PHYSIOLOGICAL AND AGRONOMIC RESPONSES OF A GRAIN SORGHUM [Sorghum bicolor (L.) Moench] HYBRID TO ELEVATED NIGHT TEMPERATURES

Vincent B. Ogunlela, Ph.D.

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Advisor: Jerry D. Eastin

Greenhouse and field experiments were conducted to study the effects of elevated night temperatures during panicle development on the yield and growth of a grain sorghum [Sorghum bicolor (L.) MoenchJ hybrid ('RS 671'). Investigations involved determination of the growth stage or stages most sensitive to elevated night temperatures and an evaluation of the effect of artificial heat preconditioning on the plant's temperature response.

Two greenhouse experiments and one field experiment consisted of imposing 26.5 C and 32 C night temperatures on plants for 4- or 5-day durations (growth stages) commencing at either panicle initiation or floret differentiation until bloom stage. The 32 C treatment signifi-cantly reduced panicle dry weight, grain yield, seed number, grams of grain/GS-3 day/plant and harvest index by approximately 14%, 14%, 19%, 12% and 11%, respectively. It also increased seed size by about 12%. The 26.5 C treatment only moderately reduced these variables. These temperature treatments hastened maturity by reducing the numbers of days from emergence to bloom and physiological maturity and the lengths of panicle expansion and grain fill periods. Such reductions were related

to yield reduction. Dry matter production and plant height were also reduced by these treatments.

Two other field experiments entailed the heat preconditioning ("heat hardening") of plants in one-half of the plots at about 3 weeks after emergence by subjecting them to brief periods of sublethal temperatures (40 to 46 C). Temperature treatments imposed were 5 C and 10 C above ambient over 7 days durations (growth stages) commencing at panicle initiation until 7 days after bloom.

Similar reductions in grain yield and shifts in components of yield occurred when treated for 7 days with 5 C or 10 C above prevailing air temperatures. Reductions in grain yield, panicle dry weight, seed number and grams of grain/GS-3 day/plant by the ambient +10 C treatment wore about 24%, 25%, 32% and 22%, respectively. About 20% seed size increase, associated with a sizeable seed number reduction, was caused by the same treatment. The 5 C-temperature elevation had lower but significant effects. Treatments had a tendency to hasten bloom and shorten the panicle expansion period but not grain fill. The ambient +10 C treatment significantly inhibited leaf photosynthetic rates by about 21% but considerably increased kernel dry weight and kernel growth rates during the first 2 to 3 weeks of grain fill period.

Artificial heat preconditioning had no significant effects on the response of grain sorghum to elevated night temperatures but tended to enhance yield-related attributes. Yield correlated positively with each yield component, but seed number correlated negatively with seed size.

The most sensitive growth stages to elevated night temperatures seemed to be during the second half of the panicle development period

(about 2 weeks). Of this period the first week after floret differentiation was generally the most sensitive.

Conclusions drawn are (1) that brief periods (a week or less) of elevated night temperatures can reduce grain sorghum yield; (2) that plant growth stage influences the plant's temperature response; (3) that a period of about one week after floret differentiation begins appears to be the most temperature sensitive; and (4) that artificial heat preconditioning provides only limited beneficial effects on the plant's temperature response.

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BY

Vincent B. Ogunlela

http://www.youtube.com/watch?v=J2nCPuqbKFA

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INTRODUCTION

Temperature ranks as one of the most critical among the various climatic factors that are known to affect grain production. Grain yields of cereals are quite often limited by higher-than-optimum growth temperatures which occur quite commonly in the arid and semi-arid regions of the world. Some parts of Nigeria fall under such higher-than-optimum temperature category. Such higher temperatures also occur in the Southwestern and Great Plains regions of the United States, which produce most of its grain sorghum [Sorghum bicolor (L.) Moench]. This makes the use of adapted crop genotypes in such areas highly desirable, if not essential, as appropriate adaptation can mean the difference between reasonable yields and in some cases crop failures in unfavorable years. Consequently, adaptation and/or resistance to high temperature becomes an important trait to consider in developing new crop varieties for use in such areas.

Grain sorghum is one of the major grain crops of the United States, ranking second to corn as the most important feed grain. In total annual production, Nebraska ranks third after Kansas and Texas, respectively. Annual production in the U.S.A. is about 20 million metric tons. A preliminary estimate for 1977 gave Nebraska's grain sorghum production as about 4 million metric tons from a harvested area of about 852,000 hectares.[1] On a world-wide basis, grain sorghum serves as a staple for many developing nations.

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[1]USDA Agricultural Statistics, 1978. pp. 52-53, U.S. Government Printing Office, Washington, D.C.

The limiting effect of high temperature on crop yields can manifest itself through short-term, high-temperature periods during critical plant growth stages. Most previous work done in this area concerned high day temperatures and was done under controlled environments. Such artificial conditions do not represent the natural, dynamic field conditions. Therefore, the potential value of such studies for extrapolation to the field is questionable. Also, most such studies failed to consider the relations between high temperature and phenological stage of the plant.

The justification for the development of research in this area is evident from the fact that short- or long-term elevated night temperatures do occur during some growth stages of the crop which result in various degrees of yield reduction.

The investigations reported here consisted of two greenhouse and three field experiments conducted in 1977, 1978 and 1979 to (1) study some physiological and agronomic responses of a grain sorghum hybrid to elevated night temperatures and (2) to determine at which growth stages the plant is most sensitive to above normal or high temperatures.

Also, an attempt was made to determine the significance of heat-preconditioning ("hardening") on the response of grain sorghum to normal and elevated night temperatures under field conditions.

LITERATURE REVIEW

Effects of High Temperature on Crop Yield and Yield Components

The amount of information on effects of temperature extremes on crop yields in general is enormous, but relatively little is available on high night temperature effects in particular. Yield reductions occur from high temperatures in temperate crops and in tropical and semi-tropical crops in arid and semi-arid zones.

Various degrees of yield reduction in various crops resulting from high temperatures have been reported (Peters et al., 1971). In comparison with yields at moderate temperatures, United States grain sorghum cultivars grown under controlled high temperatures showed depressed yields (Downes, 1972). Results of a series of experiments indicated that when plants were grown under one of five day/night temperature regimes (from 21/16 C to 33/28 C), high temperature (33/28 C) between germination and panicle initiation resulted in low grain yield. Grain yield was greatest from plants grown at low night temperatures and progressively declined with higher night temperatures. Day temperature did not affect grain yield except when accompanied by high night temperatures (Downes, 1972). He suggested that low yields in tropical environments may reflect adverse effects of high temperatures.

Eastin (1976) imposed four day/night temperature regimes (29/17 C, 29/22 C, 29/27 C and 34/22 C) on five grain sorghum genotypes from panicle initiation through maturity in growth chambers. He reported an average of 25 to 33 percent yield reduction from a 5 C above-optimum

night temperature treatment, while 10 C temperature elevation reduced grain yields by about 50 percent. These yield reductions were generally paralleled by reductions in seed number.

Asana and Williams (1965) conducted some experiments in controlled environments to determine the effects of high temperature on grain development and yield of five wheat cultivars exposed to three day (25, 28, 31 C) and two night (9 and 12 C) temperatures during post-anthesis. They observed a 16 percent mean yield reduction for the 6 C rise in day temperature, but no significant differences among cultivars. Grain weight was not significantly affected by night temperatures in these studies. However, in a subsidiary experiment using three day/night temperature regimes (24/19, 27/22 and 30/25 C) highly significant but complex interactions between temperature regime and cultivar were established.

Comparing sorghum yields with daily maximum temperatures over a period in Queensland, Australia, Skerman (1956) found that when daily maximum temperatures exceeded 100 F for three or more consecutive days, there was an adverse effect on yields. The so-called "heat waves" were most deleterious during anthesis and during the first month of grain fill. His observations were confirmed by the fact that short-term periods of heat stress during critical growth stages in grain sorghum can have detrimental effects on grain yields (Sullivan et al., 1977a). Over a decade earlier, Pasternak and Wilson (1969) reported similar findings on the effects of heat waves on grain sorghum yields. They claimed that moist or dry heat stress could accelerate anthesis resulting in a reduced seed set and ultimately reduced yields. It was also

reported that heat stress at or soon after boot stage lowered yield and when this was accompanied by low humidity, 10 to 20 percent yield reductions can occur in the field.

In many instances, high night temperatures have been more detrimental to crop growth and yields than high day temperatures (Karr et al., 1959; Langridge and McWilliam, 1969; Owen, 1971; Palis, 1971; Peters et al, 1971; Downes, 1972; Campbell and McCloud, 1977). The data presented by Karr et al. (1959) on the effect of short periods of high day and night temperatures on pea (Pisum sativum L.) yields revealed that high night temperatures proved more critical than day temperatures, resulting in a 25 percent yield reduction as against about 8 percent for high day temperatures. Conflicting opinions have, however, been expressed by some other investigators. They contended that day temperatures, rather than night temperatures, were more influential on crop yields (Nel and Small, 1973).

Based on their findings from a field study designed to assess the *effect of nighttime air temperatures on yields of corn, wheat and soy*beans, Peters et al. (1971) surmised that the largest seasonal variant experienced by a plant community would be night leaf temperature. They conducted a series of experiments in which two night temperature treatments, hot and cool air, were artificially imposed on unreplicated plots. Results showed approximately 45, 40 and 10 percent yield reductions for wheat, corn and soybean, respectively, from about 10 C above-control night temperatures.

Yield reductions occurring under elevated night temperatures were usually associated with earlier senescence and maturity; hence, the grain filling period was shortened (Chinoy, 1947; Asana and Williams, 1965; Wattal, 1965; Peters et al., 1971; Eastin, 1976). Although Eastin (1976) reported the existence of genotype x temperature interactions for each of the yield-related factors considered in his study, he attributed yield differences, at least in part, to the following: (1) time reductions in panicle development (lowered seed number) and grain filling; (2) shifts in polarization of assimilates away from flora structures to non-floral structures; and (3) differential metabolic or biological efficiency at different temperatures.

Gipson et al. (1979) conducted field experiments for two consecutive years imposing two night temperature regimes, namely 14 and 22 C, on temperature (RS 671) and tropically (ATx 623 x Tx 430) adapted grain sorghum hybrids. Temperature control was maintained on these two hybrids from emergence through maturity each year and also from emergence until bloom on these and two other genotypes during the second year. Plants were exposed to the natural field environment during daylight. Of the three phenological periods (Eastin, 1972), namely, emergence to panicle initiation (GS-1), panicle initiation to bloom (GS-2) and bloom to maturity (GS-3), the greatest temperature response occurred during GS-2. Length of the GS-2 period was the most significantly shortened. When treatments were imposed from emergence until maturity, the 8 C increase in night temperature resulted in 19 and 18 percent reductions in number of seeds per head and weight of seed per head, respectively.

Effects of high temperature stress after anthesis on wheat grain development and yield were determined by Palis (1971) using winter and spring cultivars. He subjected plants to four day/night (20/20 C, 20/40 C, 40/20 C and 40/40 C) temperature regimes during grain fill. He claimed that grain yields and yield components at the 20/20 C regime were consistently higher than or equal to those at 20/40 C and 40/20 C regimes but were lowest at the 40/40 C regime. His data suggested that warm nights were more detrimental to wheat yields than warm days even though warm days and nights severely deterred not only grain development but also physiological activities of the plants. Deleterious effects of high temperature stress on wheat grain development were shown by declining yield and yield component magnitudes with increasing levels of temperature regimes. He thought that increased dark respiration, rather than decreased potential photosynthesis, appeared to be a more determining factor of wheat yield.

Nel and Small (1973) subjected three "early" and one "late" maturing wheat cultivars to three different day and night temperatures in a factorial experiment. High day and high night temperatures consistently reduced grain yield. Although increased day temperature generally caused greater yield reduction than increased night temperature, nevertheless, high night temperatures reduced total number of kernels, number of ears, number of spikelets per ear, number of kernels per ear and straw and root yields. Low night temperature wholly or partially eliminated the adverse effect of a high day temperature. They speculated that the temperature effect on grain yield was mediated through

its effect on the formation and development of kernels, which could be explained by a higher respiratory activity at the higher temperatures.

The effects of climatic factors on the growth, reproductive development and seed yield of a cowpea genotype were investigated by Huxley and Summerfield (1976) in controlled environment cabinets. Included among the treatments were two day (27 and 33 C) and two night (19 and 24 C) temperatures. They observed warm nights hastened the onset of flowering as well as enhanced dry matter production during the vegetative period. Warm days reduced the number of pods borne on branches by about 49 percent as did warm nights. The degree of yield reduction from warm temperatures is a function of both temperature magnitude and duration. From the temperature treatment of pea plants during different growth stages, Lambert and Linck (1958) observed that with each temperature, longer treatment duration meant greater yield reduction, and for a given duration, the higher the temperature, the lower was the yield. Plants treated five days after bloom were most severely affected.

