increased toward 20 ft-c. They presented evidence which suggests that the light intensity required for photoperiodic reaction varies with different genotypes and definite thresholds were exhibited within given genotypes.

Arnold (2) subjected five varieties of sweet corn to 10, 13, and 16 hr day lengths at 75 F in growth chambers. He showed that varieties adapted to the tropics or subtropics were more likely to respond to different photoperiods than those adapted to temperate regions. He also showed that Major Belle, a photoperiodic sensitive variety, had a critical day length between 13 and 16 hrs. Long days delayed the dates of tassel initiation and tasseling.

The effects of temperature on the maturity of maize has been studied by many workers (2, 60, 94, 97, 106). In general they have shown that warmer temperatures increase the rate of maturity from planting to anthesis. Shaw and Thom (94, 95) showed that the time from anthesis to physiologic maturity is very constant. This implies that the environmental conditions during the interval from planting to anthesis have a greater effect on maturity than those after anthesis. Cassalett, Llano, Arboleda, and Sarria (10) reported that the date of silking for each of the 23 races of Columbian maize remained constant when planted in five different temperatures ranging from 29 C to 14 C. However, yield and height were reduced drastically when races adapted to the hot climates were grown in the cooler areas.

Arnold (2) reported that exposure to warm (95 F days and 80 F nights) and cool (70 F days and 55 F nights) temperatures in the periods from the 5th leaf stage to tassel initiation, tassel initiation to ear initiation, and ear initiation to row initiation, resulted in a complex situation. The time of pollen shed or silk appearance was influenced by both the time of tassel, ear, and row initiation and the number of leaves still to become visible. He found no effect on initiation, tasseling, or silking due to the temperatures from the 5th leaf stage to tassel initiation. However, warm temperatures hastened tasseling and silking when applied between tassel and ear initiation. Warm temperatures also hastened silking when applied between ear and row initiation. Francis et al. (26) reported that photoperiodic sensitivity is, in general, greater in spring planted than fall planted maize in Colombia. This demonstrates that the temperature effect is expressed partially through the photoperiodic response. Shaw and Thom (94) stated that the interval from planting to tasseling is decreased by three days for every 1 F increase in temperature. Gilmore and Rogers (32) used 15 methods to calculate the number of heat units required for silking. They concluded that "effective degrees" were adequate to classify the maturity of genetic material in different areas and years.

Studies on the genetics of maturity have been reported by several workers. Singleton (98) assigned id to a single gene which caused indeterminate growth in maize. The mutant was found in C31 sweet corn and was recessive to the gene causing normal, determinate growth and growth type. Galinat and Naylor (28) showed that the id mutant from C31 also affected vegetative proliferation of the tassel under long days after the plants have been induced to flower with short days. Yang (124) reported that 2 or 3 genes were responsible for date of silking in the crosses between early and late types that he studied. He stated that dominance of the maturity genes produced earlier plants. His results also showed that maturity genes and height genes segregate independently.

Rogers (87) studied the inheritance of photoperiodic responses in maize-teosinte crosses. He used both Guatemalan teosinte, which is very sensitive to day lengths, and Mexican types which are less sensitive. The weak photoperiodic response of the maize parent was almost completely dominant to the Mexican teosinte's response, but the Guatemalan teosinte-maize crosses exhibited a lack of dominance. He stated that there are several major genes and many modifiers controlling photoperiodic response, and these genes did not affect tillering.

Leng (60) and Siemer, Leng, and Bonnett (97) showed that heterosis affects both the time from planting to tassel initiation and from initiation to anthesis, but these intervals were under the control of different genes. Brawn (7) reports that maize yields well in southern Canada and that the short growing season is a greater problem than the long cool days in the summer.

Gaspe Flint is a very early flint corn which has been used in attempts to breed for earliness (7). Genetic studies showed that the heretibility of days to silk was 26% in Gaspe X W9 crosses and 79% in Gaspe X WF9 crosses. There appears to be about 29 and 8 genes segregating from crosses with Gaspe X W9 and Gaspe X WF9, respectively.

Arnold (1) studied 8 sweet corn varieties in 11 plantings during three seasons in relation to the time required for development. He found that "70 degree days" were more easily used than conventional heat units or degree days. Differences in the time required to reach harvest at 72% kernel moisture was primarily established by the time of pollen shed and silking and to a lesser extent by tassel initiation. He also showed that several physical characteristics were closely related to maturity rate. The interval from planting to tassel initiation and pollen shed were closely correlated to the number of leaves on the main stalk. The time from planting to silking was closely related to number of leaves and ear length. The time required from silking to harvest was closely correlated with yield and per cent oil in kernels. The rate of leaf development from the 4th to the 8th leaf was found to be the best index of rate of development. Several workers have shown other relationships between vegetative development and the maturity of maize which may be useful in breeding for rapid maturity and high yield. Hubbard and Leng (42) and Brawn (7) have attempted to relate embryonic leaf number to maturity rate. The number of embryonic leaves was usually five and was not associated with maturity. Arnold (2) states that warm and cool temperature treatments in growth chambers from planting to the fourth leaf stage had no effect on total leaf number. The warm treatments, during the period from 4th to 9th leaf stage, resulted in three more total leaves. Warm temperatures during both intervals suppressed lower internode elongation.

Chase and Nanda (13) and Arnold (2) found significant positive correlations between the leaf number of the mature plant and days to anthesis. They also showed that the interaction between photoperiod and temperature affected leaf numbers, as well as, maturity rates. The number of days per leaf was 3.7 and 3.6 from plantings in Illinois in May and Florida in November, respectively. The number of days per leaf was 4.6 in Florida from September plantings (13).

Hespeth, Chase, and Nanda (39) subjected 18 single cross maize hybrids and 2 maize races to several photoperiod and temperature regimes. They found that leaf numbers were affected by genotype, photoperiod, and temperature and were correlated with plant height and weight, photosynthetic area, and rate of maturity. The average change in leaf number per degree increased from 0.17 to .33 over the day/night temperature range 15/10, 21/16, 30/25, and 36/31 C under 16-hr day lengths. Ten-hour photoperiods produced similar results. Under 16-hr days the number of days to tasseling increased as the temperature decreased, and the days per leaf was lowest at 30 C, compared to 36, 21, and 16 C.

Hanway (36, 37, 38) described eleven stages of maize growth in relations to leaf number, floral and fruit development, and node length. Bonnett (5) described the development of maize in great detail with special emphasis on floral development. These relationships should be useful in studying maturity.

CHAPTER III

FIELD STUDY

Photoperiod and temperature effects on the maturity of sorghum have been demonstrated by various workers. The effects of these two factors have usually been studied independently. The purpose of this preliminary study was to observe the effects of photoperiods and temperatures on the maturity of sorghum by subjecting several varieties to short and long days at different planting times.

Materials and Methods

Seven pure-line sorghums which were expected to exhibit a wide range of response to photoperiod and temperature were selected for this study.

Wheatland (WD1) is an important line in the hybrid grain sorghum breeding program at the Oklahoma Agriculture Experiment Station. It was originally selected from a kafir-milo hybrid made by J. B. Sieglinger, named and distributed in 1931 (123), and re-selected for resistance to Milo Disease. A hastening of Wheatland's maturity had been observed in winter greenhouse plantings.

Combine Kafir-60 (CK-60) is a parent of several common commercial hybrids. It is a pure kafir type that was derived from a cross made in 1944 and released and distributed in 1950 by the Texas Agriculture Experiment Station (52). Quinby (76) reported that CK-60 exhibits some response to day length and temperature, but like most kafirs, its response is not nearly as great as the milos or hegaris. Quinby (76) reported the maturity genotype of CK-60 to be ma_1 Ma_2 ma_3 Ma_4.

Eighty-day Milo (80M) is one of Quinby's maturity genotype testers. Its genotype is Ma_1 ma_2 Ma_3 Ma_4, and it exhibits a very strong photoperiodic response, typical of the milos (76).

Ryer Milo (44M) carries the ma_3^R gene which makes it very early. Unlike most milos the seedlings of Ryer are very spindly with light green, narrow leaves and a very supressed tillering capacity (83). Its maturity genotype is Ma_1 ma_2 ma_3^R Ma_4 (76).

Hegari 750 is from the increase of a selection by A. B. Conner in 1910 from seed introduced from Sudan, Africa. It was distributed in 1915 and 1916, and has been grown widely as a dual purpose sorghum. Hegari is sensitive to photoperiod and temperature, and its maturity genotype is Ma_1 Ma_2 Ma_3 ma_4 (75, 76, 123).

Early Hegari is identical to Hegari except that it is earlier maturing because of a single gene difference (51). Its genotype is Ma_1 Ma_2 ma_3 ma_4 (76). This mutant hegari was increased and distributed by the Texas Agriculture Experiment Station in 1938 (51).

Belko is a tall tropical introduction from Ukiriguru, East Africa, that is very late maturing in Oklahoma, and it is very sensitive to photoperiod.

These lines were planted in the field at Stillwater, Oklahoma (latitude 36° 07' N) on June 16 and August 10, 1967. The rows were 7.6m long and 61cm apart. The lines were randomized in each of two blocks on each date. A wooden frame was constructed around one-half of each block over which black polyethylene was placed to regulate the photoperiod. One-half of each block was given 10 hours of sunlight daily during the interval of 7 to 35 days after planting. The black polyethylene was unrolled and securely fastened over the frame to exclude all light from 6:30 p.m. to 8:30 a.m. CST.

The plants grown in the half of each block not given artifically shortened days received the normal day lengths. Francis (23) reported the approximate photoperiod in hours above several light intensities of many latitudes. The number of hours from sunrise to sunset are given in Figure 1 along with the approximate number of hours per day with a light intensity of 10 ft-c and 1 ft-c or more as reported by Francis (23). Since no data has been reported on the intensity of light to which the photoperiod mechanism in sorghum is sensitive, the exact effective photoperiod is not known.

Table I shows the average minimum and maximum temperatures for the first 80 days (in 10-day intervals) following both planting dates, as recorded at the experiment station.

The data was analyzed as a split-plot in strips with the planting dates (main-plot units) arranged in a randomized complete block design. The varieties and day-lengths treatments (sub-plot units) were nested in the planting dates.

The error mean square used in calculating the LSD's for comparing the responses under different planting dates for a particular variety growing under a particular day length was composed of the variance components due to day lengths X varieties, day lengths, varieties, and trials. Six degrees of freedom were associated with this error term.

$$\text{LSD}_{(.05)} = 2.447\sqrt{\frac{2(\sigma^2_{\text{DLXV}} + \sigma^2_{\text{V}} + \sigma^2_{\text{DL}} + \sigma^2_{\text{T}})}{2}} .$$

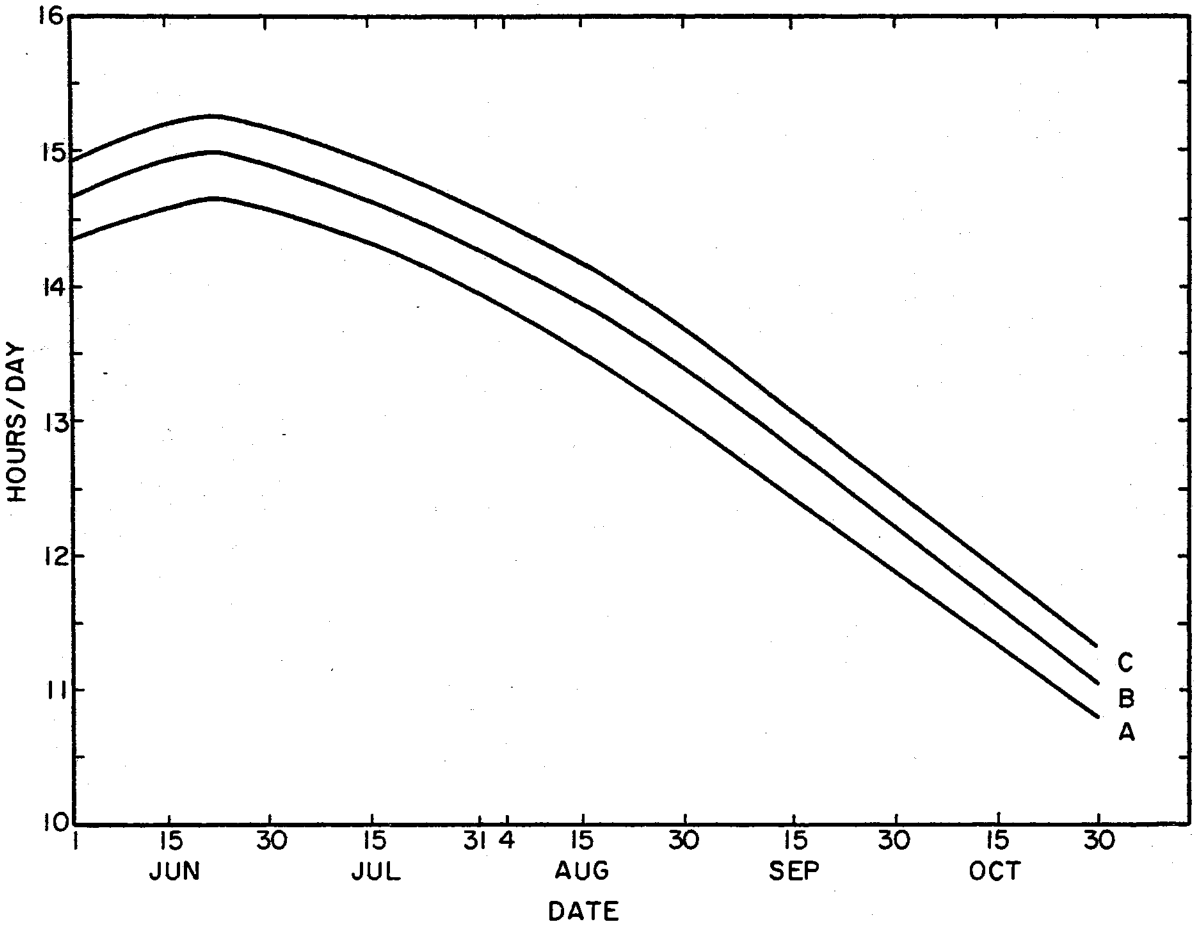

Figure 1. Length of Photoperiods From June 1 to October 30. A. Number of Hours From Sunrise to Sunset. B. Average Number of Hours per Day With the Light Intensity Greater Than 10 Ft-c. C. Average Number of Hours per Day With the Light Intensity Greater Than 1 Ft-c. Estimated From Francis (23).

TABLE I

AVERAGE DAILY MAXIMUM AND MINIMUM TEMPERATURES (C) FOR 80 DAYS (IN 10-DAY INTERVALS) AFTER PLANTING ON JUNE 16 AND AUGUST 10, 1967, AT STILLWATER, OKLAHOMA

Days After Planting	Planting Date June 16 Maximum	 Minimum	 August 10 Maximum	 Minimum
0-10	29.9	19.4	30.6	14.6
10-20	29.8	20.2	33.3	16.1
20-30	31.7	17.3	25.3	15.1
30-40	31.9	19.9	29.0	17.7
40-50	34.3	21.2	26.4	13.4
50-60	32.1	17.1	28.7	14.3
60-70	32.1	16.6	20.1	7.7
70-80	29.3	15.2	23.4	7.6

The error mean square used in calculating the LSD's for comparing two varieties grown under similar conditions was composed of the variance components due to day lengths X varieties and varieties. Ten degrees of freedom were associated with this error term.

$$LSD_{(.05)} = 2.228 \sqrt{\frac{2(\sigma^2_{DLXV} + \sigma^2_{V})}{2}} .$$

The error mean square used in calculating the LSD's for comparing the response under different day lengths for a particular variety planted on the same date was composed of the variance components due to day lengths X varieties and day lengths. Six degrees of freedom were associated with this error term.

$$LSD_{(.05)} = 2.447 \sqrt{\frac{2(\sigma^2_{DLXV} + \sigma^2_{DL})}{2}} .$$

These LSD's are for comparing the simple effects of the factor presented as the average of the two blocks at the 0.05 level.

The state of floral development in all the varieties was observed in all treatments from the 15th day after planting until about one week after floral initiation. The plants were uprooted, dissected and examined under a dissecting microscope (approximately 20X). The day that the first buds were observed to be swollen several times greater than vegetative buds and before any lobes were visible was assumed to be the day of floral initiation. Buds on which a few branch primordial lobes were visible at the base were assumed to be one day beyond floral initiation. Those buds on which several rows of lobes were visible, but the lobes did not cover the bud completely, were assumed to be two days beyond floral initiation. The time at which the whole bud was covered with lobes and the basal lobes had begun to subdivide was assumed to be three days beyond floral initiation. When all the lobes had started to subdivide once, the bud was assumed to be four days past floral initiation. The average number of days from planting to floral initiation of several plants (usually 10 or more) in each sub-plot was used in the analysis of variance.

The remaining plants (10-20 in each row) were tagged on the day of first bloom and the average of the plants within each sub-plot was used in the analysis of variance.

The floral period (interval between floral initiation to anthesis) was determined by the difference between the number of days to anthesis and floral initiation for each sub-plot.

Results and Discussion

The 10-hr photoperiods were effective in decreasing the number of days to reach anthesis for every variety under both the June and August plantings. These data are presented in Figure 2 as the mean of the two blocks. This figure also shows that the plants in most varieties sown in June reached anthesis sooner than those sown in August under short photoperiods. Wheatland and Combine Kafir-60 reached anthesis sooner after sowing under normal days in June than in August. The August planted 80-day Milo bloomed quicker under normal days than that sown in June and grown under normal days. The other varieties exhibited no significant difference due to planting dates under normal day lengths. The mean squares from the analysis of variances for floral initiation,

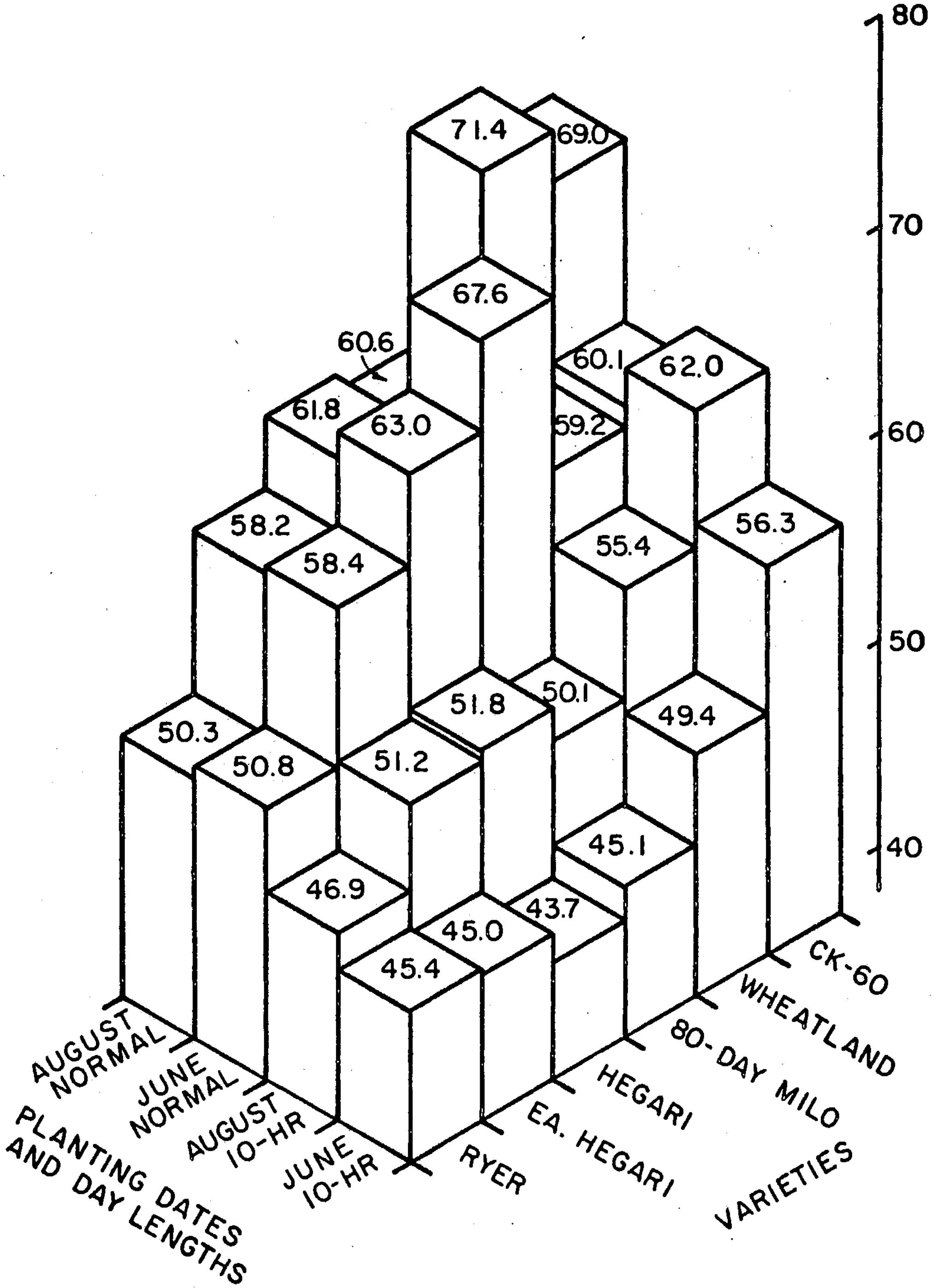

Figure 2. Field Study: Effect of Day Length and Planting Date on the Number of Days From Planting to Anthesis for Six Sorghum Varieties. LSD (.05): Planting Date = 3.7; Varieties = 2.8; Day Length = 3.0.

floral period, and anthesis are presented in Table II. Planting dates, varieties and day lengths all produced significant responses. All the interactions of these three factors were also significant except planting date X day length for floral initiation and floral period.

Figures 3 and 4 illustrate the response to these factors as measured by the number of days to floral initiation and the number of days in the floral period, respectively. Tables III and IV indicate the difference in response to day lengths and the difference in response to planting dates, respectively.

Hegari and 80-day Milo exhibited the greatest response to day lengths as measured by both days to anthesis and floral initiation when planted in June. They were hastened to anthesis only about one-half as much when planted in August. The floral period for both of these varieties was significantly shortened under 10-hr days only when planted in June.

In general, the magnitude of the response to photoperiods was similar for Early Hegari and Wheatland. The June planted Early Hegari responded more than that planted in August during all three growth stages, however, the reverse was true for Wheatland. Wheatland showed a greater response to day lengths under the conditions prevailing during the August planting.

Combine Kafir-60 and Ryer showed the least amount of response to different photoperiods of all the varieties. Ryer matured as quickly as any other variety or quicker under all the conditions. This was true for all three intervals of development. Combine Kafir-60 was as late or later than most other varieties under nearly all conditions. Like Wheatland, Combine Kafir-60 showed a greater hastening effect of

TABLE II

FIELD STUDY: ANALYSIS OF VARIANCE FOR FLORAL INITIATION (FI), FLORAL PERIOD (FI-A), AND ANTHESIS (A)

Source	DF	Mean Squares		
		FI	FI-A	A
TOTAL	47	-	-	-
Planting Date (PD)	1	96.9008**	514.6337**	164.9097*
Blocks (B) in PD (Error a)	2	.8461	4.5814	2.4450
Variety (V)	5	72.4039**	32.5252**	173.0704**
PD X V	5	9.5496**	8.0469*	30.0586**
B X V in PD (Error b)	10	.5124	2.0327	1.8923
Day Length (DL)	1	636.4178**	137.8713*	1366.7207**
PD X DL	1	16.6617NS	3.1161NS	34.1888**
B X DL in PD (Error c)	2	1.2325	1.6897	.0425
V X DL	5	27.9125**	7.6004*	49.2035**
PD X V X DL	5	9.2749**	6.0241*	25.5731**
DL X V in PD (Error d)	10	.4676	1.4413	1.4855

NSNot Significant

*Significant at 0.05 level

**Significant at 0.01 level

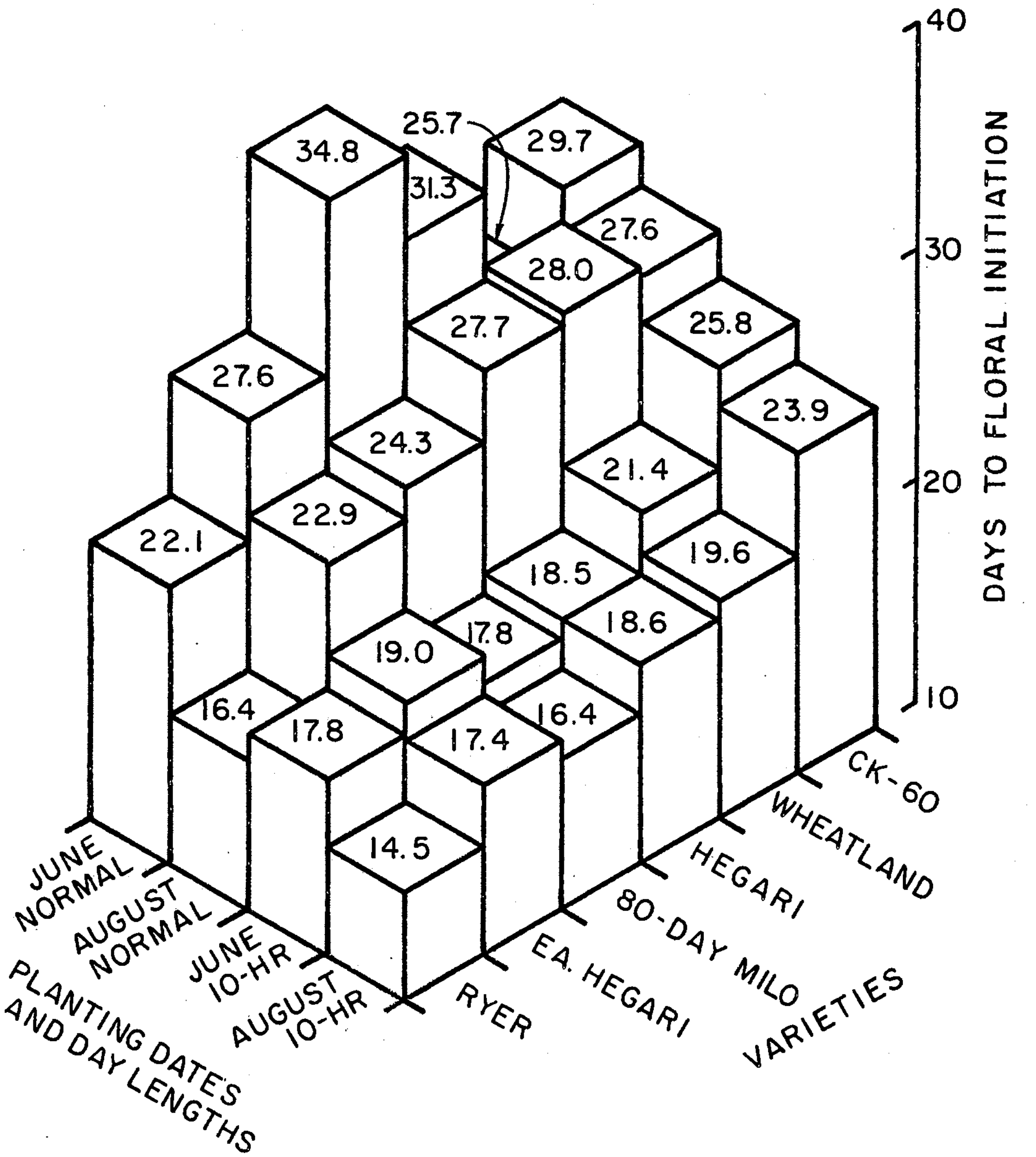

Figure 3. Field Study: Effect of Day Length and Planting Date on the Number of Days From Planting to Floral Initiation for Six Sorghum Varieties. LSD (.05): Planting Date = 1.96; Varieties = 1.54; Day Length = 1.93.