Consideration of the stage of plant development during which the plant is most sensitive to high temperature stress had led to many conflicting reports. Generally, it is believed that the vegetative phase is less critical than the reproductive. Owen (1971) subjected a semi-dwarf wheat cultivar to two temperature extremes (high and low). He observed that high temperature from floral initiation adversely affected floret development and grain filling was greatly reduced when stress occurred after ear emergence. He concluded that major effects on yields were caused by stress long before anthesis. That seems to be in accord with the conclusion by Gipson et al. (1979) claiming that the most critical

growth period for grain sorghum was between panicle initiation and bloom, and this is also true for wheat (Warrington et al., 1977). On the basis of their work on spring wheat, Ford and Thorne (1975) argued that cereal crops are more susceptible to temperature after anthesis, but this depends on grain yield being controlled more by carbohydrate supply than by sink capacity of the grains. Similarly, Eastin (1976) reported that the grain filling period appears critical to grain yield for grain sorghum.

The reason why high night temperatures hasten ripening and reduce grain yield is not yet well understood. This is further complicated by the fact that the analysis of cause and effect relationship in grain yield is complex. It has, however, been suggested that high temperature increases respiration and causes hastened ripening of rice (Yamamoto, 1954 cited by Yoshida, 1973) and significant yield reductions in wheat (Palis, 1971; Downes, 1972; Nel and Small, 1973). Moss et al. (1961) claimed that high night temperature increased respiration in the night but this in turn resulted in increased photosynthesis in the daytime. Based on their findings, they concluded that the increased respiration caused by high night temperature could not reduce grain yield. Murata (1964) had earlier believed that high night temperature reduced yield partly due to increased respiration and partly due to increased leaf senescence and decreased photosynthesis. Inadequate assimilate available to support dark respiration could also be a factor (Downes, 1972).

A shortened plant life cycle has also been associated with grain yield reduction caused by heat stress (Asana and Williams, 1965; Peters et al., 1971; Bierhuizen, 1973; Eastin, 1976). In addition,

Eastin (1976) attributed yield losses to shifts in polarization of assimilates and lower metabolic efficiency.

Temperature Effects on Plant Metabolism

Lange (1965) concluded that one of the most important climatic factors influencing biological processes is temperature since there is hardly any metabolic process not affected by it. Variations in rates of physiological processes and metabolic activities are often associated with different levels of day and night temperatures. However, this relationship is not linear and is a function of stress duration (Chabot and Lewis, 1976). Higher temperatures usually bring about faster metabolic rates but within certain limits. Photosynthesis, respiration, transpiration, translocation and nitrate reductase activity are among processes so far reported. Alexandrov (1964) and Threshow (1970) concluded that photosynthesis is a plant process that is quite sensitive to temperatures; the rate of the overall photosynthetic process being greatly affected by the physical environment perhaps more than any other growth process (Bjorkman and Berry, 1973; Pearcy et al., 1977).

There exists an optimal temperature range, determined by species and conditions, within which net carbon dioxide fixation is highest (Langridge and McWilliam, 1967; Bauer et al., 1973), and this range generally correlates with the temperature conditions of the natural environment (Mooney and West, 1964). It is also believed that the disparity of these temperature limits from these temperatures which cause lethal damage varies with species, conditions and time of year. Apart from the inhibition of carbon dioxide exchange that might occur in the presence

of extreme temperatures, these environmental conditions may also have aftereffects which could inhibit subsequent photosynthesis even at optimal temperatures (Bauer et al., 1973). The intensity of stress determines whether photosynthesis will be partially inhibited or, in extreme cases, completely stopped.

Two temperature-dependent counteracting processes involved in high temperature limit of net photosynthesis are the dark reactions of photosynthesis, which are markedly inhibited by high temperatures and the other is respiration, which increases rapidly with temperature until it finally diminishes. Such a collapse in metabolism has been associated with rapid inactivation and denaturation of enzymes that play specific roles in normal metabolism (Langridge and McWilliam, 1967; Salisbury and Ross, 1978). The heat limit of photosynthesis for a plant is influenced to a significant extent by its stage of development. Bloom stage is particularly one when high temperature stress appreciably inhibits the photosynthetic process as reported for grain sorghums by Norcio and Sullivan (1967a).

Raschke (1970) investigated the aftereffect of previous temperature on subsequent photosynthetic rate of maize (Zea mays L.) at favorable temperatures. Results showed that carbon dioxide assimilation at 25 C was not affected by previous temperatures between 10 and 35 C, but exposure to higher temperatures sharply diminished subsequent CO_2 fixation. In addition to heat reducing carbon dioxide assimilation, it also caused reduction as an aftereffect.

Norcio and Sullivan (1975, 1976a,b) conducted a series of experiments initiated in the summer of 1974 to study the effects of high

temperature on the photosynthetic and respiration rates of some sorghum and corn genotypes. The sorghum genotypes had earlier been selected for heat and drought tolerance. Genotypes selected represented low and high drought tolerance groups. Rates of photosynthesis and respiration of leaf sections were measured at 40 and 43 C during anthesis by an oxygen evolution method to estimate the thermal stability of the photosynthetic apparatus. Subjecting leaf sections to the higher temperature (43 C) in the laboratory resulted in some inhibition of the photosynthetic apparatus, both in sorghum and corn; reversal of the photosynthetic process even occurred in some of the genotypes. However, a few sorghum genotypes maintained or increased their photosynthetic rates as temperature increased up to 43 C. They concluded that the ability of the plant to photosynthesize at a higher rate under high temperature conditions may be an important character when it is under thermal stress. Sorghum species, belonging to the C_4 group of plants, are endowed with photosynthetic characteristics that are advantageous under conditions of high temperature and high irradiance (Bjorkman and Pearcy, 1971). When respiration rates were measured by Norcio and Sullivan (1975), they claimed that respiration tended to increase as the temperature increased from 40 to 43 C. This was confirmed by Eastin et al. (1976) who observed about 14% (whole-plant) respiration increases per 1 C temperature increase in the 10 to 27 C range. When the photosynthetic responses of sorghum and corn genotypes to these temperatures at panicle initiation and flowering were compared, the flowering stage was the more sensitive to elevated temperature (Norcio and Sullivan, 1976a). Thermal stability of the photosynthetic process appeared to correlate fairly well with heat tolerance as

determined by leaf-disc electrical conductivity tests (Sullivan, 1972). By means of measuring the effect of heat treatment on the photosynthetic process of six sorghum genotypes using the infrared gas analyzer, Norcio and Sullivan (1976b) observed that stomates were sensitive to high temperatures and closure of stomates was induced under heat stress. It is logical to speculate that the control of transpiration and gas exchange by high temperature would follow identical relationships. However, from his studies on plant species from contrasting thermal environments, Bjorkman (1975) observed that decline in photosynthetic rate at high temperatures was not due to a decreased conductance of the stomates to CO_2 diffusion, but on the contrary, conductance reached their maximum values at the highest temperatures measured.

When the temperature responses of photosynthesis and respiration were compared, they appeared to differ to some extent (Norcio and Sullivan, 1975). That observation was in accord with the work of Lundergardh (1925) reported about a half century earlier. He showed that the temperature curve of carbon dioxide assimilation differed considerably from that of respiration and that the optimum temperature for respiration was much higher than that for carbon assimilation. In general, because photochemical processes are not strongly temperature-dependent, leaf photosynthesis is relatively insensitive to temperature (Stoy, 1965; Cooper, 1973), at least in C_3 plant species, until later in the growing season when crop net photosynthesis is markedly decreased (Baker et al., 1972). A similar observation was reported by Halse and Weir (1974) who concluded that unfavorable effect of warm summers could not be explained by its effect on photosynthesis since it was negligible.

The temperature range within which plants photosynthesize has generally been considered as remarkably wide (Gaastra, 1962; Salisbury and Ross, 1978) and thus, when leaf temperatures of many higher plant species reach 35 C or higher in hot summers, they are still able to fix carbon dioxide. Salisbury and Ross (1978) remarked that the response of photosynthesis to temperature is a function of many factors, such as, the plant species, the environmental condition under which that plant was grown (Bjorkman and Pearcy, 1971) and those conditions during measurement.

Although it is a well-known fact that high temperatures cause heat-inactivation of the photosynthetic process in most higher plants, little is yet known about how this inhibition comes about. Bjorkman et al. (1976) compared the heat stability of photosynthesis, chloroplast membrane ractions, photosynthetic enzymes and soluble proteins in leaves of heat-adapted and cold-adapted Atriplex species. They found that complete inhibition of photosynthesis occurred before other symptoms of heat damage were detected. Consequently, it was surmised that high-temperature inhibition of photosynthesis could not result from a general breakdown of the cell's integrity. Among plausible sites of photosynthetic heat-inactivation are temperature-dependence of carboxylation reactions (Bjorkman and Pearcy, 1971; Rathnam, 1978); heat-inactivation of photosystem II resulting in the inhibition of quantum yield of photosynthesis (Bjorkman and Pearcy, 1971; Pearcy, 1977); heat-inhibition of ATP formation by photophosphorylation; and denaturation of components of soluble proteins (Bjorkman et al., 1976). Results from the series of studies conducted by Bjorkman and his colleagues at the Carnegie

Institution substantiate the hypothesis that thermal damage to specific sites of photochemical apparatus is a major factor limiting photosynthetic performance after exposure of intact tissue to damaging temperatures, even though the mechanism remains unclear.

Not too surprising, of course, is the existence of some conflicting reports claiming that the photosynthetic process of some C_4 plant species was enhanced by high temperatures. When irrigated corn plants were subjected to high temperatures during certain growth stages at Illinois, increased apparent photosynthesis was observed by Winter and Pendleton (1970). Similarly, about the same period, Downes (1970) observed increased photosynthesis with increased temperature in sudangrass (Sorghum sudanense Stapf.) in Australia under greenhouse conditions.

The influence of high temperatures on certain other vital processes of the plant other than photosynthesis and respiration has been reported. Some of such processes reported on by investigators are nitrogen metabolism such as nitrate reductase activity (Onwueme et al., 1971; Alofe et al., 1973; Maranville and Sullivan, 1976; Amos and Scholl, 1977); nucleic acid concentrations (Baker and Jung, 1970a,b; 1972); translocation (Wardlaw, 1974; Pearson and Derrick, 1977); and transpiration (Downes, 1970). Reports of decreasing nitrate reductase activity in young seedlings with increasing temperature made by various investigators have been strikingly consistent. Alofe et al. (1973) exposed seedlings of 16 corn genotypes to a high day (35 C) and three variable night (24, 16, 7 C) temperatures. The most rapid decline in nitrate reductase activity occurred at the highest night temperature (24 C) and the least rapid at 7 C. Similar results were reported by

Amos and Scholl (1977) for seedlings of ten maize hybrids exposed to two day/night temperature regimes. The nitrate reductase activity of most genotypes was reduced about 35 percent by high temperature. Reductions of reductase activity by elevated temperatures were also reported for barley seedlings by Onwueme et al. (1971) and sorghum seedlings by Maranville and Sullivan (1976).

Decrease in ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) concentrations in many grass species with increased day or night temperature was observed by Baker and Jung (1970a,b; 1972).

Wardlaw (1970) conducted a ^{14}C-label experiment to monitor the effect of high temperature on the transport of assimilate to wheat grains. He claimed that ^{14}C-labeled assimilate transport to grains was inhibited by high temperature and concluded that assimilate movement was influenced by temperature effect on the source and sink rather than on the transport system *per se*. Pearson and Derrick (1977) concluded that translocation was most sensitive to the temperature at which the plants were grown. He measured the rate of ^{14}C-label loss from leaves of three *Pennisetum* genotypes after imposing day/night temperatures ranging from 18/13 C to 33/28 C. He observed that the initial rates of percentage of ^{14}C loss were highest at 33/28 C, those at 18/13 C being only one-quarter of those at 33/28 C.

Higher transpiration rates generally associate with higher temperatures, a process through which the plant attempts to dispose of its excess heat load when under high temperature stress. Significant increases in transpiration rates with increased temperature were observed for sudangrass and wheat (Downes, 1970).

Effect of Temperature on Crop Growth and Development

Growth and developmental processes of sorghum and most other crops are influenced by a myriad of environmental variables, including temperature. Growth attributes of a plant that are influenced in one way or another are quite numerous, and it can be said that there is hardly one of them that does not respond to temperature at one point of the plant's life cycle. Vegetative growth attributes are generally more sensitive to high temperature during pre-anthesis than during post-anthesis period. The tendency is for high temperature to hasten growth rate and shorten growth duration in higher plants (Asana and Williams, 1965; Fryer et al., 1966; Pasternak and Wilson, 1969; Peters et al., 1971; Downes, 1972). An important fact, of course, is that the response of plant growth and development to temperature is extremely complex. A physiological analysis of the effect of temperature on growth and development of the plant would lead to an understanding of the adaptation of the crop to varying temperature conditions and to means for improving production (Wattal, 1965).

The relative response of higher plants to day or night temperature varies somewhat and is a function of many factors, such as, species, age, daylength and so on. A tomato plant, for instance, is known to be particularly sensitive to differences in night temperature, whereas it does not respond to a wide range of day temperatures (Went, 1950). He believed that responses to night temperature is a function of (1) the age or size of the plant, (2) the previous night temperatures, (3) the

light intensity on the previous two days and (4) the variety. This is also true of higher plants in general.