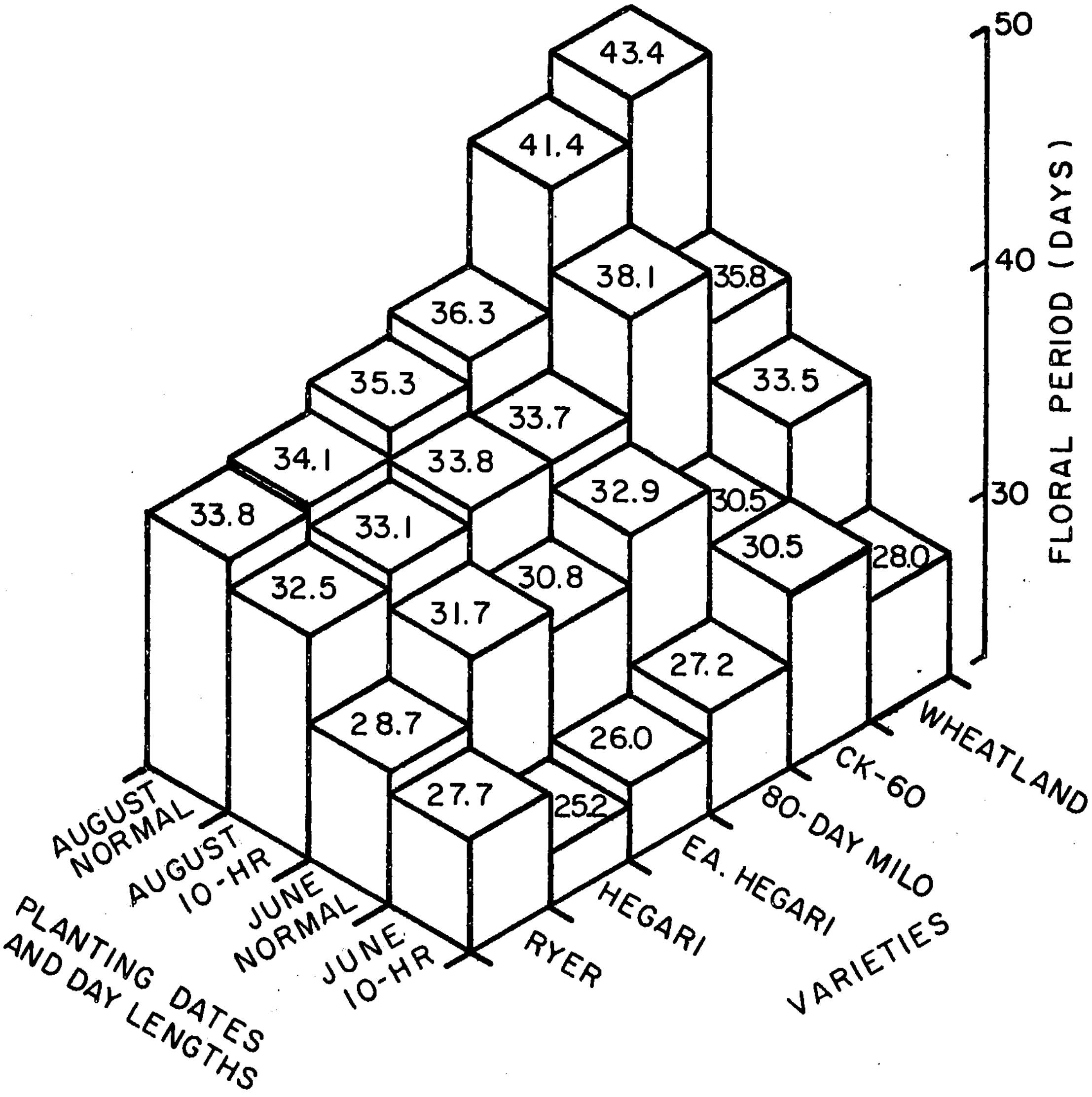

Figure 4. Field Study: Effect of Day Length and Planting Date on the Number of Days From Floral Initiation to Anthesis (Floral Period) of Six Sorghum Varieties. LSD (.05): Planting Dates = 4.8; Varieties = 2.9; Day Length = 3.0.

TABLE III

FIELD STUDY: SENSITIVITY TO PHOTOPERIODS OF SIX SORGHUM VARIETIES PLANTED ON TWO DATES AS MEASURED BY DIFFERENCES IN FLORAL INITIATION (FI), FLORAL PERIOD (FI-A), AND ANTHESIS (A)

	Developmental Intervals and Planting Dates					
	FI		FI-A		A	
Variety	June 10	Aug. 16	June 10	Aug. 16	June 10	Aug. 16
			SENSITIVITY (DAYS)[a]			
Hegari	12.8	9.1	6.5	1.0	19.3	10.0
Early Hegari	8.6	5.5	4.8	1.5	13.4	7.0
80-Day Milo	17.0	7.9	5.7	2.6	22.5	10.5
Wheatland	4.3	8.4	5.5	7.6	9.8	16.0
Combine Kafir-60	3.9	3.7	0.0	3.3	3.8	7.0
Ryer	4.3	1.9	1.0	1.3	5.4	3.4

[a] 10-hr day response subtracted from normal day response

TABLE IV

FIELD STUDY: SENSITIVITY TO PLANTING DATES OF SIX SORGHUM VARIETIES WHEN SUBJECTED TO BOTH 10-HR DAYS AND NORMAL DAY LENGTHS AS MEASURED BY DIFFERENCES IN FLORAL INITIATION (FI), FLORAL PERIOD (FI-A), AND ANTHESIS (A)

	Developmental Intervals and Day Lengths					
	FI		FI-A		A	
Variety	10-Hr	Normal	10-Hr	Normal	10-Hr	Normal
			SENSITIVITY (DAYS)[a]			
Hegari	0.1	-3.6	7.9	2.4	8.1	-1.2
Early Hegari	-1.6	-4.7	7.8	4.5	6.2	-0.2
80-Day Milo	-1.4	-10.5	6.5	3.4	5.0	-7.0
Wheatland	-1.8	2.3	7.8	9.9	6.0	12.2
Combine Kafir-60	-1.9	-2.1	7.6	10.9	5.7	8.9
Ryer	-3.3	-5.7	4.8	5.1	1.5	-0.5

[a] June response subtracted from August response

short days on the floral period during the August planting.

The number of days to floral initiation was not determined for the June planted Belko grown under normal photoperiods, because it was so late. There were only a few plants left after 50 days, and none reached anthesis. The Belko planted in June and subjected to 10-hr photoperiods produced floral tissue and bloomed. However, those plants under both photoperiods planted in August underwent floral initiation but did not reach anthesis before frost. Since there was much missing data for Belko, it was omitted from all statistical analysis, but its response to temperate conditions was probably typical of many other tropical sorghums.

The numbers of days to floral initiation, anthesis and the interval of development in between are presented in the Appendix for all varieties.(Tables XV through XVII). These data are the average of the plants in a given set of treatments and show that the blocks did not differ greatly.

In general, the magnitude of response to photoperiod for a particular variety planted on a given date as measured by anthesis was very similar to that of days to floral initiation. The response of the floral period to day lengths was usually somewhat smaller, but often significant.

The number of days required to reach floral initiation was not greatly affected by date of planting when grown under short days. However, when grown under normal day lengths the August crop, except Wheatland, initiated quicker than the June crop. During the first 20 days of growth the day temperature was higher and the night temperature was lower in August, as indicated in Table I. Apparently this temperature combination, along with slightly shorter natural day lengths during August produced rapid initiation. The prolonging effects of the cool temperature after initiation made the floral period as long or longer when planted in August under normal photoperiods than in June.

The magnitude of response to planting date for a particular variety under a given day length as measured by days to anthesis is similar to that of floral period. All varieties in the August planting required as long or longer to develop from floral initiation to anthesis than the June plantings. The cooler night temperatures slowed down the development of the head.

These data indicate that these sorghums act similar to rice. The new improved varieties of rice responded more to night temperatures than to day lengths or day temperatures, whereas, the old varieties responded greatly to photoperiods (113, 121). Wheatland and Combine Kafir-60 responded more to the planting dates under normal day lengths than the other varieties which were not developed for grain production. A significant response to planting dates was also observed for 80-day Milo under normal day lengths. This hastening of development in August was due to earlier floral initiation. Wheatland's and Combine Kafir-60's delayed response to the August planting was due to slower development during the floral period.

Hegari and 80-day Milo both have dominant alleles at the Ma_1 and Ma_2 loci. Apparently this combination of genes produces the greatest amount of photoperiodic sensitivity. The recessive allele at the ma_3 locus in Early Hegari and the ma_3^R locus in Ryer in combination with the dominant Ma_1 locus permits the plants to mature more quickly and show less response to the environment. Combine Kafir-60, and probably Wheatland, have a recessive allele at the ma_1 locus, and responds more to temperature changes and day length changes during the floral period when grown under normal day lengths.

CHAPTER IV

GROWTH CHAMBER STUDY I

The results of the field study, reported in Chapter III, and results reported by several other researchers (17, 44, 63, 64, 76, 77) suggested that temperature and photoperiod both affect the maturity of sorghums. The effect of these factors varies greatly among different genotypes.

In field studies, controlling the day length is very demanding and laborious, and controlling the temperature is impossible. Both of these factors can be controlled in growth chambers with much more precision and ease.

The purpose of this study was (1) to determine the effects of day and night temperatures and the photoperiod on sorghum's maturity; (2) to determine the age at which sorghums respond to photoperiod and temperature regimes; and, (3) to develop a technique of growing and studying sorghums in controlled environment chambers.

Materials and Methods

Three varieties, Wheatland, Early Hegari, and 80-day Milo, were selected from the seven previously used in the field study. Wheatland showed a moderate response to both day length and temperature. Early Hegari and 80-day Milo had been observed to be very sensitive to photoperiod, but temperature modified this response somewhat. These three varieties were intermediate in maturity, but the maturity genotype was different for each. This provided the opportunity to observe different genotypes without greatly prolonging the time required to make observations when they were delayed in maturity.

These three varieties were subjected to night temperatures of 16 C and 21 C; day temperatures of 27 C and 32 C; and 10-, 12-, and 14-hr photoperiods.

The day temperature was provided during the time that the lights were on in the chambers and the night temperatures prevailed during the dark period. Between one and two hours were required for the temperature changes. The temperature was maintained within 1 C of that stated.

Approximately 150 ft-c of incandescent light were supplied during the first and last 15 minutes of each light period. During the rest of the light period, a combination of these incandescent lights and Sylvania cool white, very high output, florescent bulbs provided about 3500 ft-c of light at the top of the plants.

Twelve seeds of each of the three varieties were planted in each of 24 (9 inch plastic) pots. The growing medium was a mixture of 2 parts sterilized loamy sand, one part peat, and one part perlite. About 3g of 11-5-6 fertilizer was applied every two to three weeks as needed by the plants depending upon the amount of vegetative growth. Water was applied to the top of the soil when fertilizer was applied. The rest of the time water was applied in a saucer below the pot. Both tap water and distilled water were used. Distilled water seemed more satisfactory. Approximately 15 days after planting all but the six most vigorous plants of each variety were removed. One plant of each variety in each pot was available, when necessary, to determine the date to dissect the varieties for floral initiation. The number of days from planting to initiation of four plants from each variety in each pot were averaged. In the regimes which included a 21 C night temperature, the sixth plant of each variety in each pot was left until anthesis. The number of days from planting to the day the first floret bloomed on each plant was recorded. In order to observe more photoperiod -- temperature combinations in less time, no anthesis data were collected for those regimes which included a 16 C night temperature.

Each combination of day length and temperature was run at least two times. When, for some reason, the results of the two trials differed greatly, that combination was rerun and the two most logical sets of results were used in the analysis.

The data were analyzed as a split-plot with the main plot consisting of day lengths, day temperature and night temperature. The varieties were the sub-plots. Within both the main plot and the sub-plot the design was completely randomized.

The LSD used to compare the responses of two day temperatures, night temperatures, or day lengths for a particular variety with the other treatments held constant was calculated from

$$2.447\sqrt{\frac{2(\text{Error a})}{48}}\ .$$

The LSD used to compare the responses of two varieties under the same treatment combinations was calculated from

$$2.306\sqrt{\frac{2[2(\text{Error a}) + \text{Error b}]}{96}}\ .$$

Both of these LSD's are for comparing the simple effects of the factor presented as the means of the two trials at the 0.05 level.

Results and Discussion

The Field Study reported in Chapter III confirmed other reports that the rate at which sorghums mature is highly dependent upon the environmental conditions in which they were grown. The varieties varied in their response to different photoperiods and temperatures. This growth chamber study was designed to study the effects of day lengths, day temperatures, and night temperatures on the maturity of three sorghum varieties.

Rate of development was measured by both the number of days from planting to floral initiation and to anthesis. Three intervals of development were established. The vegetative period was from planting to floral initiation. The floral period or period of flower development was from floral initiation to anthesis. The floral period was determined by subtracting the number of days from sowing to floral initiation from the number of days from sowing to anthesis. The interval from sowing to anthesis includes the other two periods. To reduce the time required to observe the effects of all the factors on maturity only the number of days from planting to floral initiation were recorded for one-half of the treatment combinations (those with 16 C night temperature).

Both the vegetative and floral periods are important from a sorghum breeding standpoint. In general, the longer the vegetative period, more leaves are produced, thus more photosynthetic area. Also, the longer the floral period, more time is available for the production of panicle branches and florets, thus more seed. It seems desirable to develop varieties that produce a large number of both leaves and seeds in a minimum amount of time.

The nighttime temperature for the data presented in Figures 5, 6, and 7 was 21 C.

The three-dimensional graph of data in Figure 5 shows that Wheatland, 80-day Milo, and Early Hegari all reached anthesis quickly under 10-hr days with no significant difference due to daytime temperatures. The varieties were significantly different from each other (0.05 level) under 10-hr days except 80-day Milo and Early Hegari at 32 C daytime temperature, and 80-day Milo and Wheatland at 27 C daytime temperature.