Methods of growth analysis are widely used to study the quantitative responses of plant growth to various environmental factors, especially temperature and light. This entails destructive harvesting of a suitable number of plants within a given land area at certain regular time intervals and determining dry matter production. Even though temperature extremes to which plants are subjected are insufficient to kill the protoplasm, it may still inhibit growth, impair vigor and suppress production (Threshow, 1970). Precise growth responses are often difficult to detect in the field and, therefore, often go unrecognized, even when production losses from the reduced growth may be significant long before visible symptoms appear. Nevertheless, temperature level remained a vital factor influencing plant growth, development and yield, at least from an agronomic point of view (Palmer, 1973).

The realization that high temperatures, especially if they occur during certain critical growth phases, could be detrimental to growth and development of higher plants had come about many years ago. Salmon (1941) described the interaction of various climatic factors with small grains, such as, wheat, oats and barley. He explained that high temperatures, especially if accompanied by hot winds, when the plant is at the heading stage or between heading and ripening, may seriously interfere with its growth and development. Delayed flowering in rice was associated with high temperature (Yoshida, 1973). He concluded that the optimal temperature appears to shift from high to low as growth stage advances from the vegetative to the reproductive stage. At the early

growth stages, the growth rate of rice plants in growth chambers increased as the temperature was raised from 22 C to 31 C; however, the effect of temperature on growth rate decreased with time (Yoshida, 1973).

Wilson (1966) compared the net assimilation rates and other growth attributes of widely spaced rape, sunflower and maize plants at 10, 16, 27, 28 and 34 C temperatures. The temperature coefficient of net assimilation rate (NAR) was lower than that of relative growth rate (RGR), and this corresponds to an increase in leaf area ratio (LAR) with rise in temperature. This increase was associated with change in leaf area per leaf weight since temperature had little effect on leaf weight/plant weight (leaf weight ratio). Leaf area ratio provides a measure of the proportion of the total plant active in photosynthesis (Friend et al., 1965). Its study should be of interest in any investigation on the physiology of a whole plant active in photosynthesis. Increasing temperature from 10 to 25 C increased LAR because the growth of leaves was promoted to a greater extent than the growth of stems and roots, and because leaves were thinner (Friend et al., 1965; Robson, 1973), with day temperature having a greater effect than night temperature. A further increase in temperature to 30 C lowered the LAR because of an increased proportion of stem and thicker leaves. When maize was grown at 21 C, a greater leaf area per plant and, consequently, higher leaf area index (LAI) was obtained than when grown at 18 or 25 C. This resulted in a higher dry weight increase after silking (Wilson et al., 1973). Similar results reported by Robson (1973) indicated that leaves of tall fescue (Festuca arundinacea) produced at night temperatures from 20 to 30 C were progressively shorter and smaller in leaf area, leaf length and

area being halved when the night temperature was raised from 20 to 30 C, at the expense of day temperature. Sheaths were similarly affected by temperature, although shorter than laminae.

On the whole, day temperature had a greater effect than night temperature on leaf growth, with the effect of increasing day temperature being positive over almost all ranges used, whereas night temperature above 20 C depressed it. Total leaf number per plant is also influenced by temperature. Positive relations between leaf number and temperature were reported for corn within 15/10 to 36/31 C day/night temperature regimes (Duncan and Hesketh, 1968) and also for sorghum in the warmer night temperature (29 C) than in the cooler (23 C) temperature (Quinby et al., 1973). The results from a study of temperature effects on the partitioning of daily weight gain into new leaf area weight measured on soybean, cotton, pigweed, johnsongrass and cocklebur under 21/10, 32/21 and 38/27 C day/night temperature regimes corroborate earlier results (Potter, 1975). The relative growth rates were greatest at 32/21 C and lowest at 21/10 C for all species, and this correlated well with partitioning of daily weight gain into new leaf area. The rapid growth rate observed under 32/21 C regime was presumed to have resulted from a combined effect of relative values of NAR, leaf weight and leaf area partitioning. Controversial results have, however, been reported recently by some workers (Ruegg and Nosberger, 1977) who claimed that when 16/11, 21/16 and 26/21 C temperature regimes were compared between panicle emergence and full anthesis in tall fescue, the largest leaf area per plant was from 16/11 C. Their results contrasted those of Pearson (1975) who reported that when seedlings of two Pennisetum

cultivars were grown at 33/28, 24/19, 18/13 and 15/10 C day/night temperatures in a natural environment, total green leaf area per plant was highest at 33/28 C when compared to other regimes at the same age.

Considered among suitable growth attributes for use in analysis of variation in yield are the size of the photosynthetic system and its efficiency. The leaf area of a plant is the best measure of photosynthetic size, while photosynthetic efficiency can be measured by the rate of dry matter increase per unit leaf area otherwise called, net assimilation rate (Watson, 1963).

Five tropical grass species were grown in growth chambers under several day/night temperature regimes by Ivory and Whiteman (1978). Both day and night temperatures significantly affected growth in all the species, high night temperatures causing between average to severe reductions in leaf growth in some species. Also, alfalfa (Medicago sativa L.) plants grown under cool night temperatures produced significantly more top growth than those under warm night temperatures (Henderson, 1969). Maize seedlings grown in climate room and glasshouse under various constant temperatures increased in relative growth rate from 0.068 to 0.230 $g\ g^{-1}\ day^{-1}$ as temperature was raised from 15 to 25 C (Brouwer et al., 1973). Even though various processes that determine growth rate were not equally affected by temperature, about 50 percent of the overall growth response could be ascribed to changes in morphology. Day temperature has been considered a more significant factor than night temperature in regard to relative growth rate. Raising night temperature from 10 to 20 C increased RGR of tall fescue but only half as much as raising the day temperature over the same range (Robson, 1973), but

when night temperature was raised above that of day, the RGR was drastically reduced.

Munakata (1976) believed that temperature directly exerts significant influence on both processes of dry matter production and differentiation through entire physiological and biochemical reactions other than the biological clock. He further claimed that it is difficult to analyze how relationships between plant growth and climate at certain growth stages are affected by previous climatic conditions. One would, therefore, expect that temperature requirements differ between species as well as during different stages of growth and development in the life cycle of a plant (Downs and Hellmers, 1977).

Top growth can be reduced by high temperature stress depending upon the stage of occurrence, its intensity and its duration. Baker (1969) and Baker and Jung (1970a) grew four temperate grass species under various temperature regimes and observed that growth produced by each species decreased when plants were subjected to heat stress of various duration and intensities. They attributed the growth reduction to the detrimental effect heat stress might have on nucleic acids, especially RNA.

Total dry weight production and the pattern of its distribution within the plant were found to be modified by temperature when raising temperature by 10 C hastened the phenological development of tall fescue (Ruegg and Nosberger, 1977). The highest dry weight for all growth stages was found at the lowest temperature regime (16/11 C). Under the warm (21/16 C) and the hot (26/21 C) regimes, with their corresponding shorter growth durations, dry weight was decreased. The effect of

temperature on dry weight distribution within the plant was considerable. The root dry weight as a percentage of the total dry weight of the plant dropped remarkably and rapidly under two warm regimes (Pearson, 1975; McWhorter and Jordan, 1976), and root growth was enhanced when night temperature was lowered for tobacco, pea and potato (Went, 1948). As root growth is favored over stem growth, the top:root ratio declines. The effect of high temperature on root dry weight was the reverse of that on stem dry weight (Brouwer, 1973; Ruegg and Nosberger, 1977).

High temperatures have commonly been associated with reduced stem height in higher plants (Jones, 1947; Friend, 1965; McWhorter and Jordan, 1976). McWhorter and Jordan (1976) found that the primary culm height and weight of johnsongrass [Sorghum halepense (L.) Pers] were greater at 24 C than at 40 C, regardless of the illumination. Growth of bean (Vicia faba) plants under high night temperatures (15 and 20 C) resulted in significant decreases in shoot height in comparison with plants grown at low (5 and 10 C) night temperatures (Said et al., 1967). Even though higher night temperatures initially had an accelerating effect on stem elongation, that effect disappeared as plants grew older, with a downward shift in night temperature optimum. Conversely, high temperatures have been observed to accelerate plant growth and cause greater plant height than cool temperatures (Schuster and Okuyucu, 1976). Increasing plant height with increasing night temperature was also reported for soybeans (Warrington et al., 1976) but at the expense of dry matter production (Downs and Hellmers, 1977).

Work on some aspects of grain growth in cereals as affected by temperature has been reported. It is commonly accepted that the rate of

grain growth in cereals is accelerated by high temperatures, but the duration of growth is shortened (Spiertz, 1974, 1977; Gallagher et al., 1976). Exceptionally high temperatures were associated with very fast wheat grain growth rate during the linear growth phase, but this was more than offset by a sharp decline in the duration of that phase (Gallagher et al., 1976). Work in controlled environments suggests that temperature rather than moisture stress stops grain growth prematurely (Asana and Saini, 1962; Asana and Williams, 1965; Spiertz, 1974). Gallagher et al. (1976) surmised that if cereals are to yield well in regions where drought and high temperatures during grain filling are frequent, varieties must be bred which not only increase the rate but also sustain the duration of grain growth.

When high temperatures were applied on rice at the beginning of grain fill, the development of the rice grain was hastened but depressed it when applied later (Nagato and Ebata, 1966). A recent study by Chowdhury and Wardlaw (1978) showed that rice kernel development was less affected by temperature extremes than sorghum but was more sensitive to low temperature than wheat. Rice kernels showed a relatively small change in weight over a 21/16 to 30/25 C temperature range.

Accelerated leaf senescence and ripening of the kernels by higher temperatures were more important for the ultimate wheat grain yield than increase in grain growth rate (Spiertz, 1974). Temperature influences the supply of assimilate to the grain in many ways such as, acceleration of leaf senescence by raised temperatures and increased respiration of leaves, stem and ear.

Reasons for the curtailment of grain growth duration under high temperatures have been speculated by investigators. Gallagher et al. (1976) proposed three possible reasons why grain growth stops: either the extent of translocation may ultimately be limited by the need to retain sufficient dry matter in the stems to support the ears, the transport system to the growing grain was inadequate, or starch synthesis stopped prematurely.

Temperature relations of time of maturity and growth duration of higher plants have been studied for some time. High temperatures are known to hasten the period between planting and anthesis and that from bloom to physiological maturity (Skerman, 1956; Fryer et al., 1966; Pasternak and Wilson, 1969; Peters et al., 1971; Downes, 1972; Eastin, 1976). The rate of development of three sorghum varieties grown in controlled environments was found to be highly dependent upon day and night temperatures (Caddel and Weibel, 1971), all reaching anthesis faster at the warmer night temperature. Similar results were earlier reported by Pasternak and Wilson (1969) for high night temperatures. Flowering delay resulting from drops in temperature was reported for Pennisetum (Pearson, 1975) and from drops in night temperature for bean (Said et al., 1967). Hastening of sorghum maturity by about 70 F day temperatures and night temperatures greater than 70 F or below 70 F for the first 30 days after emergence was reported by Fryer et al. (1966). Maturity generally was retarded by day temperatures below 70 F and night temperatures in the sixties.

Heat Injury, Tolerance and Adaptation in Higher Plants

General Concepts and Terminology

Heat tolerance is fairly commonly used for referring to plant-temperature relationships of living organisms. Reference to heat tolerance often follows the terminology of Levitt et al. (1960), and it is defined as the ability of plant tissues to live and function under conditions of high temperatures. A very difficult plant condition to quantify is, of course, "heat stress." Evaluating a high temperature stress on an absolute basis is, therefore, rather difficult, and this makes a quantitative definition of heat stress impossible. Plants that belong to the group "mesophiles" grow and develop at temperatures above 10 to 30 C. Heat stress to such plants may be any temperature above about 35 C, and the degree of stress is also a function of duration (Levitt, 1972). In a qualitative sense, therefore, specific heat stress for any organism would increase with the temperature above the lowest that causes stress. The lowest temperature that causes stress would again vary from crop to crop.

Threshow (1970) defined temperature in molecular terms as it relates to living organisms. It is defined as a measure of the activity of molecules and the energy involved in their motion. When temperatures are too high, molecular motion is believed to be extremely rapid, and thus the complex protein molecules disintegrate. Threshow considered plant temperature as a function of the difference between the gain and the loss of heat energy by the plant. This forms the very basis upon which some mechanisms of heat injury were developed.

Plant response to an environment is quite a broad and complex phenomenon, but it can be categorized. Itai and Benzioni (1974) suggested two main kinds of plant response, namely: (1) a direct response, which is proportional to the appropriate environmental factor involved, and (2) an induced response, the plant responding only when the relevant factor exceeds a given magnitude. They concluded by saying that plant responses to changes in any of the microclimatic complex are regulated along similar lines.

Variability does exist in the degree of heat tolerance possessed by a given plant as this property is characterized by numerous variables other than heat per se. To this end, Lange (1965) regarded the high temperature tolerance of a plant as a phenomenon that is not constant, being subject to continuous modification by both internal and external factors.

The stage of development is one factor that ought to be considered when determining the degree of high temperature tolerance of a plant. Young seedlings may have a level of heat tolerance much different from that of older plants. Laude and Chaugule (1953) observed the highest level of heat tolerance in bromegrass seedlings just after emergence. There was no visible heat injury at that stage, whereas older material was substantially injured. Earlier studies by Heyne and Laude (1940) showed that young corn seedlings 10 to 20 days after planting possessed considerably higher resistance to a given level of heat stress than older seedlings.

Light has also been considered among external factors influencing the degree of heat tolerance of a plant. Laude (1939), Heyne and Laude

(1940) and Laude and Chaugule (1953) have demonstrated that heat injury in plants kept in the dark was far greater than that of plants which had received light. Exposing corn seedlings previously kept in the dark to light for 1 hour considerably increased their heat resistance. A daily cycle of heat resistance in plants of corn, wheat, barley, sorghum and alfalfa was reported some decades ago (Laude, 1939). He found that the daily maximum resistance was attained by plants about mid-day and during the afternoon, while the minimum occurred early in the morning.

In describing plants' temperature tolerance research, Laude (1964) considered the testing of plant materials in such a way that the responses to high temperature are clearly separable from those attributable to associated conditions as a difficult task. A typical example is that of distinguishing temperature response from that due to the moisture deficiency caused by high temperature, particularly under field conditions (Laude, 1964; Sullivan et al., 1977a). Laude (1964) recommended an evaluation of the many factors that alter the degree of plant response to high temperature in order to properly interpret plant behavior. Among such factors are the previous conditioning of the plant, the stage of development, the variety or ecotype, the criteria selected for measurement, the test condition, the exposure duration and the moisture regime.

Threshow (1970) expanded the discussion by stating that apart from the optimum temperature for a given metabolic activity varying among individuals of a single species, different temperature optima also exist for different plant organs and for each successive stage of plant development.

The phenomenon of heat injury translocation was demonstrated in higher plants by Yarwood (1961b) using leaves of Phaseolus vulgaris (L.), Vigna sinensis or the cotyledons of Cucumis sativus (L.). Translocation of injury occurred as a result of the abrasion of heated leaves. He claimed that translocated heat injury was favored by light and high temperatures in the environment and increased plant age. He later demonstrated an acquired sensitivity of bean plants to heat injury after a disposition heat treatment (Yarwood, 1962). Its manifestation was said to depend on high soil moisture and exposure to dark prior to treatment.

Mechanisms of Heat Injury in Plants

Over the years, a number of mechanisms of heat injury have been proposed, some of which are popular. One of such earlier proposed theories is that high temperatures induce thermal oscillations which readily break H and S-S protein bridges (Levitt, 1956), thus resulting in protein denaturation. Bound water is believed to strengthen protein bridges and prevent its denaturation. According to the speed of resynthesis concept, heat killing occurs when the rate of resynthesis of an essential component lags behind its degradation. Levitt (1956) supported this concept as the obvious explanation for direct heat injury since many proteins are denatured at heat killing temperatures for many plants.

Alexandrov (1964) conjectured that protein denaturation theory of heat injury explained some of his data. He, therefore, concluded that specific doses of different kinds of stimulants produce similar denaturing

changes in the protoplasmic protein.

Principal points of the denaturation theory are as follows: (1) the reaction of the protoplasm toward the action of injurious agent is quite non-specific; (2) specific peculiarities characteristic of the injurious action of each given agent exist; (3) the stimulation and the injury are consecutive phases of the cell's response; and (4) at the bases of both the injury and the stimulation are denaturing changes of the protein molecules of different protoplasmic components (Alexandrov, 1964).

Leopold and Kriedemann (1975) considered the formation of toxic substances as an associative event of protein denaturation. An accumulation of such by-products, including nitrogen and ammonia, would lead to auto-intoxication that would result in death of the plant (Petinov and Molotkovsky, 1959).

Also associated with protein denaturation is the disruption of the normal function of enzymes which could lead to some metabolic imbalance in the plant. The general conclusion drawn from a survey of high temperature lesions is that many of them may occur, at least partly, as a result of inactivation of heat-labile enzymes (Langridge, 1963b).

Other theories of secondary effects of heat injury that have been considered are metabolic disturbances, especially increased respiration rate; rapid dissipation of reserve carbohydrates; and apparent drop in photosynthesis (Wilsie, 1962).

Mechanisms of heat injury were summarized by Threshow (1970) and the following conclusions were made: (1) the temperature limit for a plant is determined largely by the capacity of the component molecules

to maintain their structure; (2) if high temperatures persist, bonds in the protein molecule become irreversibly disrupted; (3) indirect injury may occur at temperatures below the point of protein denaturation; (4) cellular damage could result from the formation of toxic substances; and (5) regardless of the mechanisms involved, when the temperature exceeds the extremes to which the plant is adapted, growth is impaired and expressions of stress and malfunction appear.

The genetics of high temperature response of higher plants have so far received limited attention. High temperature defects are said to be possibly inherited as single genes which probably control thermolabile homeostasis as a buffering phenomenon upon which the genetic ability of a plant to resist injurious effect of extreme temperatures rests. The high frequency with which mutation produces temperature-sensitive alleles which specify enzymes and other proteins, the structures of which are so altered that they become inherently unstable at high temperatures. Abnormal phenotypes occurring only when above-optimum temperatures have denatured these unstable proteins.

Acquired Heat Tolerance and Adaption in Plants

When some plants are subjected to some form of mild environmental stress, be it artificially or otherwise, they sustain biochemical, biophysical and/or physiological changes that enable them to tolerate greater stress at a later time in their life cycle (Kinbacher et al., 1967). Heat hardening process was described by Leopold and Kriedemann (1975) as a plant's metabolic response to temperature that embodies instantaneous effects; e.g., enzyme activity, membrane permeability and

substrate concentration, and cumulative reactions, whereby the plant "remembers" a temperature experienced and adapts its physiology accordingly. Such a property allows the plant to endure more intense heat conditions and is considered to be of ecological significance. The conclusion drawn by Schroeder (1963) was that heat tolerance can be induced in plant tissues in vivo and in vitro.

Coffman (1957) found that winter oats exposed to 48-54.5 C temperatures for 45 min at early boot, after exposure to sunlight, developed greater heat tolerance than plants under shade. His results corroborate those of Heyne and Laude (1940) who had earlier reported that heat tolerance of corn seedlings kept in the dark for 12 to 18 hr was increased considerably by exposure to light for as brief a time as 1 hr, younger seedlings being generally considered as more heat tolerant than older plants (Heyne and Laude, 1940; Coffman, 1957).

Further reports of successful artificial heat-hardening in higher plants had also been made known. Heat-hardened bean plants were claimed to have significantly higher heat tolerance than unhardened plants (Kinbacher et al., 1967; Sullivan and Kinbacher, 1967). The thermostability of fraction I protein isolated from bean plants exposed to 44 C for 2-4 hr per day for 3 to 10 consecutive days was found to be higher than that extracted from control (unhardened) plants. Maleic dehydrogenase extracted from leaves of high-temperature hardened greenhouse-grown bean plants was significantly more heat stable than that extracted from unhardened plants (Kinbacher et al., 1967). Similarly, Feldman (1968) claimed that artificial heat hardening of cucumber and wheat plants increased the heat resistance of various leaf enzymes.

Thermal adaptation of photosynthetic processes in higher plants were reported by Mooney and West (1964), Bjorkman et al. (1972), Berry (1975) and Pearcy et al. (1977). They observed that plants adapted to high temperatures had remarkably higher photosynthetic rates than non-adapted species under high temperature conditions. High growth temperature induced a substantial increase in the thermal stability of the photosynthetic process of Atriplex lentiformis, a C_4 species. Heat treatment of 46 C on leaves of unhardened plants caused marked reduction of photosystem II activities of chloroplasts but not in those of chloroplasts from high-temperature grown plants (Pearcy et al., 1977).

Extremely brief period of exposure to heat is sometimes sufficient to bring about heat hardening. Alexandrov (1964) observed increased heat tolerance of some grass species after very brief heat shocks of even a few seconds. Acquired plant tolerance to heat was demonstrated in bean, cowpea, corn, cucumber, fig, soybean and tobacco after exposing them to elevated temperatures no higher than 50 C for 20 sec (Yarwood, 1961; 1967). Laude and Chaugule (1953) adopted three different procedures to determine the degree of heat hardiness that can be attained by bromegrass. A significant degree of heat hardiness compared to its control was attained by each of the three bromegrass species used.

Successful artificial heat hardenings of crop seedlings were reported for grain sorghum by Smith (1973) and Sullivan et al. (1977a) and for soybeans by Specht et al. (1977). Two-week old seedlings of sorghums differing in maturity were heat hardened at high subinjurious temperatures in growth chambers for 2 to 4 hr per day for four consecutive days before they were transplanted to the field (Smith, 1973;

Sullivan et al., 1977a). The earlier maturing hybrids showed higher heat tolerance up to 26 days after the heat treatment but not thereafter. Heat hardened plants averaging about 7-8.3 percent higher grain yields than the unhardened plants.

Specht et al. (1977) conducted field and greenhouse experiments to assess the phenotypic and agronomic consequences of short-term temperature hardening of soybean seedlings. They exposed seedlings to "cold" (under 10 C) or "hot" (above 40 C) temperature in growth chambers for 7 days before transplanting them to the field. It was claimed that yield, height and leaf area differences occurred between control and hardened plants. Higher membrane thermostability induced by the heat hardening persisted throughout the growing season.

The duration for which induced heat hardening in higher plants persists has been a subject of controversy. While Schroeder (1963), Alexandrov (1964) and Specht et al. (1977) claimed that the heat-hardened condition may persist throughout life cycle, other conflicting claims exist. Alexandrov (1964) indicated that dehardening of plant cells occurred after 24 hr, but only after 2 days did Sullivan et al. (1976) observe a diminishing effect in hardened cabbage plants. Langridge and McWilliam (1967) concluded that adaptation of phenotype to temperature may be transient and reversible or may be irreversible.

Mechanisms of Heat Hardening and Adaptation in Plants

Many different theories explaining the phenomenon of heat hardening and adaptation in plants have been postulated. Of these, only a few can be considered popular and tenable. Heat tolerance or hardening is

generally attributed to increased heat stability of protoplasmic proteins (Koffler et al., 1951; Levitt, 1956; Langridge and McWilliam, 1967; Threshow, 1970), and it has also been proposed that rapid resynthesis of heat-damaged protein molecules brings about heat stability (Levitt, 1956; Langridge and McWilliam, 1967). One of the more plausible explanations is that thermophilic organisms possess relatively heat-stable proteins (Koffler and Gale, 1957) resulting from a relatively stable molecular architecture of the proteins conferred by H-bonding (Koffler et al., 1957). This led Kinbacher et al. (1967) to speculate on the basis of their data that heat hardening probably alters the protein configuration allowing for a greater degree of heat tolerance without denaturation. Sullivan and Kinbacher (1967) suggested that there may be a disulfide (S-S) interchange during hardening which causes a repositioning of the S-S bonds in a manner that thermal stability of fraction I protein increases. Possibly, heat hardening of higher plants increases the resistance of their proteins to the denaturating action of various agents other than heat per se (Lomagin et al., 1963).

Based on the assumption that heat hardening results from an increased resistance of proteins to heat, Langridge and McWilliam (1957) suggested the following three classes of molecular mechanisms: (1) that hardened cells have their protein protected by an increased concentration of antidenaturants, (2) that change in protein structure increases their stability, and (3) that hardening occurs in plants able to accelerate their rate of protein synthesis at high temperatures.

Another popular theory of heat hardening is that cells of heat resistant organisms possess protective factors or substances. Laude

(1939) reasoned that the photosynthetic production of organic material suggests itself as an explanation for the increased heat resistance of plants. This argument was supported by Petinov and Molotkovsky (1959) and Schroeder (1963) whose data suggest an accumulation of substances, such as organic acids, which provide protection against extreme temperatures. Plants treated with organic acids showed much less evidence of heat damage (Petinov and Molotkovsky, 1959; Emmerikh, 1973). Treatment of tomato plants with adenine after the onset of flowering markedly increased their resistance to high temperatures (Emmerikh, 1973). Langridge and McWilliam (1967) believed that high temperature-induced defects can be circumvented by nutritional supplementations such as the addition of biotin or sucrose.

Coffman (1957) concluded that heat resistance is a heritable trait in oats, and it is recessive to susceptibility. He speculated that possibly three factors are involved in the inheritance of heat resistance. In general, the genetic basis of an organism's adaptation to climate rests on a coordination of very many, if not all, of the constituent genes (Langridge, 1963a). The genetic ability to resist the injurious effects of extreme temperatures is believed to rest on a buffering phenomenon called "homeostasis" (Langridge and McWilliam, 1967). Any new molecule resulting from a change in environment requires a shift and adjustment in genetic background. The environment influences the selection of alleles and gene combination.