Under 12- and 14-hr days the varieties were significantly different from each other at both daytime temperatures, except Wheatland and 80-day Milo in the 14-hr 32 C regime. Under 12-hr photoperiods the rate of maturity was highly dependent on the temperature. When grown in the 12-hr, 32 C regime, the three varieties reached anthesis in about the same number of days as under the 10-hr photoperiods. In the 12-hr 27 C regime these same varieties were delayed greatly. The 5 C decrease in temperature under 12-hr photoperiods delayed anthesis 15.1, 15.5, and 15.8 days for Wheatland, 80-day Milo, and Early Hegari, respectively.

Anthesis was delayed significantly under 14-hr photoperiods at both daytime temperatures as compared to 10-hr photoperiods. Under 14-hr days, only Wheatland's maturity was significantly affected by a 5 C difference in day temperature. The long photoperiods and warm daytime temperature delayed both Wheatland and 80-day Milo in reaching

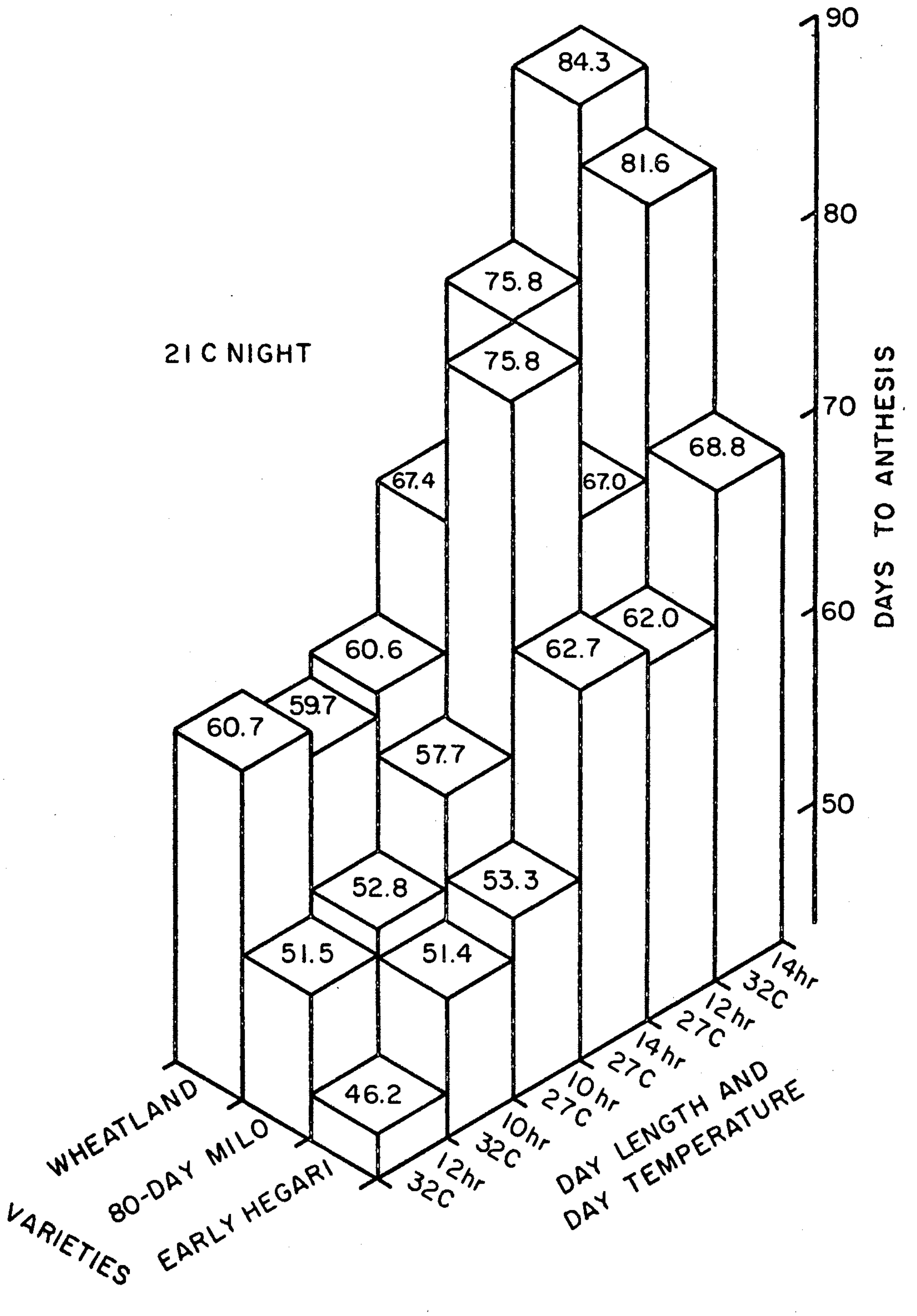

Figure 5. Growth Chamber Study I: Effect of Day Length and Temperature on the Days to Anthesis of Three Sorghum Varieties. LSD: (.05) Day Length and Temperature = 8.8; Varieties = 4.2.

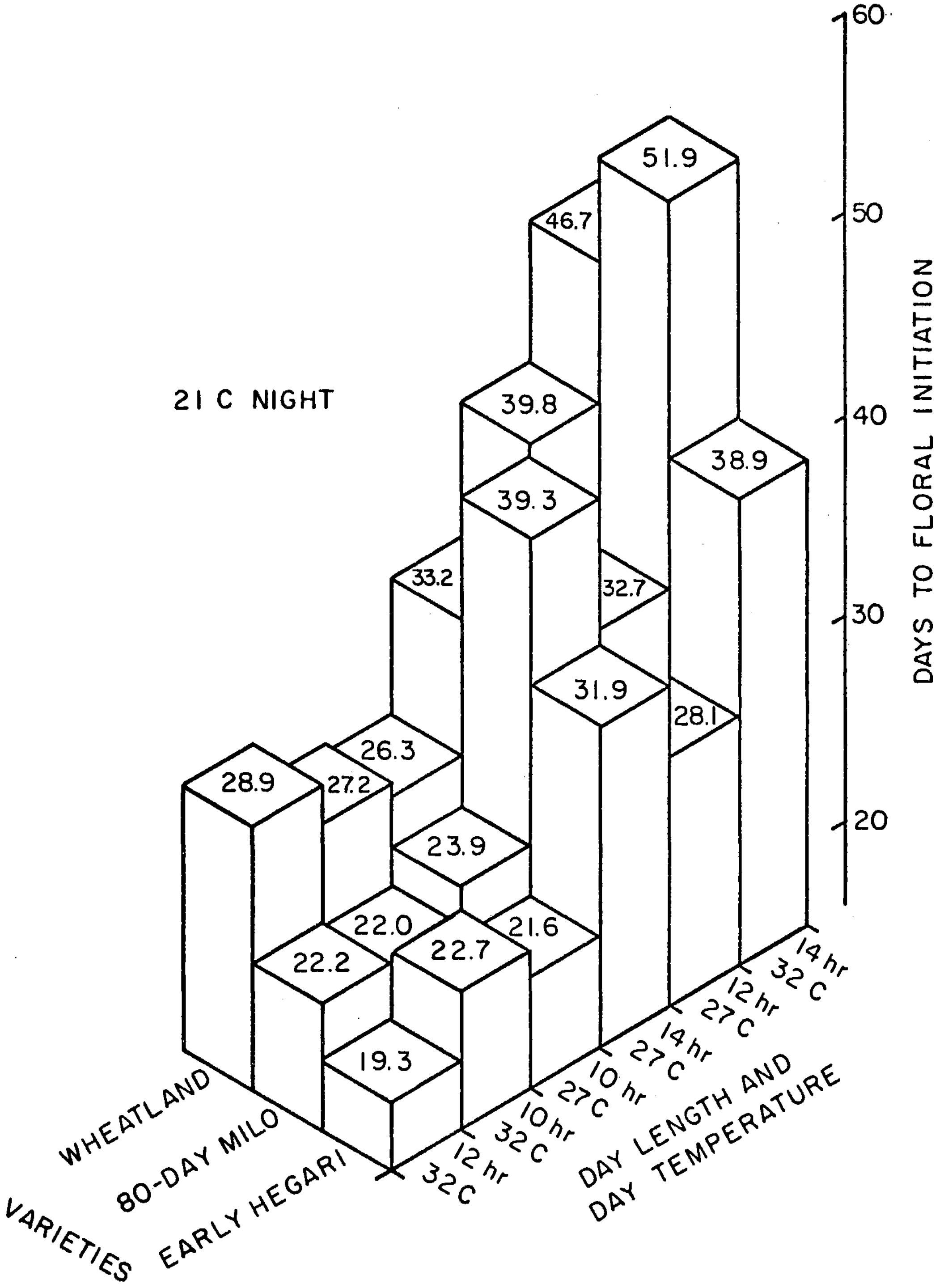

Figure 6. Growth Chamber Study I: Effect of Day Length and Temperature on the Floral Initiation of Three Sorghum Varieties at 21 C Night Temperature. LSD: (.05) Day Length and Temperature = 10.5; Varieties = 4.9.

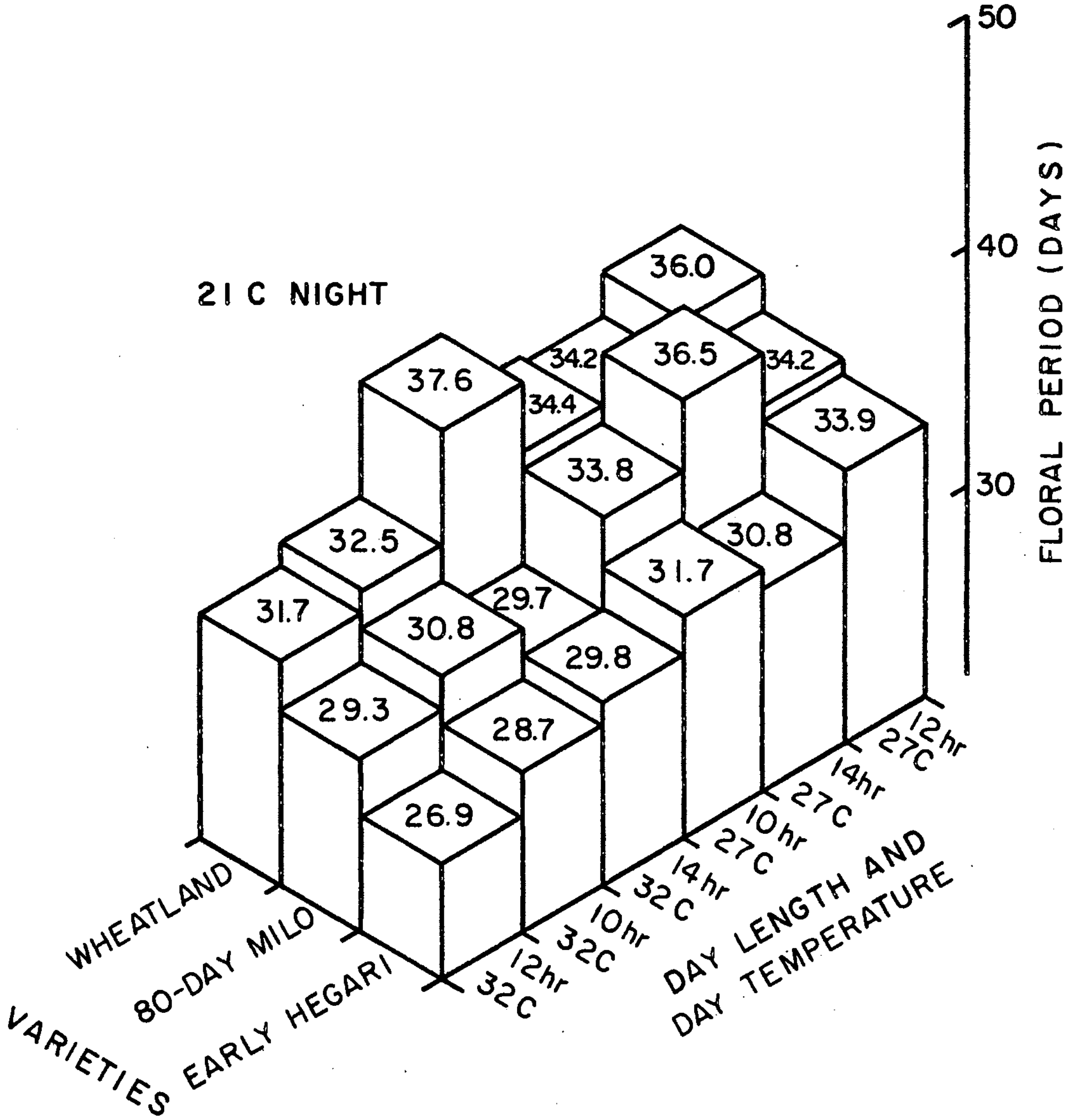

Figure 7. Growth Chamber Study I: Effect of Day Length and Temperature on the Floral Period of Three Sorghum Varieties. LSD: (.05) Day Length and Temperature = 3.6; Varieties = 2.4.

anthesis more than Early Hegari.

Wheatland reached anthesis later under the 12-hr, 27 C regime than under the 14-hr, 27 C condition. This situation suggested a heat accumulation type of reaction, but the delay exhibited under the 14-hr, 32 C condition does not support such a concept.

The data presented in Figure 6 indicates that the number of days from planting to floral initiation follows a similar pattern to that of days to anthesis. However, the only significant difference among the varieties in the 10-hr days was between Wheatland and 80-day Milo at 32 C. Under 10-hr days the daytime temperatures produced no significant differences on these varieties.

Under the 12-hr, 32 C regime the plants initiated at about the same age as under a 10-hr day. Wheatland was significantly later than the other varieties under the 12-hr, 32 C days. With a decrease in temperature of 5 C in 12-hr photoperiods, 80-day Milo and Early Hegari initiated at an age which was intermediate and not significantly different from either the 10- or 14-hr days.

Wheatland initiated its floral tissue insignificantly sooner under the 14-hr, 27 C regime than under the 12-hr, 27 C condition. Wheatland and 80-day Milo reached floral initiation 13.5 and 12.6 days later under the 14-hr photoperiod with an increase of 5 C. Early Hegari was delayed less by the long days than the other varieties at 32 C.

The reason that days to floral initiation and anthesis seemed to follow the same pattern in Figures 5 and 6 is illustrated in Figure 7. The magnitude of response exhibited by the floral period to these differences in environmental conditions is much smaller than the other two intervals of development.

The data in Figure 7 illustrates that the floral period of the three varieties was not significantly affected by daytime temperatures under the 10-hr day. Under the 12-hr days all three varieties were delayed significantly by the 27 C temperature as compared to 32 C.

Wheatland's floral period was significantly longer than Early Hegari under every photoperiod-temperature combination except the 12-hr, 27 C regime. The floral period for Wheatland was longer than 80-day Milo only under the 14-hr, 32 C condition. The 12-hr, 32 C and 14-hr, 27 C regimes caused 80-day Milo to have a significantly longer floral period than Early Hegari.

All three day lengths produced about the same length of floral period at each daytime temperature for Early Hegari or 80-day Milo. Wheatland's floral period was also about the same over the three photoperiods at 27 C, but the 14-hr, 32 C condition caused a delay over the 10- and 12-hr, 32 C regimes.

The mean squares for the analyses of variance for each of the intervals of development are presented in Table V. They show that day lengths are highly significant in determining the length of the vegetative period (days to floral initiation) and the number of days to anthesis, but do not affect the floral period. On the other hand, the day temperature does not affect the days to floral initiation or anthesis, but it does affect the length of the floral period. Even though day temperatures did not significantly affect days to floral initiation or anthesis, the interaction of day temperature and photoperiod is highly important. These data suggest that maximum yields might be obtained under long days, for greatest vegetative development, and cool days for a longer period for floral development. However, these

TABLE V

GROWTH CHAMBER STUDY I: ANALYSIS OF VARIANCE FOR ALL TREATMENT COMBINATIONS WITH 21 C NIGHT TEMPERATURE FOR FLORAL INITIATION (FI), FLORAL PERIOD (FI-A), AND ANTHESIS (A)

Source	DF	Mean Squares		
		FI	FI-A	A
TOTAL	863	-	-	-
Day Length (DL)	2	20531.1374**	121.8232^{NS}	23724.9178**
Day Temperature (DT)	1	21.4074^{NS}	2146.8345**	1753.8900^{NS}
DL X DT	2	8038.6157**	299.2720^{NS}	11322.2928**
Error a	6	441.3411	86.6299	307.5567
Variety (V)	2	3369.8030**	1217.4792**	8493.6678**
DL X V	4	1238.0047**	44.4939**	1185.1453**
DT X V	2	41.8082**	301.0660**	541.6956**
DL X DT X V	4	175.6464**	193.8587**	264.4578**
Error b	564	3.6116	8.5547	8.4542
Residual	276	1.9879	5.0290	19.9598

^{NS}Not Significant

*Significant at 0.05 level

**Significant at 0.01 level

conditions produce slow maturing plants which must be grown under near ideal conditions for maximum yield expression.

The significant mean squares for the interactions of varieties and the treatment combinations point out the obvious genotype by environment interactions shown in Figures 5, 6, and 7.

The analysis of variance for floral initiation (Table VI) which included two night temperatures, in addition to the previously discussed treatment combination, shows that day temperatures do not significantly affect time of floral initiation while day lengths, night temperatures, and varieties are statistically different. For this reason the response to day lengths and night temperatures with 27 C day temperature is graphed in Figure 8 and with 32 C day temperature in Figure 9. Differences in the two figures illustrate the interactions with day temperature.

These figures indicate that 10-hr photoperiods hastened floral initiation of all three varieties under all four combinations of temperatures. Early Hegari and 80-day Milo always initiated in about 20 to 24 days from planting under short days. Wheatland initiated its floral tissue 3 to 7 days later than the other varieties under 10-hr days, all differences being significant except Wheatland and 80-day Milo in the 10-hr 27/21 C regime.

In all cases these varieties initiated their floral tissue later under 14-hr than 10-hr photoperiods. However, the difference for Wheatland under 10-hr, 27/16 C (10-hr photoperiod, 27 C day, and 16 C night) was not significantly different from the 14-hr, 27/21 C at the 0.05 level.

TABLE VI

GROWTH CHAMBER STUDY I: ANALYSIS OF VARIANCE OF FLORAL INITIATION FOR ALL TREATMENT COMBINATIONS

Source	DF	Mean Square
TOTAL	1727	--
Day Length (DL)	2	45233.9307**
Night Temperature (NT)	1	4613.5140**
Day Temperature (DT)	1	399.6302^{NS}
DL X NT	2	1493.7597*
DL X DT	2	11158.8142**
NT X DT	1	180.8339^{NS}
DL X NT X DT	2	942.1013^{NS}
Error a	12	256.4782
Variety (V)	2	28306.6532**
DL X V	4	2374.3030**
NT X V	2	10786.3965**
DT X V	2	957.9200**
DL X NT X V	4	4152.5219**
DL X DT X V	4	2514.1055**
NT X DT X V	2	553.8258**
DL X NT X DT X V	4	1605.3964**
Error b	1128	2.7412
Residual	552	3.1825

^{NS}Not significant

*Significant at 0.05 level

**Significant at 0.01 level

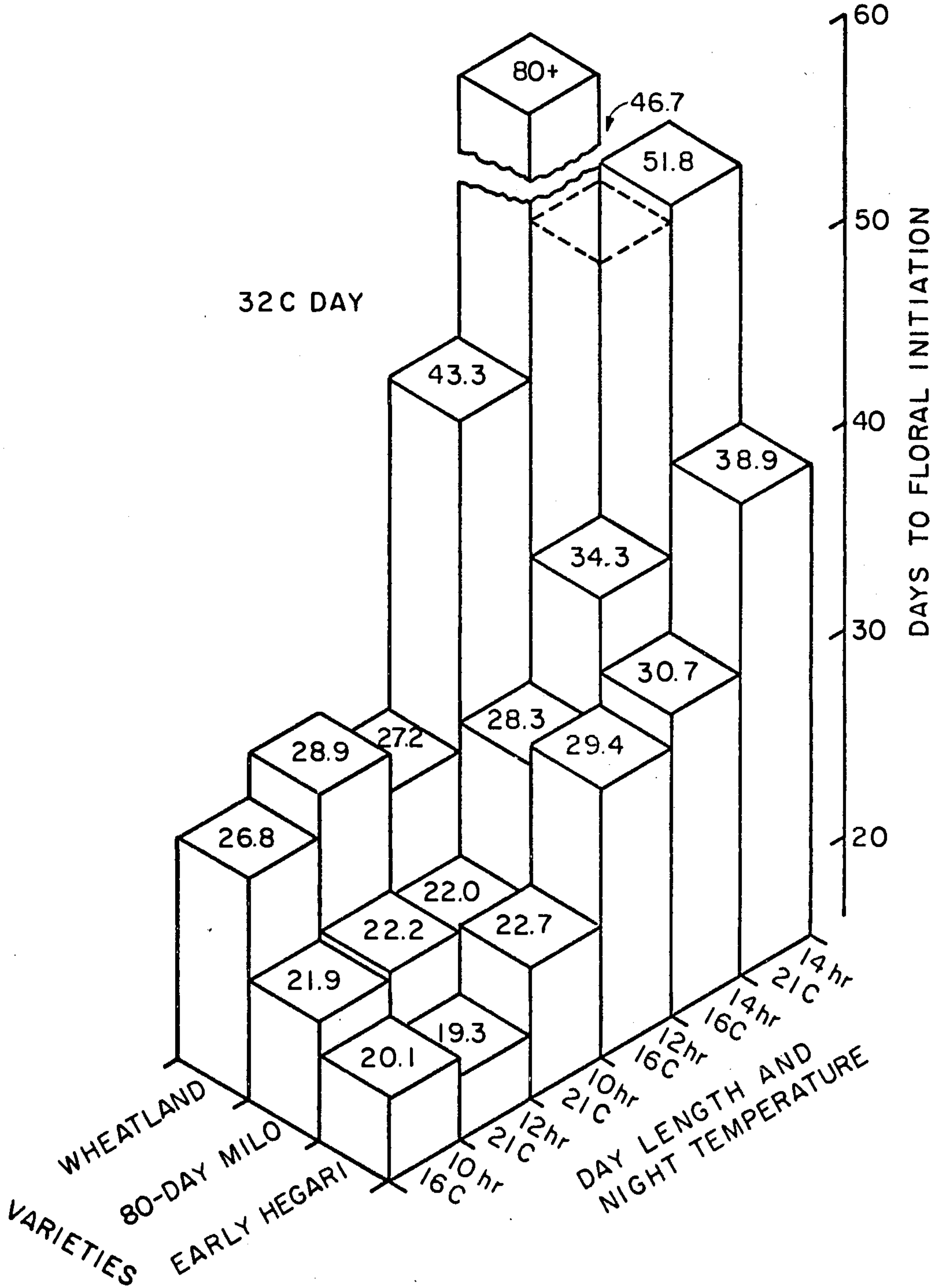

Figure 8. Growth Chamber Study I: Effect of Day Length and Night Temperature on the Floral Initiation of Three Sorghum Varieties at 32 C Day Temperature. LSD: (.05) Day Length, Day Temperature, and Night Temperature = 7.1; Varieties = 3.8.

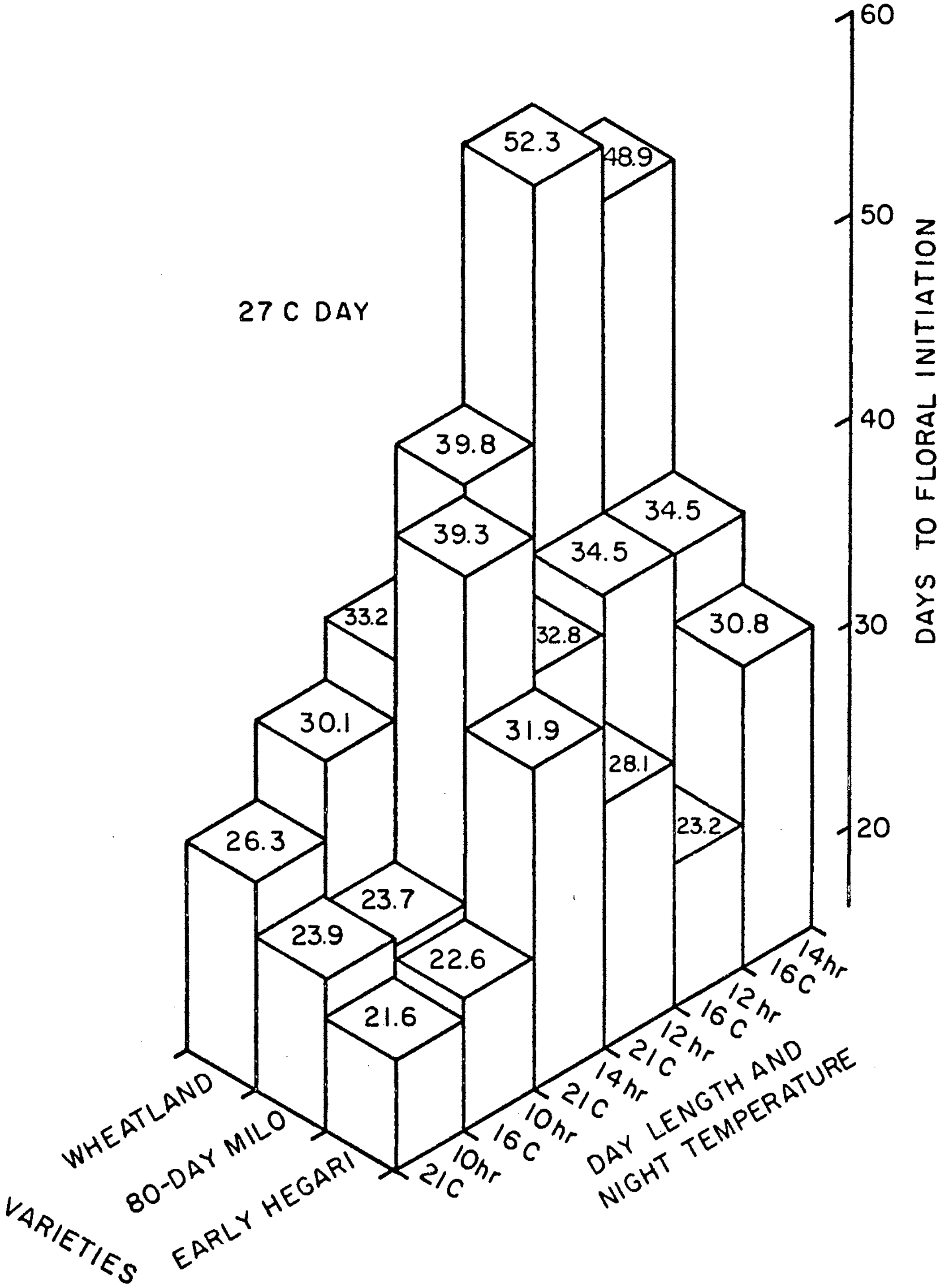

Figure 9. Growth Chamber Study I: Effect of Day Length and Night Temperature on the Floral Initiation of Three Sorghum Varieties at 27 C Day Temperature. LSD: (.05) Day Length, Day Temperature, and Night Temperature = 7.1; Varieties = 3.8.

Under 14-hr days Early Hegari initiated about 31 days after planting in both night temperatures with 27 C day temperature (Figure 9) in a 16 C night and 32 C day temperature (Figure 8). However, the 14-hr, 32/21 C regime delayed initiation significantly (8 days). A somewhat similar pattern of results was obtained for 80-day Milo, but it reached floral initiation much later than Early Hegari during the 14-hr, 32/21 C regime.