MATERIALS AND METHODS

Experiments I and II were conducted in a quonset style fiberglass greenhouse during the summers of 1977 and 1978, respectively. Experiments III, IV and V were field experiments conducted at the University Agronomy Farm, Lincoln, with a Sharpsburg silty-clay loam soil, during the summers of 1977, 1978 and 1979, respectively. RS 671 (Redlan x Tx 415), an open-pedigree temperate-adapted grain sorghum [Sorghum bicolor (L.) Moench] hybrid, having a medium-late maturity, was used in each of the experiments.

Experiment I

RS 671 grain sorghum seed was sown in a 1:1:1 sand:vermiculite: peat medium in 10-liter plastic pots. Six seeds were sown in each pot but later thinned to two plants per pot at about two weeks after emergence. Those retained were considered the most vigorous and representative seedlings. Plants received daily watering and a modified Hoagland-Arnon nutrient solution (C. Y. Sullivan, personal communication; Appendix Table A1) on alternate days. Adequate moisture level was maintained in the rooting medium during the growth cycle in order to eliminate soil drought which would otherwise confound with temperature treatments. Tillers were removed as they appeared and only main shoots were allowed to grow. Prior to treatment application, plants with uniform growth and vigor were selected as experimental units. A "Tempscribe" temperature recorder[1] was placed in the center of the experimental area to

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[1]Manufactured by Bacharach Instrument Co., Pittsburgh, PA.

continuously record ambient air temperatures (Appendix Table A2). Plants received one spray of "Carzol" SP., an acaricide, at the rate of 1 tablespoonful per 4.5 liters of water for spider-mite control at the soft-dough stage.

Pots to be used for the experiments had their plants individually tagged and arranged on benches in a randomized complete block design (Cochran and Cox, 1957) with each plot representing a treatment replication. Spacings between plants and between greenhouse benches were 30 cm and 1 m, respectively. Ten replications were used in this experiment.

At periodic intervals, plant samples were taken from extra pots and growing points dissected and examined under a microscope to determine the phenological growth stage reached, a procedure similar to those described by Friends (1965), Taylor and Frey (1972) and Lee et al. (1974). Elevated night temperature treatments were initiated when plants had reached floret differentiation (FD) stage--the appearance of pistil and stamen primordia; night temperature treatments imposed being 26.5 and 32 C air temperatures for 12 hr, between 20:00 hr and 08:00 hr the next morning. In order to impose these temperatures, plants to be treated were removed from benches and arranged at designated areas inside the greenhouse just prior to the start of treatment application each evening. The ten pots (replicates) for each temperature treatment were set together and covered with a 1.08 m x 1.12 m x 1.08 m clear plastic movable chamber, similar to those described by Peters et al. (1971). Clear plastic was used so that light quality reaching plants during early sunrise would be altered only at the barest minimum. Temperature treatments were effected by means of thermostat-controlled

heat boxes consisting of blowers (fans) forcing hot air from two cone heaters (made of resistance wires) into the plastic enclosure via a dryer hose. The heat box model resembled that described by Maun et al. (1969). Connected to each heat box was a calibrated thermistor placed among plants enclosed inside the plastic chamber for air temperature regulation. At 08:00 hr each morning, plants treated the previous night were returned to the benches where they remained until the following evening when temperature treatment was again imposed. Precaution was taken to see that pots were rotated each evening prior to start of treatment to alleviate any position effects. Heat boxes were checked at periodic intervals for adequate precision and efficiency.

The experiment consisted of 11 treatments (including a check) composed of various combinations of five growth stages (phases) and two higher-than-ambient night temperatures (26.5 and 32 C). Commencing at floret differentiation stage, plants were subjected to these temperatures for four consecutive nights up till bloom. This gave four 4-day periods receiving temperature treatments. In addition, a 16-day period from floret differentiation through bloom was included among growth stages involved in this experiment. Described below are the five different growth periods during which the two elevated night temperatures were imposed:

Stage	Description[a]	Treatment Duration (no. of nights)
1	$FD_{(1)}$ thru $FD_{(4)}$	4
2	$FD_{(5)}$ thru $FD_{(8)}$	4
3	$FD_{(9)}$ thru $FD_{(12)}$	4
4	$FD_{(13)}$ thru Bloom	4
5	FD thru Bloom	16

[a]Numbers in parentheses are the numbers of days after floret differentiation (FD) when temperature treatments were initiated or terminated.

Each plant was dated for time of panicle emergence (heading), of bloom and of physiological maturity (appearance of blacklayer). Time of blacklayer formation was used as an index of physiological maturity according to Eastin et al. (1973). At the bloom stage, one of the two plants in the pot was sampled for dry weight and total leaf area determination. Leaf area was measured with a Li-cor Model 3100 belt-type area meter.[2]

Harvested plants were then dissected into leaf laminae, sheaths, stems and panicles and dried in a drying oven at 105 C for 72 hr. Dried plant samples were weighed with a "Sartorius" Model 2354 electronic top-loading balance. Plant height, panicle length and panicle exertion were other growth attributes measured at the bloom stage.

Total above-ground dry weight and dry weights of leaf laminae, sheaths, stems and panicles were also determined at physiological maturity in addition to measurement of plant height and panicle length.

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[2]Manufactured by Li-cor Instrument Corp., Lincoln, NE.

At that point, roots were carefully extracted from pots and washed free of extraneous matter. Root samples were later dried in an oven and their dry weights determined by a procedure similar to those described earlier.

Analysis of plant growth consisted of taking leaf area, plant dry weight and height, panicle length and exertion, and root dry weight determined at bloom and/or at physiological maturity.

Leaf growth and expansion were determined on the basis of specific leaf area (SLA), leaf weight ratio (LWR), leaf stem ratio (LSR) and leaf area ratio (LAR) derived from formulae described by Friend et al. (1965) as follows:

$$\text{Specific leaf area } (dm^2\ g^{-1}) = \frac{\text{leaf area/plant}}{\text{leaf dry weight/plant}}$$

$$\text{Leaf weight ratio } (g\ g^{-1}) = \frac{\text{leaf dry weight}}{\text{total plant dry weight}}$$

$$\text{Leaf area ratio } (dm^2\ g^{-1}) = \frac{\text{leaf area}}{\text{total plant dry weight}}$$

$$\text{Leaf stem ratio } (g\ g^{-1}) = \frac{\text{leaf dry weight}}{\text{stem dry weight}}$$

Plant development was assessed on the basis of number of days from seedling emergence to panicle emergence (heading), to anthesis (bloom), to physiological maturity (blacklayer formation) and duration of grain fill (GS-3). These attributes were determined on individual plant basis for a more reliable determination.

After panicles had been harvested, they were dried in an oven at 100 C for 72 hr before being weighed and threshed singly. Yield and yield components considered in the experiment were panicle dry weight,

grain yield/plant, number of grains/head, seed size (1000-seed weight), threshing percent, number of primary panicle branches/head and grain growth per GS-3 day (defined below).

$$\text{grain growth/GS-3 day} = \frac{\text{grain yield/plant (g)}}{\text{duration of GS-3 (days)}}$$

(expressed as g grain plant^{-1} day^{-1})

Data analyses were accomplished by conducting a separate analysis of variance (ANOV) for each variable in a factorial design where temperature and growth stages were main effects. Tests of significance were done using F-tests at both 5% and 1% probability levels. Associations existing between various pairs of variables were determined by means of tests of correlation using partial correlation coefficients at 5% probability level. Mean comparisons among the various growth stages were accomplished using the Duncan's multiple range test and test of least significant difference (LSD) described by Steel and Torrie (1960). Those comparisons were done in order to determine the relative sensitivity of the various plant growth stages to the two elevated night temperatures imposed on the sorghum plants.

Experiment II

The various procedures employed in this greenhouse experiment, conducted in the summer of 1978, were identical to those described for Experiment I above with the exception of a few details. More variables were measured in this experiment in addition to those included in Experiment I.

Procedures adopted for plant culture were the same as those used in Experiment I except that there were eight pots (replicates) per treatment in this particular experiment. At about 3 1/2 weeks after emergence, "dy-syston," a granular, systemic insecticide was applied against aphids. Two applications of "Carzol" SP were also given for spider-mite control. Appendix Table A3 contains the ambient temperatures recorded within the greenhouses during experimentation.

There was a total of 19 treatments comprised of combinations of nine different growth stages and two elevated night temperatures (26.5 and 32 C) in this experiment. Treatment application was started at the panicle initiation (PI) stage and continued for sets of fine consecutive nights through five days after bloom. This made up six 5-day treatment periods (growth stages). Three additional longer duration growth stages (periods) also included in this experiment were (1) the first half of GS-2, i.e., PI through floret differentiation (FD); (2) the second half of GS-2, i.e., FD through bloom; and (3) the entire GS-2 period, i.e., PI through bloom. The nine various growth stages (periods) during which the two elevated night temperatures were imposed are indicated below:

Stage	Description[a]	Treatment Duration (no. of nights)
1	$PI_{(1)}$ thru $PI_{(5)}$	5
2	$PI_{(6)}$ thru $PI_{(10)}$	5
3	$PI_{(11)}$ thru $PI_{(15)}$	5
4	$PI_{(16)}$ thru $PI_{(20)}$	5
5	$PI_{(21)}$ thru $PI_{(25)}$	5
6	$PI_{(26)}$ thru $PI_{(30)}$	5
7	PI thru FD	13
8	FD thru Bloom	13
9	PI thru Bloom	26

[a]Numbers in parentheses are the numbers of days after panicle initiation when temperature treatments were commenced or terminated.

Plant growth and development were characterized by measurements similar to those employed in Experiment I. The gross plant growth rate over the entire growth cycle, representing the average plant dry matter accumulation above ground, was determined using the following formula:

$$\text{Plant growth rate (g day}^{-1}) = \frac{\text{total plant dry weight}}{\text{no. of days from emergence to maturity}}$$

It was realized that this was a gross simplification of plant growth rate determination and the linearity of plant growth throughout its entire life cycle was assumed. The rate of leaf senescence was estimated from the number of green leaves present on the plant at physiological maturity. The duration of panicle expansion (GS-2) was determined by the number of days between panicle initiation and bloom, as per the terminology of Eastin (1972). GS-2 is considered to be a critical growth period since

potential for seed number is set then. Harvest index, a measure of plant efficiency, was determined in this experiment through the relationship indicated below:

$$\text{Harvest index} = \frac{\text{grain yield/plant}}{\text{total plant dry weight}}$$

The inclusion of harvest index as one of the variables measured in this study was justified by the fact that it integrates many responses of the plant to its environment throughout the whole growth cycle. Grain yield and various yield components considered in Experiment I were measured as well.

Data analyses closely followed the statistical procedures previously described for Experiment I.

Experiment III

This field experiment was conducted at the University Agronomy Farm, Lincoln, in the summer of 1977. Its design, scope and objectives were essentially the same as those for Experiments I and II described earlier.

The experiment was planted in 0.75-m (30-in) rows on May 5. Prior to planting, 130 lb/A of N was soil incorporated in the experimental area in the form of ammonium nitrate. And, at about three weeks after emergence, plant stands were thinned, leaving 15 cm (6 in) between plants to give a plant population of approximately 86,000 plants/ha.

A completely randomized design with 17 treatments replicated 10 times was used in this experiment. The treatments were composed of eight growth stages (periods) and two elevated night temperatures (26.5

and 32 C). The elevated night temperature treatments were applied by supplying regulated heat from the same heat boxes used in Experiments I and II.

There were 10 plants per plot, plants being selected on the basis of size and vigor uniformity, with each representing a treatment replicate. A "Tempscribe" temperature recorder was placed in the middle of the experimental area to continuously record ambient air temperatures (Appendix Table A4). This was in addition to climatological data of the site extracted from Nebraska Climatological Data (published by National Climatic Center, Asheville, North Carolina; Appendix Tables A5 and A6).

Starting from about 8-10 leaves stage, plant samples were taken from plots at periodic intervals for phenological growth stage determination by the procedure described in Experiment I. Night temperature treatment was initiated when plants had reached floret initiation stage (FI), a few days past panicle initiation. Plots were covered with 1.08 m x 1.12 m x 1.08 m clear plastic chambers and hot air blown from heat boxes onto plants enclosed within these chambers. Each nightly treatment application lasted from 20:00 hr through 08:00 hr the next morning, a period of 12 hr. Plastic chambers were kept outside the plots during daytime when plants were exposed to normal field environment. Heat boxes were checked periodically for temperature precision and performance.

Treatment application during each growth stage lasted for four consecutive nights starting from the floret differentiation stage until bloom, giving five 4-day treatment periods. Additional longer treatment durations (periods) included among the treatments were (1) floret initiation through floret differentiation, (2) floret initiation through

bloom, and (3) floret differentiation through bloom. All the treatment periods were within GS-2 period as per the schedule below.

Stage	Description[a]		Treatment Duration (no. of nights)
1	FI	thru FD	5
2	FI	thru Bloom	25
3	FD	thru Bloom	20
4	$FD_{(1)}$	thru $FD_{(4)}$	4
5	$FD_{(5)}$	thru $FD_{(8)}$	4
6	$FD_{(9)}$	thru $FD_{(12)}$	4
7	$FD_{(13)}$	thru $FD_{(16)}$	4
8	$FD_{(17)}$	thru $FD_{(20)}$	4

[a]Numbers in parentheses are the numbers of days after floret differentiation when the temperature treatments were initiated or terminated.

Plants were singly tagged for records of dates of panicle emergence, of bloom and of physiological maturation. Durations of panicle expansion (GS-2) and grain fill (GS-3) periods were computed from dates of phenological events. Plant height and panicle length were measured at physiological maturity, while stover dry weight was determined after harvest. Stover dry weights on a per plant basis were obtained after drying harvested stovers in an oven at 105 C for 96 hr.

About a week after plants had reached physiological maturity, panicles were harvested, dried at 100 C for 72 hr and then singly weighed and hand-threshed. Yield-related attributes measured included panicle dry weight, grain yield/plant, number of grains/head, seed size

(1000-seed weight) and harvest index. The average plant metabolic efficiency (sink activity) was estimated from the grams of grain accumulated per plant per day during grain fill (GS-3) period.

Data collected were statistically analyzed using the various procedures described for Experiment I.

Experiment IV

This field experiment was conducted at the University Agronomy Farm, Lincoln, in the summer of 1978 and was planted with RS 671 grain sorghum on May 26.

A split-block design (Federer, 1955) with various temperature and growth stage combinations as the whole-plots and precondition/no precondition as the subplots, was used in this experiment. Eleven main treatments were randomized within the whole-block at three replications. A whole-plot consisted of two 0.75 m rows, 1.5 m (5 ft) long. Plant stands were thinned to desired spacing, 12.5 cm (5 in) apart, at two weeks after emergence. The plant density was approximately 105,000 plants/ha (42,000 plants/A). The experimental area received 148 kg/ha of N in the form of ammonium nitrate soil-incorporated prior to planting. A pre-emergence application of 5.7 kg/ha of ramrod/atrazine was given on the day of planting as a weed control measure. Plots also received periodic hand-weeding to maintain a weed-free condition during the growing season.

At about two weeks after seedling emergence, a "Tempscribe" temperature recorder was placed in the middle of the plots to continuously record ambient air temperatures for the duration of temperature treatment

(Appendix Table A7). Climatic data for the site were also extracted from Nebraska Climatological Data (Appendix Tables A8 and A9). Periodic sampling of plants for microscopic examination of growing points to determine phenological growth stage (described in previous experiments) was initiated at about three weeks after emergence and continued until floret differentiation (the appearance of pistil and stamen primordia).

In order to effect heat preconditioning ("heat hardening"), plants in one of the two rows in each plot were exposed to 40.5 C temperature for 1 hr, for two consecutive days, followed by exposure to 46 C for 1 hr for another two consecutive days, beginning at three weeks after emergence (i.e., in the vegetative growth phase). Oblong 1.8 m x 0.6 m x 0.6 m (72 in x 24 in x 24 in) clear plastic structures (enclosures) were used to cover the rows of plants to be "heat-hardened" and heat was blown into these enclosures from thermostat-controlled heat boxes, previously described in these investigations. Consequently, only one row of plants in each plot was heat-preconditioned, while the other row was not.

Application of the two elevated temperatures began when plants reached the panicle differentiation stage (appearance of primary panicle branch primordia). The main treatments were combinations of two elevated night temperatures relative to the ambient (5 C above-ambient and 10 C above-ambient) imposed during each of five various 7-day growth stages (periods) starting at panicle initiation through the seventh day after bloom. The schedule of treatment application is as follows:

Stage	Description[a]		Treatment Duration (no. of nights)
1	$PI_{(1)}$	thru $PI_{(7)}$	7
2	$PI_{(8)}$	thru FD	7
3	$FD_{(1)}$	thru $FD_{(7)}$	7
4	$FD_{(8)}$	thru Bloom	7
5	$Bloom_{(1)}$	thru $Bloom_{(7)}$	7

[a]Numbers in parentheses are the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were commenced or terminated.

Each nightly treatment was applied from 20:00 hr through 08:00 hr the next morning, a period of 12 hr. To apply the elevated temperatures, movable 1.75 m x 1.05 m x 1.05 m (70 in x 42 in x 42 in) clear plastic chambers were placed over plants in plots to receive the temperature treatments. Portable thermostat-controlled electrical heat boxes were used to continuously elevate air temperatures around the plants 5 C or 10 C above the prevailing ambient air temperature. Ambient temperature refers to the air temperature outside the chamber. Two calibrated thermistors were installed on each heat box; one of which was placed within the plant canopy inside the chamber, while the other was placed outside the chamber to monitor the ambient air temperature. The circuit system of the heat boxes was constructed such that the heat supplied by the resistance-wire cone heaters can be continuously thermostat-regulated to maintain 5 C or 10 C temperature above the ambient temperature. The heat boxes were calibrated to supply heat to keep the temperature within the chambers at 5 C or 10 C above ambient but could be calibrated for

any desired differential. The two elevated night temperatures can be referred to as ambient + 5 C and ambient + 10 C temperatures.

Data obtained and analyzed were predominantly attributes of grain yield and plant growth. Yield attributes considered in this experiment include panicle dry weight, grain yield/plant, number of grains/head, seed size (1000-seed weight) and metabolic efficiency (sink activity). Plant growth and development parameters determined were number of days from seedling emergence to panicle emergence (heading), to anthesis (bloom) and to physiological maturity (blacklayer formation); durations of GS-2 and GS-3 periods; and plant height and panicle length at bloom stage.

Analysis of variance procedure and orthogonal comparisons were used to test treatment significance using F-tests. Partial and general correlation coefficients between various pairs of variables were determined to test associations at the 5% probability level. Duncan's multiple range test and the test of least significant difference were employed for mean comparisons, also at the 5% probability level.

Experiment V

This field experiment, conducted at the University Agronomy Farm, Lincoln, in the summer of 1979, was identical to Experiment IV in many respects. Although results from the previous year's experiment (Experiment IV) indicated significant responses of yield and growth attributes to various treatments, it was deemed necessary to repeat the experiment and include more detailed physiological studies in this experiment.

Seed was sown on June 5 along 0.75 m rows and plant stands thinned to 10 cm (4 in) apart at two weeks after seedling emergence, giving a plant density of approximately 130,700 plants/ha (52,300 plants/A). The experimental site received 143 kg/ha of N applied preplant as ammonium nitrate. A pre-emergence application of 5.7 kg/ha of ramrod/atrazine was given on the day of sowing, as a weed control measure. However, plots also received a few occasional hand-weedings during the season to keep them relatively weed-free. The experimental design and layout used in this experiment were similar to those adopted in Experiment IV, with each plot containing two 0.75 m rows and 1.5 m in length.

Plant phenological growth stages were determined by the same procedure as that used in Experiment IV and similarly, temperature application was commenced at panicle initiation stage. Heat preconditioning ("hardening") was effected by exposing plants to sublethal high temperatures starting from the 24th day after seedling emergence and following the same procedure employed in Experiment IV. In addition, 12 extra plots, each also consisting of one heat-preconditioned and one non-heat preconditioned rows, were devoted to laboratory heat tolerance tests (Sullivan, 1972), which represented tests of membrane thermostability.

The application of the two elevated night temperatures (5 and 10 C above ambient) in this experiment followed exactly the procedure described earlier for Experiment IV, with the nightly treatment duration and growth period interval being identical. The treatment schedule for temperature application entailed five 7-day growth stages (periods) from panicle initiation stage through the seventh day after bloom. Each treatment growth period had a duration of seven consecutive nights of

12 hr as in Experiment IV. During the duration of treatment application, i.e., from PI through bloom + 7 days, the relative humidity of air within the plastic enclosures was recorded with a "Durotherm" hygrometer[3] at 08:00 hr in the morning and at 20:00 hr in the evening (Appendix Table A10). The ambient air temperatures within the plots were also continuously recorded with a "Tempscribe" temperature recorder (Appendix Table A11).

Growth and yield related data obtained and analyzed on this experiment were the same as those determined on Experiment IV. However, some plant physiological measurements such as cell membrane thermostability, leaf CO_2 assimilation and kernel growth (sink activity) were made. These physiological studies are described in detail as follows.

Cell Membrane Thermostability

A temperature-mediated leaf injury laboratory technique developed by Dexter et al. (1932) and modified by Sullivan (1972) was used to measure heat tolerance differences between heat hardened and non-hardened plants at various intervals during the growing season. This technique essentially measures the heat stability of cell membranes (Specht et al., 1977).

Twelve plots, each containing two rows, were used for the study. Each plot represented a treatment replication, with one row of plants heat hardened, while the other row of plants was the control. There were, therefore, 12 replications used for the treatment in this heat tolerance study.

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[3]Manufactured by Abbeon Cal., Inc., Santa Barbara, Calif.

Leaf disc electrical conductivity method was used to determine heat tolerance levels on five dates at weekly intervals. The five different test dates represented the following growth stages: (1) floret initiation stage (PI + 7 days), (2) floret differentiation, (3) boot (FD + 7 days), (4) bloom and (5) milk stage (bloom + 7 days). The stepwise leaf disc electrical conductivity procedure is described as follows:

1. Twenty leaf discs, 1 cm in diameter, were cut with a leaf disc cutter (a cork borer would do just as well).
2. Leaf discs were cut from laminae only (avoiding midribs) of the 2nd fully expanded leaves, counting from the top, from about eight plants.
3. Two sets of 20 leaf discs were required--one set for control and the other set for heat treatment.
4. Leaf discs were placed in deionized water in test tubes immediately after cutting.
5. Leaf discs were thoroughly washed in deionized water for two hours, with four changes of water.
6. Water was then drained from test tubes but ensuring that leaf discs remained moist, and test tubes were covered with plastic wrap.
7. One-half of the test tubes (i.e., one set) were kept in a 53.5 C water bath for 15 min to effect heat treatment. The second set of tubes (controls) were held at room temperature (about 25 C) during that 15-min period.

8. The heated tubes were allowed to cool after which 30 ml of deionized water was added to each test tube, i.e., both the heated and the control tubes.
9. The tubes were held overnight in a 8 C incubator.
10. The next morning, each tube was shaken thoroughly with a test tube shaker, then placed in a 25 C water bath. The duration of shaking should be kept fairly uniform among the samples as this could influence heat injury levels (Onwueme, 1979).
11. When solutions in test tubes reached 25 C, their electrical conductivity was measured with a model RC 1632J conductivity bridge.
12. The tubes were then covered with plastic wrap and placed in a 80-90 C autoclave for 15 min to kill the cells.
13. The tubes were allowed to cool in the room.
14. The test tubes were later placed in a 25 C water bath, and the conductivity of the solutions measured a second time when they had equilibrated at 25 C.

Since all measurements were in terms of resistance to current flow through the various solutions, resistance readings were converted to conductivity values, on the basis of the inverse relationship between these two properties, thus:

$$\text{conductivity} = \frac{1}{\text{resistance}}$$

The formula used for calculating percent heat injury (sensitivity) from conductivity readings is as shown below (C. Y. Sullivan, personal communications):

$$\% \text{ Heat Injury} = 1 - \frac{1 - \frac{T_1}{T_2}}{1 - \frac{C_1}{C_2}} \times 100$$

where, T_1 = 1st conductivity reading of treated sample before killing

T_2 = 2nd conductivity reading of treated sample after killing

C_1 = 1st conductivity reading of control sample before killing

C_2 = 2nd conductivity reading of control sample after killing

Paired comparisons using the Student's t test (Steel and Torrie, 1960) were employed to compare means of percent heat injury between heat hardened and control plants. The heat tolerance (membrane thermostability) levels at different growth stages (test dates) were compared across the growth cycle, and thus the relative heat sensitivity of various critical growth stages to heat stress.

Carbon Dioxide Exchange

Carbon dioxide exchange measurements were done on intact sorghum leaves in the field on the third day after the termination of each 7-day treatment duration. Gas exchange measurements essentially measured the photosynthetic rates of leaves after exposure to elevated temperatures (ambient + 5 C and ambient + 10 C). The main objectives of this study were to evaluate the response of the photosynthetic system to elevated

night temperatures and to investigate the effect of heat hardening on the response of this system to elevated temperatures.

Gas exchange measurements were accomplished with an infrared gas analysis system described by Clegg and Sullivan (1976), Sullivan et al. (1976) and more recently by Clegg et al. (1978). This is a portable small chamber field system of sampling followed by laboratory gas analyses.