Wheatland responded quite differently from the other two varieties. Wheatland initiated its floral tissue as late or later than Early Hegari under every 14-hr day and was earlier than 80-day Milo only during the 21 C night regimes. The 14-hr-27/21 C combination made Wheatland initiate its floral tissue in 33.2 days. This was only a few days later than the 10-hr responses. Wheatland underwent initiation at about the same age when it was subjected to 14-hr days with 32/21 C and 27/16 C. The Wheatland had not initiated 80 days after planting, when the experiment was terminated, under the 14-hr-32/16 C regime.

The temperature by variety interactions showed that an environment which produces the slowest response in one variety may not significantly delay another variety.

Wheatland reached initiation significantly later than Early Hegari and 80-day Milo under every 12-hr day. Early Hegari was earlier than 80-day Milo when the 12-hr day was combined with the cool daytime temperature.

The 16 C nighttime temperature caused a significant delay in floral initiation for Early Hegari in the 12-hr, 32 C regime and for Wheatland in the 12- and 14-hr, 27 C conditions. Early Hegari and

80-day Milo were significantly later under the 21 C night combined with the 14-hr, 32 C days, while Wheatland had not initiated after 80 days under the 14-hr, 32/16 C regime.

The response of Early Hegari to the 12-hr days with 32/21 C and 27/16 C was about the same as a 10-hr day response. However, the other two temperature combinations produced a response which was intermediate to the 14- and 10-hr day response. Early Hegari did not exhibit any real threshold in response except where the warmer day and night temperatures (32/21 C) were combined with the longest day (14-hr) in which it underwent floral initiation in 38.9 days following planting.

Floral initiation occurred as quickly under 12-hr, 32/21 C treatment combination as under the 10-hr day treatments for 80-day Milo. The other three temperature combinations combined with the 12-hr days produced responses that were intermediate to the short and long day responses. Like Early Hegari, 80-day Milo was delayed most by 14-hr day with the warmer temperatures during both days and nights.

Wheatland also exhibited no delay in floral initiation with 12-hr days and 32/21 C temperatures. Wheatland produced an intermediate response to 12-hr days combined with both 32/16 C and 27/21 C temperatures. Unlike the other varieties, especially Early Hegari, Wheatland was greatly delayed by a 12-hr day with 27/16 C temperatures. Under the 32 C day temperature, Wheatland seems to have a threshold in response with a critical photoperiod of about 12-hr. The night temperature appeared to determine the exact length of the critical photoperiod. However, when grown in 27 C days, this threshold and critical photoperiod does not exist, even to the extent that it may develop more quickly under some 14-hr days than 12-hr days.

These data showed that these three varieties all responded to day lengths, but in many cases the day and night temperatures change the response to the photoperiod drastically. From these results, it can be concluded that 10-hr days in all four temperature combinations hastened floral initiation. Some day length greater than 14-hr might be long enough to delay floral initiation and consequently anthesis under all reasonable temperatures.

The results pertaining to the effect of photoperiod and temperature on the floral period showed that it responded very little to day lengths. Various temperatures did produce some fluctuation in the floral period which influenced the time of anthesis. These responses were probably small enough to be ignored since the days to floral initiation and anthesis followed a very similar pattern across most of the treatment combinations for each variety. Therefore, these data indicate that days to floral initiation is a reasonable point in the development of sorghum plants from which maturity rate may be estimated.

The mean of each trial is presented in the Appendix (Tables XVIII and XIX) for the three varieties and all combinations of treatments. It was not uncommon for the mean of the trials in the growth chamber to differ by three days or more for each of the intervals measured. Difference between blocks in the field study were not this great. Apparently there are some environmental conditions that were not constant from trial to trial in chamber. These factors may have been slight differences in humidity, light intensity, light quality, soil fertility, etc. It may be possible to stabilize these, as well as other factors, which are not generally considered to be of great importance in affecting maturity. In this manner the response to a given set of conditions may be more repeatable.

CHAPTER V

GROWTH CHAMBER STUDY II

The preceding studies have clearly shown that the rate at which sorghums mature depends, at least partially, on the photoperiod. To utilize diverse germ plasm existing in the genus, crosses need to be made involving widely differing types. Often the two lines to be crossed do not reach anthesis at the same time. Crosses could be made with more ease if the environment could be controlled to make the lines to be crossed bloom at the same, predictable time. Some set of conditions, producible in growth chambers might be very useful to plant breeders.

Another use of growth chambers in sorghum breeding programs is the testing of segregating populations for photoperiodic sensitivity. Making crosses and observing segregating populations in growth chambers is both expensive and time consuming. The amount of time required in the growth chambers needs to be minimal. The purpose of this study was to determine the age at which sorghums become sensitive to photoperiods and how many inductive periods are required for floral induction.

Materials and Methods

Three photoperiodic sensitive varieties (Early Hegari, 80-day Milo, and Ryer Milo) were used in this series of experiments. They were grown in controlled environment chambers under long (17 hr) and short (10 hr) days. The day temperature was 32 C (± 1 C) and the dark period temperature was 21 C (± 1 C).

Approximately 150 ft-c of incandescent light were supplied for the first and last 15 minutes of every light period. During the rest of the light period, a combination of these incandescent lights and Sylvania cool white, very high output, florescent bulbs provided about 3500 ft-c of light at the top of the plants.

Twelve seeds of each variety were planted in each 9-inch pot containing two parts sterilized loamy sand soil, one part peat, and one part perlite. The pots were fertilized with approximately 3g of 11-5-6 every two to three weeks or as needed, depending upon the amount of vegetative growth. Water was supplied to the top of the soil when fertilizer was applied. The rest of the time water was supplied in saucers below the pots as needed.

In Experiments A through E four pots containing three varieties were subjected to a set of experimental conditions. The number of days from planting to floral initiation was determined for four plants from each variety in every pot by dissection and observation under a dissecting microscope (approximately 20X) as described in Chapter III. There were two trials of Experiments A through D and three trials of Experiment E.

In Experiment A (short to long) four pots, each containing the three varieties, were subjected to 0, 5, 10, 15, 20, or 25 short days, beginning with the day of planting, and then transferred to long days until floral initiation.

In Experiment B (short to long to short) the plants were subjected to 5 long days after being grown for 0, 5, 10, 15, 20, or 25 days from planting under short-day conditions. After the 5 long days, the plants were transferred back to the short days until floral initiation.

In Experiment C (long to short) the plants were subjected to 0, 5, 10, 15, 20, or 25 long days, beginning with the day of planting, and then transferred to short days until floral initiation.

In Experiment D (long to short to long) the plants were subjected to 0, 5, 10, 15, 20, or 25 long days, beginning with the day of planting, and then they were given five short days. After this five-day treatment they were returned to the long days until floral initiation.

In Experiment E (long to short to long) the plants were grown under the long-day conditions except for three short days. The short days were applied between 13 and 16, 16 and 19, 19 and 22, or 22 and 25 days of age. The results of the three trials of this experiment differed so greatly that they were not subjected to statistical analysis.

In Experiment F four pots, each containing 6 plants of the three varieties, were subjected to short days from the 13th to the 25th day after planting. In one pot all the leaves beyond the fourth leaf were cut off daily even with the ligule of the fourth leaf. In a second pot all the leaves beyond the fifth leaf were cut off daily. In the third pot the leaves that emerged after the sixth leaf were cut off daily. In the fourth pot the leaves beyond the seventh leaf were cut off daily. Since the number of plants and pots was so small these data were not statistically analyzed.

Experiments A through D were analyzed separately. Each was analyzed as a split-plot with the day length treatments as main plot units and the varieties used as sub-plots.

The LSD's (.05) for comparing day length treatments for a particular variety was calculated as

$$2.571 \sqrt{\frac{2(\text{Error a})}{32}} .$$

The LSD's (0.5) for comparing varieties in a given day length treatment was calculated as

$$2 \sqrt{\frac{2\left[2(\text{Error a}) + \text{Error b}\right]}{64}} .$$

These LSD's are for comparing the mean of two trials.

Results and Discussion

The graph in Figure 10A illustrates the results of Experiment A (short to long) in which the plants were sown under short-day conditions and transferred to long days after the number of days indicated on the abscissa. The ordinate is days of age at floral initiation. Each of the points in this figure, as well as, all the others to follow, represents the mean of 32 plants.

When 0, 5, or 10 short days were supplied, beginning with the day of planting, all the three varieties differed greatly and initiated their floral tissue relatively late. After the plants reached 15 to 20 days of age under short-day conditions, there was a response to the short days. Each variety exhibited a threshold in sensitivity at about 15 days of age. All three varieties initiated their floral tissue shortly after 20 short days. In fact, the plants which were supposed to receive the long days after 25 short days, initiated before the long

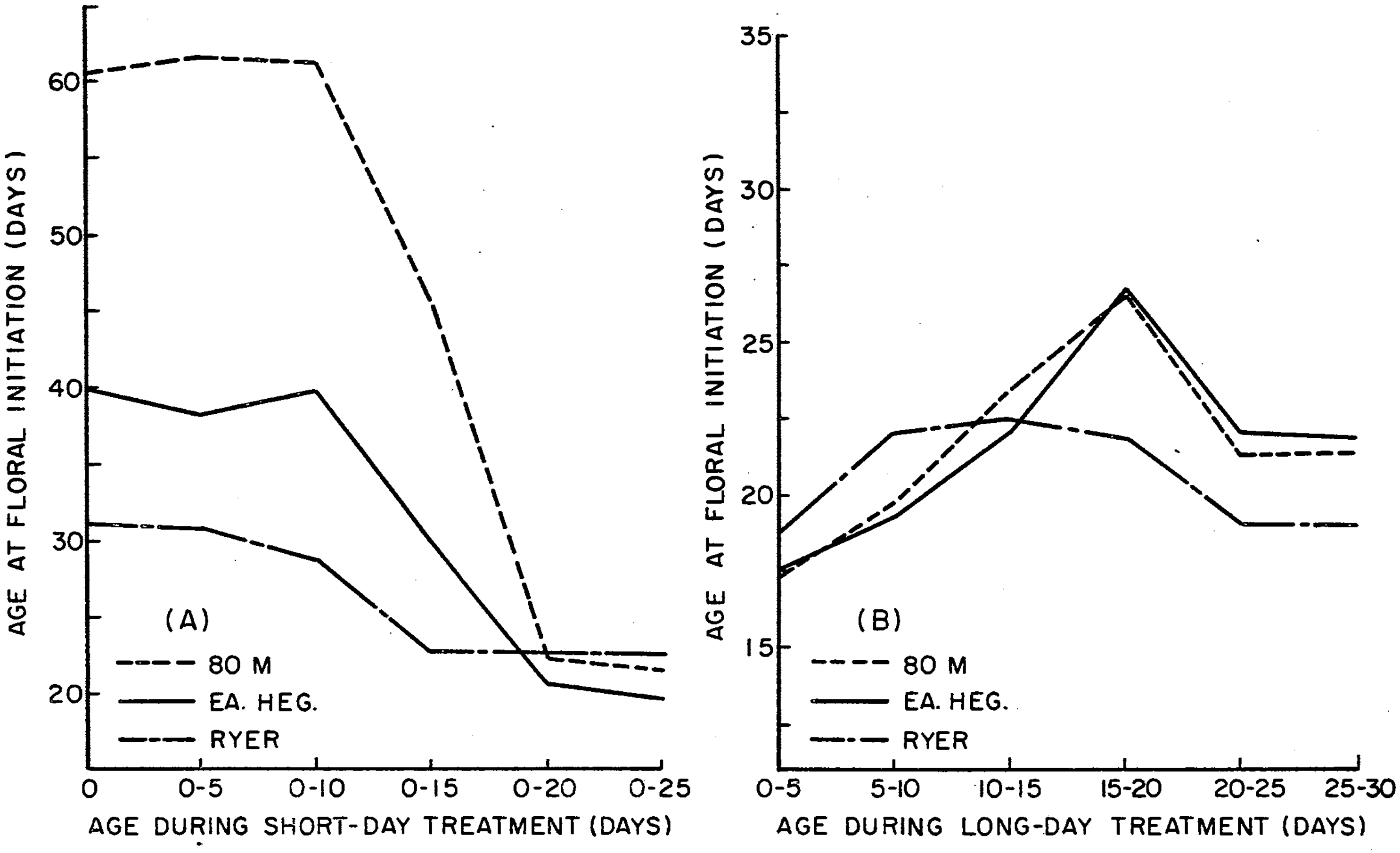

Figure 10. Growth Chamber Study II A and B: Age at Floral Initiation for Three Sorghum Varieties. A. Subjected to Different Numbers of Short Days Followed by Long Days. LSD (.05) Treatments = 4.0; Varieties = 3.7. B. Subjected to Five Long Days at Different Ages Preceded and Followed by Short Days. LSD (.05) Treatments = 0.97; Varieties = 1.24.

days were started.

Table VII presents the results of this experiment as the mean number of days to floral initiation for 16 plants (four plants in each of four pots). These means show that the two trials for each treatment are in close agreement when the plants received 20 or more short days. The trials differed more when an intermediate number of short days were supplied. This probably indicates that very slight differences in the growth chambers affect the age at which plants become sensitive to short days.