Carbon dioxide exchange in sorghum leaves was measured by enclosing the middle portion of the second fully expanded leaf (counting from the top) in a portable 2.18-liter plexiglas assimilation chamber. Inside the assimilation chamber were installed two small, battery-operated fans which properly mixed air inside the chamber. The second fully expanded leaf was chosen for the single-leaf CO_2 fixation measurement based on the fact that Fischer and Wilson (1971) claimed that 75% of grain sorghum yield was assimilated by the upper four leaves. Measurements were made between 11:00 hr and 13:00 hr from six randomly selected plants per plot; that is, three heat-hardened and three non-hardened plants. About 8 cc each of initial and final air samples were drawn from the assimilation chamber with lubricated glass syringes and the needles quickly stoppered with Teflon caps. The time interval between the initial and final air sampling was 20 sec. Glass syringes containing air samples were stored in a Styrofoam insulation box in which they were conveyed to the laboratory for analysis. The dimensions of intact leaf sections enclosed in the assimilation chamber were measured and their areas determined. At regular intervals during the duration of air sampling from leaves in the field, ambient air temperatures were

measured with an Atkins model 23463-10 electronic thermometer[4] and photosynthetically active radiation (PAR--within the range of 400-700 nm) was also measured with a Li-cor model LI-185A quantum radiometer.[5]

Samples were quickly conveyed to the laboratory where the concentrations of CO_2 in them were determined. The difference in the CO_2 concentrations of the initial and the final air samples is a measure of the amount of CO_2 taken up by the leaf section as photosynthetic fixation. From this, the photosynthetic rate of the leaf per unit area and time (mg CO_2 dm^{-2} hr^{-1}) was determined. The CO_2 exchange formula of Eastin and Sullivan (1969) was employed to determine rates of leaf photosynthesis as shown below:

$$\text{Net photosynthetic rate (expressed as mg } CO_2 \text{ dm}^{-2} \text{ hr}^{-1}) = \frac{44{,}000 \text{ mg } CO_2 \text{ mole} \times 10^{-6} \times \text{chamber volume (liters)} \times \Delta \text{ ppm } CO_2 \text{ sec}^{-1} \times \frac{273}{To} \times \frac{760}{atm} \times 3600}{\text{leaf area (dm}^2)}$$

where, chamber volume = 2.18 liters,

Δ ppm = (ppm CO_2 initial sample - ppm CO_2 final sample) divided by 20 sec,

T = ambient temperature in ^{o}K,

atm = atmospheric pressure (mm Hg),

3600 = conversion factor from sec to hr.

Leaf photosynthetic rates were measured on three plots (replications) of the two elevated night temperature treatments and the control.

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[4]Manufactured by Atkins Technical Inc., Gainesville, FLA.

[5]Manufactured by Li-cor Instrument Corp., Lincoln, NE.

Since there were six measurements on each plot, there was a total of 18 single-leaf measurements from which temperature treatment means were determined. Means for the heat preconditioning vs no preconditioning were determined from nine replications. Data obtained were statistically analyzed to compare photosynthetic rates among two elevated night temperatures and the control and between the heat-hardened and the non-hardened plants.

Grain Dry Matter Accumulation

Measurement of kernel growth was undertaken to partially evaluate the plant's metabolic efficiency in terms of dry matter partitioning to the grains (sink). In sink activity evaluation factors to consider are the weight per grain (mg), a function of assimilate translocation; sink efficiency, reflected partly by grain growth rate (mg day^{-1}); and the relative grain growth rate (mg mg^{-1} day^{-1}) which relates to sink strength (Spiertz, 1974). The main objectives of this study were to determine the effect of elevated night temperatures imposed during panicle expansion (GS-2) on kernel growth during grain fill (GS-3) and also to compare among the various growth stages with regard to temperature effects on the plant's metabolic efficiency (sink activity).

The study basically entailed repeated sampling of kernels from single heads by a procedure which was a modification of that developed for corn by Duncan and Hatfield (1964). Attributes of kernel growth measured in the study included: (1) kernel dry weight (mg), (2) kernel growth rate (mg day^{-1}), (3) relative kernel growth rate (mg mg^{-1} day^{-1}), and (4) average duration of kernel growth (days).

Plants were tagged for tip-bloom and full-bloom dates and from these three plants having identical tip-bloom dates were randomly selected in each of the two rows of every plot in two reps. Plants having identical tip-bloom dates were selected to ensure that kernels extracted from panicles would be reasonably identical in age. Starting from the tenth day after tip-bloom, when kernel development was obvious, one primary panicle branch in the middle portion of the panicle was harvested from each of the three designated plants in each row. Spikelet samples were taken to the laboratory where kernels were extracted from them. Fifty kernels were then randomly selected from each 3-spikelet sample and placed in a 6.25 cm x 11.25 cm coin envelope. Kernel samples were dried in a ventilated oven at 70 C for 48 hr and kernel dry weights determined by weighing dried kernel samples on a Mettler type H15 balance. Kernel samplings were done at weekly (7-day) intervals through the seventh day after physiological maturity (blacklayer formation).

From kernel dry weight data for the various sampling dates, kernel growth attributes considered in this study were determined through mathematical computations as follows:

$$\text{Kernel dry weight (mg)} = \frac{\text{dry weight of kernels}}{\text{number of kernels}}$$

$$\text{Kernel growth rate (mg day}^{-1}\text{)} = \frac{\text{kernel DW}_2 - \text{kernel DW}_1}{t_2 - t_1} = \frac{\Delta DW}{\Delta t}$$

$$\text{Relative kernel growth rate} = \frac{\text{kernel DW}_2 - \text{kernel DW}_1}{(t_2 - t_1) \times (\text{kernel DW}_1)}$$

(expressed as mg mg^{-1} day^{-1})

where, DW_1 = initial dry weight (at t_1),

DW_2 = final (or succeeding) dry weight (at t_2)

ΔDW = dry weight differential between two succeeding sampling dates,

t_1 = initial sampling date,

t_2 = final (or succeeding) sampling date,

Δt = time interval (days) between two succeeding sampling dates.

Kernel growth duration was estimated as the time interval (in days) between the start of grain fill and when kernels ceased to increase in dry weight with time (blacklayer).

Data obtained were analyzed on separate sampling date basis. Temperature and growth stage means were compared for each of the variables measured using the Duncan's multiple range test and the test of least significant difference at the 5% probability level after tests of treatment significance had been done with F-tests at the 1% and 5% probability levels.

RESULTS AND DISCUSSION

Experiment I

The main objectives of this greenhouse experiment were to determine the response of 'RS 671' grain sorghum to elevated night temperatures (26.5 and 32 C) with respect to yield and plant growth and to determine the specific most critical growth stage(s) during panicle development when grain sorghum is most vulnerable to elevated night temperatures.

Yield and Yield Components

Analyses of variance for grain yield and its components indicated significant effects of the two elevated night temperatures (26.5 and 32 C) and the various growth stages when temperature treatments were imposed (Table A12). Highly significant temperature x growth stage interactions were also observed for the various yield-related attributes, indicative of some influence of temperature level on the response of some of the various growth stages to elevated temperatures. There were significant effects of temperature treatments on panicle dry weight, grain yield per plant, number of seeds per panicle, and number of primary panicle branches but not on 1000-seed weight nor threshing percent. However, the effects of growth stages and the temperature x growth stage interactions were highly significant for all these variables. Also, the control (ambient) differed quite significantly from the two temperature treatments with regard to all these variables, with the exclusion of 1000-seed weight and number of primary panicle branches.

The two elevated night temperatures (26.5 and 32 C) imposed on grain sorghum plants for short (4-day) periods caused significant reductions in panicle dry weight, grain yield per plant, number of seeds per panicle and grams of grain/GS-3 day/plant (Table 1). Although there was no significant difference between the ambient and the 26.5 C temperature treatments with regard to 1000-seed weight, the 32 C temperature treatment significantly increased seed weight by approximately 12%. It was observed that approximately 19%, 21%, 24% and 20% reductions from the ambient were caused by the 32 C treatment for panicle dry weight, grain yield per plant, seed number per panicle and grams of grain/GS-3 day/plant, respectively, with much lower reductions being observed for the 26.5 C treatment (Table 1). The brief four-day period of elevated night temperature during GS-2 caused surprising reduction in yield and shifts in yield components of grain sorghum. Sullivan et al. (1977) had earlier shown that a very short environmental stress may have a very marked influence on the performance of a plant throughout its life cycle. Average ambient temperatures inside the greenhouse during the various growth stages were for, all practical purposes, similar (Table A2). Thus, comparisons made among these growth stages regarding their relative responses to the two elevated night temperature treatments could be considered appropriate. Comparable degree of grain sorghum reduction was reported by Eastin (1976) having observed yield reduction of about 25% for two hybrids when night temperature was elevated by 5 C above near optimum. The reduction in seed number also observed as temperature was increased closely related to yield reduction.

Table 1. Panicle dry weight, grain yield/plant, number of seeds per panicle, 1000-seed weight and grams of grain/GS-3 day (averaged over growth stages) of RS 671 grain sorghum as influenced by two night temperatures: Greenhouse Experiment I, 1977.

	Temperature Treatment			$LSD_{(.05)}$
	Control[2]	26.5 C[1]	32.0 C[1]	
Panicle dry weight (g)	52.3	48.2 (7.8)	42.3 (19.2)	3.09
Grain yield/plant (g)	43.7	39.1 (10.7)	34.6 (20.9)	2.84
Seeds/panicle	2061	1928 (6.5)	1517 (23.8)	113.5
1000-seed weight (g)	21.64	20.77 (-4.0)	24.28 (+12.2)	1.37
Grams grain/GS-3 day /plant (g/day)	1.34	1.22 (8.3)	1.10 (20.0)	0.09

[1]Values in parentheses are percent reductions from controls except in the case of seed size where one represents percent increase from control.

[2]Average control (ambient) temperature was 22.5 C.

When the various 4-day growth stages (during which the two elevated night temperatures were imposed) were compared, it was observed that no significant differences occurred with respect to panicle dry weight, grain yield per plant and grams of grain/GS-3 day/plant (Table 2). However, the longer-duration growth stage—floret differentiation (FD) through bloom—caused significant reductions in these yield-related attributes, indicative of the significance of duration in temperature effects on yield and its components. The various 4-day growth stages differed significantly with regard to number of seeds per panicle and 1000-seed weight. Generally, an inverse relationship existed between seed number and seed weight with seed weight compensating for seed number reductions in the 4-day treatments. Elevated night temperatures caused reductions in seed numbers when imposed at earlier growth stages during panicle development (Table 2). This result was in accord with the popular view that the potential for seed number in grain sorghum is determined early in the panicle development (GS-2) period. And, since the potential for seed size (weight) is a later-determined trait, the relationship between seed size and growth stage was a reversal of that for seed number and growth stage; greater seed weight reductions having occurred for later-occurring growth stages than earlier-occurring ones. On the whole, a longer temperature treatment duration (from floret differentiation through bloom) resulted in greater reductions in yield and yield components (excluding seed weight) than a shorter treatment duration.

Table 2. Panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight and grams of grain per GS-3 days of RS 671 grain sorghum exposed to two night temperatures at various growth stages during panicle development (averaged over temperature treatments): Greenhouse Experiment I, 1977.

Treatment (Growth stage)[1]	Panicle dry weight (g)[2]	Grain yield/ plant (g)[2]	Seeds per panicle[2]	1000-seed weight (g)[2]	Grams grain/GS-3 day/plant (g/day)[2]
FD_1-FD_4	48.3 a	40.2 a	1606 c	26.04 a	1.27 a
FD_5-FD_8	47.7 a	38.4 a	1733 b	22.49 bc	1.21 a
FD_9-FD_{12}	47.5 a	38.2 a	1903 ab	20.46 ed	1.21 a
FD_{13}-FD_{16}	47.8 a	38.9 a	2037 a	19.43 d	1.13 a
FD_1-$Bloom_1$	34.9 b	28.6 b	1336 d	24.21 a	0.98 b

[1]Numbers in subscripts are the numbers of days after floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[2]Means followed by the same letter within a column are not significantly different at P=0.05.

Plant Growth and Development

Based upon analyses of variance results and statistical tests, it was found that both elevated night temperatures and the various growth stages produced highly significant effects on plant growth and development (Table A13). Besides, there were highly significant temperature x growth stage interactions, as was the case for yield-related attributes. Number of days from emergence to physiological maturity, length of grain fill (GS-3) period, panicle exertion and plant height were reduced significantly by elevated night temperatures (Table 3), but numbers of days to heading and bloom were not. The higher temperature level caused reductions in plant growth and development periods. Plant development appeared to be much less affected by the two elevated night temperatures than was plant growth; at least, much less noticeable.

Dry matter production by plants and its partitioning was determined. Elevated night temperature, growth stage and temperature x growth stage interactions were significant for dry weights of leaf sheaths, stem, panicle and aboveground plant total but not on leaf laminae dry weight (Table A14). Temperature did effect significant changes in laminae dry weight. The reason why growth stage did not have significant effects on total leaf area and consequently leaf laminae dry weight could be explained by the fact that this parameter was probably almost fully determined by the time temperature treatments were imposed. Not too unexpected, however, were greater reductions in dry weights of leaf laminae, sheaths, stem and aboveground plant total observed for the higher temperature level (32 C) than either the lower temperature level (26.5 C) or the control (ambient). Means for the ambient and for the

Table 3. Numbers of days to heading, bloom and physiological maturity, duration of grain fill (GS-3), panicle exertion and plant height (averaged over growth stages) of RS 671 grain sorghum as influenced by two night temperatures: Greenhouse Experiment I, 1977.

	Temperature Treatment			LSD(.05)	Mean
	Control[2]	26.5 C	32.0 C		
Days to heading	59.6	59.8	59.7	0.62	59.7
Days to bloom	66.2	65.8	65.2	0.48	65.7
Days to physiological maturity[1]	99.1	97.9	96.7	0.69	97.9
Duration of GS-3 (days)	32.9	32.1	31.5	0.81	32.2
Panicle exertion (cm)	16.0	12.8	10.5	1.13	13.1
Plant height (cm)	124.0	114.6	107.1	2.52	115.2

[1]Dark layer appearance at tip of basal panicle branches.