Figure 10B illustrates the results of Experiment B in which the plants were moved from short to long and back to short-day lengths. It shows a fairly normal short-day response when 5 long days began at 0 and 5 days of age. The long-day treatments had no effects in these cases since the plants all initiated at about 20 days. Those plants that received five long days beginning on the planting days initiated earlier than those that received long days beginning on the fifth or tenth day. This was probably because the seeds germinated faster and the seedlings emerged and grew more rapidly under the long days. This was not a photoperiodic response since the seeds and seedlings were under the soil for three to four of the five days. When these varieties were subjected to five long days beginning at 10 days of age there was a slight delay in initiation. Early Hegari and 80-day Milo showed a delay when the long days were applied between 15 and 20 days of age. These plants must have become sensitive during this period since the long days had their main delaying effect in this interval. Long days after 20 days of age had little or no effect because the plants had started the initiation process, at least physiologically, before the

TABLE VII

GROWTH CHAMBER STUDY II A: AGE AT FLORAL INITIATION FOR THREE VARIETIES OF SORGHUM SUBJECTED TO SHORT DAYS FOR SIX DIFFERENT INTERVALS, AND THEN GROWN UNDER LONG DAYS

	Age During Short-Day Treatments (Days) and Trials											
	0[a]		0-5		0-10		0-15		0-20		0-25	
Variety	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari	36.3[b]	40.8	36.3	40.2	35.4	44.2	26.6	32.9	20.1	21.1	19.1	20.5
80-Day Milo	62.1	59.1	64.2	59.3	62.4	60.1	42.9	48.3	22.6	22.2	21.9	21.8
Ryer	30.1	32.0	30.1	31.6	28.4	29.4	23.5	22.0	22.2	22.8	21.9	23.1

[a] Received no short days

[b] Each number is the mean of 16 observations (four plants in each of four pots).

long-day treatment. The five long days did not affect Ryer nearly as much as the other varieties. Early Hegari and 80-day Milo were not delayed more than five days by the long days during the 15-20 day interval. This indicates that the long days did not remove or destroy any of the preceding short day effect and the effect of the long days did not prevent the action of the following short days.

Table VIII indicates a very good agreement between the two trials of this experiment.

The graphs in Figure 11 show the results of Experiment C in which the plants were exposed to long days first and then transferred to short days. Figure 11-1 illustrates how the number of days to floral initiation was affected by these treatments. When the short days began at zero and five days of age, all three varieties initiated at about 20 days. The longer the plants were subjected to long days, the later they initiated their floral tissue. These data indicate a simple quantitative response except for those plants that germinated and emerged under the short days. These plants received less of the warm daytime temperature and grew more slowly as small seedlings. The varieties did not differ significantly at any treatment.

Figure 11-2 illustrates this same experiment in another respect. Instead of the number of days to floral initiation, it presents the number of short days preceding floral initiation. As the plants grew under long-day conditions for a longer period of time fewer short days elapsed before floral initiation was observed. When 25 long days preceded the short days, these varieties initiated at about 33 days of age -- about six days after the first short day. This is not necessarily the number of short days required for floral initiation. It is

TABLE VIII

GROWTH CHAMBER STUDY II B: AGE AT FLORAL INITIATION FOR THREE VARIETIES OF SORGHUM SUBJECTED TO FIVE LONG DAYS AT SIX DIFFERENT AGES, PRECEDED AND FOLLOWED BY SHORT DAYS

	Age During Long-Day Treatments (Days) and Trials											
	0-5		5-10		10-15		15-20		20-25		25-30	
Variety	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari	16.7[a]	18.4	18.9	19.5	21.8	22.2	26.4	27.0	22.0	22.1	21.8	22.1
80-Day Milo	16.8	18.0	19.8	19.8	23.1	23.9	26.6	26.8	21.1	21.4	20.8	21.8
Ryer	18.5	19.2	21.8	22.1	22.2	22.8	21.5	22.2	18.7	19.7	18.7	19.3

[a] Each number is the mean of 16 observations (four plants in each of four pots).

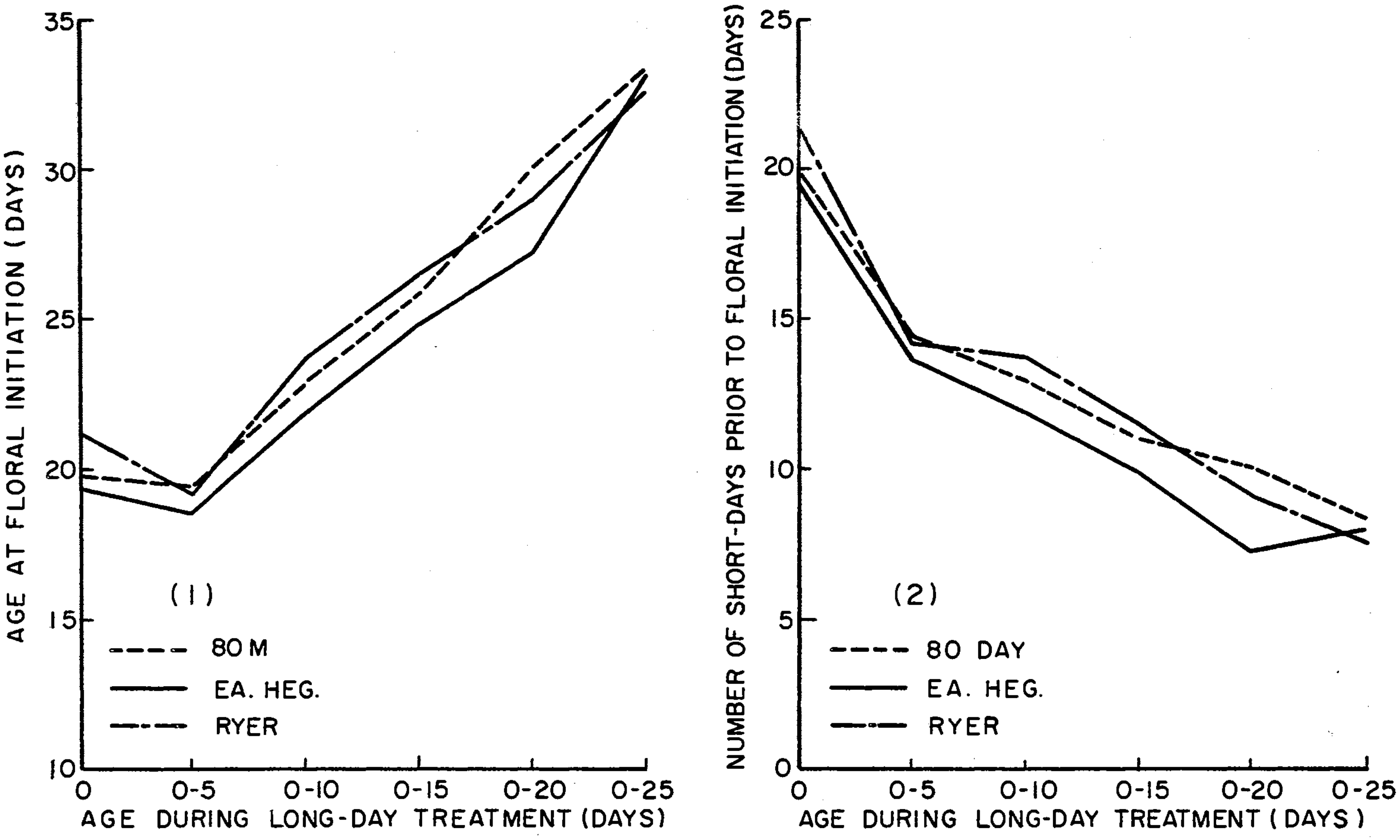

Figure 11. Growth Chamber Study II C. 1. Age at Floral Initiation of Three Sorghum Varieties Subjected to Different Numbers of Long Days Followed by Short Days. LSD (.05) Treatments = 7.4; Varieties = 5.8. 2. Number of Short Days Prior to Floral Initiation for Three Sorghum Varieties Subjected to Different Numbers of Long Days Followed by Short Days.

the number of days from the first short day until floral initiation was observed morophologically.

Table IX shows that there was relatively close agreement between trials. Slight differences in the environment had less effect when many short days were provided.

Experiment D, in which the plants were moved from a long day condition to a short day for five days and then back to long days, is summarized by Figure 12. Figure 12-1 illustrates how days to floral initiation was affected by these short-day treatments. Short days given before the 80-day Milo and Early Hegari were about 15 days old, had no hastening effect on floral initiation. Ryer was slightly stimulated by the short days earlier than the other varieties. There was a delay in floral initiation after the plants were 20 days old because the stimulus for early initiation was not applied until after the plants were sensitive for several days. For earliest floral initiation short days must be applied at about 15 days of age.

Figure 12-2 shows that the number of days from the first short day to floral initiation decreases greatly as the plants become older. When five short days were applied to 25 day old plants, initiation followed the first short day by less than 10 days.

Table X shows that when the short days were given either early or late, the trials produced similar results. When the short days were applied at about 15 days of age, the trials differed greatly. This was especially true for the 80-day Milo that was subjected to five short days from 15 to 20 days of age. This indicates that the length of the photoperiodic insensitive juvenile stage of sorghum is under the control of environmental conditions which were not constant. The large

TABLE IX

GROWTH CHAMBER STUDY II C: AGE AT FLORAL INITIATION FOR THREE VARIETIES OF SORGHUM SUBJECTED TO LONG DAYS FOR SIX DIFFERENT PERIODS, THEN GROWN UNDER SHORT DAYS

	Age During Long-Day Treatments (Days) and Trials											
	0[a]		0-5		0-10		0-15		0-20		0-25	
Variety	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari	18.9[b]	20.0	18.8	18.6	23.9	19.8	28.2	21.6	26.9	27.6	33.2	32.9
80-Day Milo	18.9	20.4	19.9	19.1	24.8	20.8	27.8	24.1	30.9	29.4	34.2	32.4
Ryer	20.7	21.8	18.6	19.9	26.0	21.4	28.3	24.8	30.6	27.5	32.7	32.4

[a] Received no long days

[b] Each number is the mean of 16 observations (four plants in each of four pots).

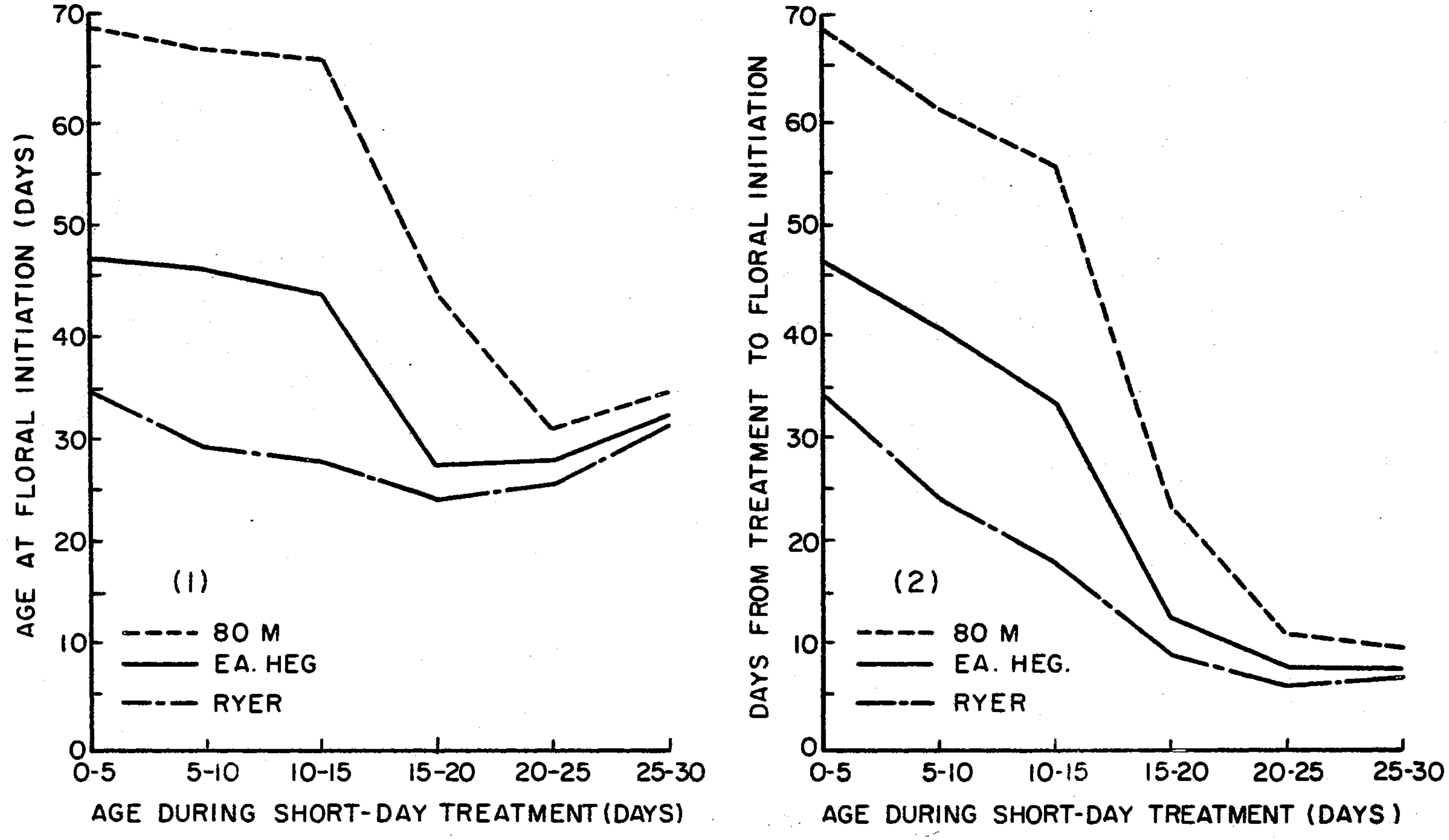

Figure 12. Growth Chamber Study II D. 1. Age at Floral Initiation for Three Sorghum Varieties Subjected to Five Short Days at Different Ages Preceded and Followed by Long Days. LSD (.05) Treatments = 20.9; Varieties = 16.6. 2. Number of Days From the First of Five Short Days, Provided at Different Intervals, to Floral Initiation for Three Sorghum Varieties.

TABLE X

GROWTH CHAMBER STUDY II D: AGE AT FLORAL INITIATION FOR THREE VARIETIES OF SORGHUM SUBJECTED TO FIVE SHORT DAYS AT SIX DIFFERENT AGES, PRECEDED AND FOLLOWED BY LONG DAYS

	Age During Short-Day Treatments (Days) and Trials											
	0-5		5-10		10-15		15-20		20-25		25-30	
Variety	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari	44.2[a]	48.4	43.3	48.4	43.6	42.8	24.1	30.4	26.6	29.2	31.1	34.2
80-Day Milo	72.6	65.1	68.9	63.9	69.8	61.4	24.9	61.4	27.2	34.8	33.8	35.6
Ryer	33.6	35.6	29.7	29.4	30.3	25.6	23.0	24.9	25.6	26.2	30.2	33.6

[a] Each number is the mean of 16 observations (four plants in each of four pots).

amount of discrepancy between trials of this experiment produced a large LSD, but this emphasizes the sensitivity of sorghum plants to the environment. For this reason, Figure 12 indicates trends, some of which are not statistically significant.

The analyses of variance for Experiments A through D are given in Table XI and indicate that in each experiment the treatment, varieties, and treatment X varieties interactions are significant.

Table XII presents the means for each of three trials for Experiment E, in which the plants were subjected to three short days at four different ages. Since Trial 1 was terminated after 45 days and Trial 2 after 33 days, it is not known when 80-day Milo would have initiated.

Even though these data are very inconsistent, the results show that only three short days may produce a full short-day response in some sorghum varieties. This experiment also shows that there is a very precise set of conditions that must be met for sorghum to respond to short days.

The results of removing all the leaves except the first four, five, six, or seven and subjecting the plants to short days are presented in Table XIII (Experiment F). With seven intact leaves, Ryer and 80-day Milo produced a nearly normal short-day response. When fewer leaves were allowed to remain intact, the plants initiated later. The experiment was terminated after 60 days.

If the plants with only four, or perhaps five, leaves had responded to the short-days normally, it could have been concluded that the juvenile insensitive stage of sorghum ended with some biochemical change. Since this is not the case, the change from insensitive to sensitive may be due physically to an increased leaf area to perceive

TABLE XI

GROWTH CHAMBER STUDY II: ANALYSIS OF VARIANCE FOR EXPERIMENTS A, B, C, AND D

Source	DF	Mean Squares			
		A. SHORT TO LONG	B. SHORT TO LONG TO SHORT	C. LONG TO SHORT	D. LONG TO SHORT TO LONG
TOTAL	575	-	-	-	-
Trials (T)	1	283.3611	58.7778	375.3906	1042.7517
Treatment (TR)	5	11062.6861**	557.6528**	2718.6434**	8404.7642*
Error a	5	38.7361	2.2861	132.8906	1062.3142
Variety (V)	2	19160.8403**	69.6997**	81.4236**	25261.5330**
V X TR	10	1981.2799**	85.9372**	14.8215**	2105.0663**
Error b	84	31.2522	2.2033	3.2373	89.6619
Pots in TR in T	36	3.5509	2.3796	3.5850	4.8953
Plants in V, Pots, TR and T	432	2.0278	1.1620	.8235	1.6777

*Significant at .05 level

**Significant at .01 level

TABLE XII

GROWTH CHAMBER STUDY II E: AGE AT FLORAL INITIATION FOR THREE VARIETIES OF SORGHUM SUBJECTED TO THREE SHORT DAYS AT FOUR DIFFERENT AGES

		Age During Short-Day Treatment (Days)			
Variety	Trial	13-16	16-19	19-22	22-25
Early Hegari	1	22.9[a]	21.8	26.9	27.5
	2	31.0	33.0	32.1	31.2
	3	45.8	26.2	37.8	36.3
80-Day Milo	1	45+[b]	31.0	33.9	36.9
	2	33+[b]	33+[b]	33+[b]	33+[b]
	3	58.6	51.7	58.9	58.4
Ryer	1	22.5	22.8	26.5	27.7
	2	24.8	28.7	30.4	31.5
	3	29.9	26.5	31.4	31.2

[a] Each number is the mean of 16 plants.

[b] Did not initiate before termination of experiment

TABLE XIII

GROWTH CHAMBER STUDY II F: AGE AT FLORAL INITIATION OF THREE SORGHUM VARIETIES WITH ONLY 4, 5, 6, OR 7 LEAVES EXPOSED TO SHORT DAYS

	Number of Leaves Remaining			
Variety	4	5	6	7
Early Hegari	60+[a]	37.0	31.2	30.0
80-Day Milo	60+[a]	39.5	31.2	23.2
Ryer	46.5[b]	29.8	28.5	22.0

[a] Did not initiate before termination of experiment at 60 days

[b] Each number is the mean of four plants.

the stimulus or to some change in the plant's chemistry. In this, and other experiments, a trend was noted that healthier, more vigorously growing plants, usually initiate sooner, even when the same treatment was applied.

From the results of Growth Chamber Study I (in Chapter IV), as well as the results reported by other researchers, it is known that temperature has an important effect on the photoperiodic response. At temperatures different from 32 C in the day and 21 C in the dark period the results may be different from those reported here. Slight differences in the environment, which were not controllable, caused greater responses to long days. Short days seem to hasten maturity, with little difference caused by other factors.

These experiments show that sorghum breeders could probably make use of controlled environment chambers to more easily make crosses involving late, photoperiod sensitive lines. To minimize the time required in the chambers for any group of plants, long warm days should be used to germinate the seeds and grow the seedlings up to about 15 days. After this age, the plants should be photoperiod sensitive, and short days should hasten floral initiation. To be more effective, more than five short days should be applied. At least 10 short days would probably be safe. The Field Study and Growth Chamber Study I showed that warm temperatures hasten the interval from floral initiation to anthesis, and that this interval showed little response to day lengths. Long warm days during the floral period would probably produce the largest heads in the shortest amount of time.

Using techniques such as these, sorghum breeders and geneticists may be able to handle more generations per year than using greenhouses or winter nurseries in the tropics. Additional studies need to be conducted to determine the efficiency of starting plants in the growth chambers and transplanting them into the field. Such a procedure would also allow the breeder to select for characteristics other than photoperiodic response.

CHAPTER VI

SUMMARY AND CONCLUSION

The field study was conducted to determine the effects of 10-hr and normal photoperiods on the maturity of 7 sorghum varieties planted in June and August. The 10-hr days were produced by covering half of each block with black polyethylene. The results of this study showed that short days hastened maturity of these varieties as measured by the number of days to floral initiation and anthesis. However, the amount of response to different day length changed with planting dates and genotypes. The day lengths and planting dates studied affected the length of the interval from planting to floral initiation more than the interval from floral initiation to anthesis.

A growth chamber study was conducted to observe the effects of 10-, 12-, and 14-hr photoperiods and 27 and 32 C day temperatures on the time required for Early Hegari, 80-day Milo, and Wheatland to reach floral initiation and anthesis. The effects of 16 and 21 C night temperatures on the time required for floral initiation were also determined.

Ten-hour days hastened the floral initiation and anthesis of each variety in all temperature combinations. Fourteen-hour days usually, but not always, delayed the maturity as compared to 10-hr days. The rate of maturity of these three varieties under 12-hr days was highly dependent upon the day and night temperature. The response to 12-hr days ranged from as early as under 10-hr days, to intermediate between the 10- and 14-hr days, and to later than some 14-hr days.

The interval between floral initiation and anthesis was not significantly affected by day length. However, a statistically significant effect was observed due to day temperature. The warmer temperature often hastened development. The overall effect was small and not of great importance in determining the rate at which a variety reached anthesis. The time required to reach anthesis followed a very similar pattern to that of the time required to reach floral initiation.

Growth chamber studies were conducted in which Early Hegari, 80-day Milo, and Ryer plants were moved from one day length to another at different ages to determine the age at which sorghum became sensitive to short days. These studies showed that these sorghum varieties must be about 15 days of age before a short-day treatment gave a stimulating effect. After they reached this age, they became sensitive to short days and initiated floral tissue quickly following the stimulus. As they increased in age beyond 15 days, less time was required for floral initiation following the stimulation.

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APPENDIX

TABLE XIV

FIELD STUDY: AGE AT FLORAL INITIATION FOR SEVEN SORGHUM VARIETIES SUBJECTED TO DIFFERENT DAY LENGTHS AND PLANTING DATES

DAY LENGTH	10-Hr Day				Normal Day			
PLANTING DATE	June 10		Aug. 16		June 10		Aug. 16	
BLOCK	1	2	1	2	1	2	1	2
VARIETY								
Hegari	18.4[a]	18.5	18.5	18.8	29.7	32.8	27.8	27.5
Early Hegari	19.2	18.8	17.3	17.4	27.8	27.4	23.7	22.2
80-Day Milo	18.2	17.6	16.6	16.2	34.0	35.5	24.3	24.3
Wheatland	21.1	21.7	19.4	19.7	24.3	27.1	28.0	28.0
Combine Kafir-60	26.6	25.1	23.8	24.0	29.6	29.8	28.0	27.2
Ryer	17.2	18.2	14.8	14.1	22.3	21.9	16.1	16.8
Belko[b]	29.9	28.5	30.3	31.8	-d	-d	40.0[c]	40.0[c]

[a] Each number is the mean of a row.

[b] Not included in analysis

[c] Very few plants examined

[d] No plants initiated

TABLE XV

FIELD STUDY: AGE AT ANTHESIS FOR SEVEN SORGHUM VARIETIES SUBJECTED TO DIFFERENT DAY LENGTHS AND PLANTING DATES

DAY LENGTH	10-Hr Day				Normal Day			
PLANTING DATE	June 10		Aug. 16		June 10		Aug. 16	
BLOCK	1	2	1	2	1	2	1	2
VARIETY								
Hegari	43.6[a]	43.9	52.0	51.5	61.9	64.0	62.9	60.6
Early Hegari	45.2	44.8	51.1	51.2	57.6	59.1	56.8	59.7
80-Day Milo	46.3	43.8	51.5	48.7	68.8	66.5	60.5	60.7
Wheatland	49.0	49.8	55.3	55.4	60.4	58.0	72.2	70.6
Combine Kafir-60	58.2	54.5	61.8	62.2	61.0	59.2	69.8	68.2
Ryer	44.4	46.5	47.7	46.2	51.6	50.1	50.7	49.9
Belko[b]	72.0[c]	69.7[c]	-d	-d	-d	-d	-d	-d

[a] Each number is the mean of a row.

[b] Not included in analysis

[c] Very few plants

[d] No plants bloomed.

TABLE XVI

FIELD STUDY: NUMBER OF DAYS FROM FLORAL INITIATION TO ANTHESIS (FLORAL PERIOD) FOR SEVEN SORGHUM VARIETIES SUBJECTED TO DIFFERENT DAY LENGTHS AND PLANTING DATES

DAY LENGTH	10-Hr Day				Normal Day			
PLANTING DATE	June 10		Aug. 16		June 10		Aug. 16	
BLOCK	1	2	1	2	1	2	1	2
VARIETY	FLORAL PERIOD (DAYS)							
Hegari	25.2[a]	25.3	33.5	32.8	32.2	31.2	35.1	33.1
Early Hegari	26.0	26.1	33.8	33.8	29.9	31.7	33.1	37.5
80-Day Milo	28.2	26.3	34.9	32.6	34.8	31.0	36.2	36.3
Wheatland	27.9	28.0	35.9	35.7	36.1	31.0	44.2	42.6
Combine Kafir-60	31.6	29.4	38.0	38.2	31.5	29.4	41.8	41.0
Ryer	27.2	28.2	32.9	32.1	29.3	28.2	34.6	33.1
Belko[b]	42.1[c]	40.1[c]	-[d]	-[d]	-[d]	-[d]	-[d]	-[d]

[a] Each number is the mean of a row.

[b] Not included in analysis

[c] Very few plants

[d] No plants bloomed.

TABLE XVII

GROWTH CHAMBER STUDY I: AGE AT FLORAL INITIATION (FI) AND ANTHESIS (A) AND NUMBER OF DAYS FROM FLORAL INITIATION TO ANTHESIS (FI-A)[a]

DAY TEMPERATURE	27						32					
DAY LENGTH	10		12		14		10		12		14	
TRIAL	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari												
FI	19.7[b]	23.6	29.3	26.9	28.2	35.6	22.0	23.3	19.5	19.1	42.3	35.6
FI-A	33.2	30.1	34.3	33.5	33.1	28.6	29.7	27.7	26.1	27.6	30.0	29.7
A	53.0	53.7	63.7	60.4	61.3	64.2	51.7	51.0	45.7	46.7	72.2	65.3
80-Day Milo												
FI	22.3	25.6	34.6	30.9	37.1	41.5	21.0	23.0	22.4	22.0	54.4	49.3
FI-A	34.0	33.5	33.5	35.0	38.7	34.4	31.7	52.9	29.8	28.8	29.9	29.5
A	56.2	59.2	68.1	65.9	75.8	75.8	52.7	29.8	52.2	50.8	84.3	78.8
Wheatland												
FI	25.1	27.5	42.2	37.4	31.1	35.2	26.9	27.4	31.2	26.6	47.0	46.4
FI-A	34.3	34.4	36.2	35.8	34.6	33.8	32.4	32.7	33.4	30.1	38.2	37.0
A	59.3	62.0	78.4	73.2	65.8	69.0	59.3	60.1	64.6	56.8	85.2	83.4

[a] 21 C night temperature

[b] Each number is the mean of 24 pots.

TABLE XVIII

GROWTH CHAMBER STUDY I: AGE AT FLORAL INITIATION

DAY TEMPERATURE	27						32					
DAY LENGTH	10		12		14		10		12		14	
TRIAL	1	2	1	2	1	2	1	2	1	2	1	2
Early Hegari												
16 C Night	23.6[a]	21.6	23.3	23.2	29.2	32.3	20.0	20.2	30.8	28.0	30.6	30.8
21 C Night	19.7	23.6	29.3	26.9	28.2	35.6	22.0	23.3	19.5	19.1	42.3	35.6
80-Day Milo												
16 C Night	24.4	23.0	34.6	34.4	33.1	35.9	22.2	21.7	28.0	28.7	36.6	32.0
21 C Night	22.3	25.6	34.6	30.9	37.1	41.5	21.0	23.0	22.4	22.0	54.4	49.3
Wheatland												
16 C Night	30.3	29.9	52.0	52.5	48.0	49.8	27.6	26.1	40.4	46.2	80+[b]	80+[b]
21 C Night	25.1	27.5	42.2	37.4	31.1	35.2	26.9	27.4	31.2	26.6	47.0	46.4

[a] Each number is the mean of 24 pots.

[b] Did not initiate in 80 days

VITA

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