[2]Average control (ambient) temperature was 22.5 C

26.5 C treatment were similar for the various variables. There were about 12%, 6%, 18% and 15% reductions in dry weights of leaf laminae, sheaths, stem and aboveground plant total, respectively, from the 32 C treatment (Table 4).

Temperature effects on root dry matter production and shoot:root ratio were not significant. However, root dry weights differed significantly at different growth stages, and there was a significant temperature x growth stage interaction (Table A15). There was a tendency for root dry weight to be increased by elevated night temperatures, with about 20% increase over the control (ambient) under the 32 C treatment while shoot ratio was decreased by these temperatures. About a 19% decrease in shoot:root ratio occurred under the 32 C treatment as against the ambient, suggesting that dry matter partitioning between the shoot and the roots was significantly influenced by elevated night temperatures. Apparently, photosynthate partitioning was influenced by elevated night temperatures. Polarization of photosynthate away from the sink (head) could, therefore, partly account for the lower grain yield observed under elevated night temperatures.

Also, both growth stage and temperature x growth stage interactions were significant for both root dry matter production and the partitioning of dry matter between the shoot and the roots (Table A15). Mean comparisons for the various growth stages revealed that shoot:root ratios were not significantly different among growth stages with the exception of a larger means for the growth stage closest to bloom (FD_{13} to FD_{16}). Since root dry weight for the various growth stages differed appreciably, and the value for FD_{13} to FD_{16} was the lowest amongst them,

Table 4. Dry weights of leaf laminae, sheaths, stems, roots, aboveground total (shoot) and shoot/root ratios (averaged over growth stages) of RS 671 grain sorghum as affected by two night temperatures: Greenhouse Experiment I, 1977.

	Temperature Treatment			$LSD_{(.05)}$
	Control[2]	26.5 C[1]	32.0 C[1]	
Laminae (g)	16.02	15.45 (3.6)	14.09 (12.1)	0.91
Sheaths (g)	9.58	9.65 (~0)	8.98 (6.3)	0.57
Stems (g)	20.80	19.33 (7.07)	17.17 (17.5)	1.43
Root (g)	9.39	9.30 (~0)	11.27 (20.0)	1.83
Aboveground total (g)	102.35	95.18 (7.0)	86.73 (15.3)	5.46
Shoot/root ratio	5.42	5.58 (3.0)	4.41 (18.6)	0.87

[1]Values in parentheses are percent reductions (or increases) in dry weights from those of the control.

[2]Average control (ambient) temperature was 22.5 C.

this observation could have been related to an increasing effect on shoot dry weight and/or a decreasing effect on root dry weight (Table 5). The longer the application of heat treatment was delayed during GS-2, the greater were the chances for root dry weight reduction.

Correlations

Table A16 contains partial correlation coefficients between various pairs of yield-related variables. Highly significant positive correlations were found between grain yield and panicle dry weight (r= 0.98), seed number (r= 0.64), seed weight (r= 0.30) and threshing percent (r= 0.67). A highly significant negative correlation was observed between seed number and seed weight (r= -0.44). The negative relationship between seed number and seed weight clearly demonstrates why temperature treatments that bring about fewer seed numbers also produce larger seed sizes. The reduced seed number ("sink") under such circumstances might have been less than adequate for the available "source" and hence the increased seed size observed from smaller-sized panicles.

The correlations between grams of grain/GS-3 day/plant (approximate metabolic efficiency) and panicle dry weight, grain yield, seed number, seed weight and threshing percent were also significantly positive, with correlation coefficients (r) of 0.94, 0.93, 0.64, 0.25 and 0.60, respectively (Table A16).

Experiment II

The main objectives of this experiment were the same as those for Experiment I discussed above; however, treatments spanned the entire

Table 5. Dry weights of leaf laminae, sheaths, stems, roots, aboveground total (shoot) and shoot/root ratios (averaged over temperature treatments) of RS 671 grain sorghum exposed to two night treatments at various growth stages during panicle development: Greenhouse Experiment I, 1977.

Treatment (Growth stage)[1]	Laminae dry weight (g)[2]	Sheath dry weight (g)[2]	Stem dry weight (g)[2]	Root dry weight (g)[2]	Aboveground total (g)[2]	Shoot/root ratio[2]
FD_1-FD_4	14.39 a	9.49 ab	19.96 a	13.84 a	95.38 ab	3.65 b
FD_5-FD_8	14.48 a	9.04 bc	18.01 a	9.28 bc	90.66 b	4.81 b
FD_9-FD_{12}	15.26 a	9.72 ab	18.73 a	9.44 bc	94.07 ab	5.05 b
FD_{13}-FD_{16}	15.58 a	10.07 a	19.73 a	7.65 c	102.94 a	6.83 a
FD_1-$Bloom_i$	14.16 a	8.25 c	14.82 b	11.24 ab	71.73 c	4.63 b

[1]Numbers in subscripts are the numbers of days after floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[2]Means followed by the same letter within a column are not significantly different at P=0.05.

panicle expansion (GS-2) period here. This was in accord with the claim made by Warrington et al (1977) and Gipson et al (1979) that the GS-2 period is the most temperature-responsive among the three phenological periods of grain sorghum. Similar reports were also made by Skerman (1956), Pasternak and Wilson (1969) and Downes (1972).

The analysis of variance in Table A17 indicates that there were highly significant effects of temperatures and growth stages for panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight and harvest index but not for number of primary panicle branches. The temperature x growth stage interactions were also significant. These results were consistent with those observed in Experiment I reported above, with the exception of primary panicle branch number, which was significantly affected by temperature in the previous experiment.

It is now obvious that plant growth stage can place an important control on the degree to which high temperatures influence the yield and yield components of grain sorghum.

Plant growth and development were influenced by main effects of temperatures and growth stages (Tables A18 and A19), but number of days to physiological maturity and panicle length were not influenced by either of the two elevated night temperatures.

Temperature Effects

Yield and yield components

Means for the lower temperature level (26.5 C) and those for the ambient were not significantly different (Table 6). However, these differed significantly from those under the higher temperature level

Table 6. Panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight and harvest index (averaged over growth stages) of RS 671 grain sorghum as affected by two night temperatures: Greenhouse Experiment II, 1978.

	Temperature Treatment			LSD (.05)
	Control[2]	26.5 C[1]	32.0 C[1]	
Panicle dry weight (g)	56.3	57.0 (1.1)	52.6 (6.7)	2.74
Grain yield/plant (g)	49.9	49.9 (0)	46.5 (6.9)	2.59
Seeds/panicle	1973	1982 (0.5)	1612 (18.3)	80.73
1000-seed weight (g)	24.08	25.24 (+4.8)	29.54 (+22.7)	1.22
Harvest index	0.49	0.48 (2.0)	0.46 (6.1)	0.011

[1]Values in parentheses are percent reductions from control except in the case of seed size where they represent percent increases from control.

[2]Average control (ambient) temperature was 26.3 C.

(32 C). This observation could be accounted for by the seemingly high average ambient night temperatures that prevailed inside the greenhouse during experimentation (near the 26.5 C level), with a mean of 26.3 C for the GS-2 period. This, presumably, could partly explain why the magnitudes of reductions caused by the 32 C treatment were much lower here than those observed on Experiment I. Another possibility could be that temperature treatment in this experiment included the entire GS-2 period, whereas only the latter half of that period was included in Experiment I. Nevertheless, reductions caused by 32 C treatment were still significant. And, as usual, a corresponding reduction in seed number (18%) and increase in seed weight (18%) occurred.

Plant growth and development

There seemed to be a general tendency for numbers of days to heading, bloom and physiological maturity to be increased by the higher temperature level (32 C), and this treatment consequently increased the length of panicle expansion (GS-2) period (Table 7). This result was at variance with the findings of Eastin (1976) showing a reduction in panicle expansion period by elevated night temperature imposed throughout GS-2 period. Conversely, however, metabolic efficiency (g grain/GS-3 day/plant) and length of grain fill (GS-3) period were significantly reduced by the 32 C treatment. These results were in accord with those Eastin (1976) reported from a growth chamber study. Cinoy (1947), Asana and Williams (1965), Wattal (1965) and Peters et al (1971) have also reported reductions of grain fill period by elevated temperatures.

Table 7. Days to heading, bloom, and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3), and grams of grain per GS-3 day (averaged over growth stages) of RS 671 grain sorghum as affected by two night temperatures: Greenhouse Experiment II, 1978.

	Temperature Treatment			$LSD_{(.05)}$
	Control[2]	26.5 C	32.0 C	
Heading (days)	51.9	52.2	53.0	0.54
Bloom (days)	56.8	57.2	58.0	0.48
Physiological maturity (days)[1]	87.1	87.1	87.3	0.41
GS-2 (days)	26.8	27.2	28.0	0.48
GS-3 (days)	30.4	29.9	29.2	0.38
Grams grain/GS-3 day /plant (g/day)	1.65	1.69	1.59	0.09

[1]Dark layer appearance at tip of basal panicle branches.

[2]Average control (ambient) temperature was 26.3 C.

Elevated night temperatures and temperature x growth stage had significant effects on plant growth as determined through measurement of plant height and panicle exertion. Both elevated night temperatures (26.5 and 32 C) significantly reduced plant height and panicle exertion (Table 8), whereas other measures of plant growth such as total plant leaf area, leaf:stem ratio and leaf area ratio were not significantly affected by temperatures (Table A20). However, specific leaf area (SLA) and leaf weight ratio (LWR) were highly significantly influenced by temperatures and growth stages. Here also, the milder temperature treatment did not differ from the ambient with regard to their effects on both specific leaf area and leaf weight ratio, and while the 32 C treatment decreased SLA, it increased LWR (Table 8). Went (1944) had earlier claimed that elevated night temperatures significantly decreased shoot height.

Growth Stage Effects

Yield and yield components

When the various 5-day growth stages from panicle initiation through bloom were compared, it seemed rather difficult to identify precisely the most critical growth stages with regard to treatment effects on various yield attributes (Table 9). Not unexpectedly though, temperature treatments had the least effect on seed number when imposed during the last growth stage (PI_{26} to PI_{30}), and these temperature treatments had the greatest effect on seed weight reduction at that particular growth stage.

Table 8. Threshing percent, total leaf area, specific leaf area (SLA), leaf weight ratio (LWR), panicle exertion and plant height (averaged over growth stages) of RS 671 grain sorghum as affected by two night temperatures: Greenhouse Experiment II, 1978.

	Temperature Treatment			$LSD_{(.05)}$
	Control[1]	26.5 C	32.0 C	
Threshing %	88.5	87.4	88.3	0.67
Leaf area (dm^2)	25.15	24.26	24.67	1.22
SLA ($dm^2\ g^{-1}$)	1.80	1.80	1.73	0.05
LWR ($g.g^{-1}$)	0.23	0.23	0.24	0.01
Panicle exertion (cm)	17.2	12.1	8.7	1.10
Plant height (cm)	123.5	115.5	112.0	2.15

[1]Average control (ambient) temperature was 26.3 C.

Table 9. Panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight and harvest index of RS 671 grain sorghum exposed to two night temperatures at various growth stages during panicle development (averaged over temperature treatments): Greenhouse Experiment II, 1978.

Treatment (Growth stage)[1]	Panicle dry weight (g)[2]	Grain yield/ plant (g)[2]	Seeds/Panicle[2]	1000-seed weight (g)[2]	Harvest index[2]
PI_1 -PI_5	55.5 abc	47.7 bc	1939 b	24.66 de	0.47 bc
PI_6 -PI_{10}	54.2 bc	47.5 bc	1814 b	26.55 cd	0.47 bc
PI_{11}-PI_{15}	61.1 a	54.7 a	1979 b	29.00 abc	0.49 ab
PI_{16}-PI_{20}	53.9 bc	48.0 bc	1803 b	27.01 cd	0.48 ab
PI_{21}-PI_{25}	59.0 ab	52.4 ab	1946 b	27.01 cd	0.50 a
PI_{26}-PI_{30}	55.8 abc	47.5 bc	2150 a	22.24 e	0.46 bc
PI_1 -FD_1	56.6 abc	50.3 abc	1802 b	28.12 bc	0.48 ab
FD_1 -$Bloom_1$	46.3 d	41.3 d	1389 c	30.20 ab	0.45 cd
PI_1 -$Bloom_1$	50.6 cd	44.4 cd	1455 c	31.69 a	0.43 d

[1]Numbers in subscripts are the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[2]Means followed by the same letter within a column are not significantly different at P=0.05.

The difficulty of not being able to precisely discern the most critical growth stage within the GS-2 period in this experiment could, at least in part, be ascribed to the rather higher-than-average ambient temperatures that prevailed during most of that period (Table A3). However, it was observed that if the two halves of GS-2 period—from panicle initiation (PI) through floret differentiation (FD) and from floret differentiation through bloom—are compared, the second half of GS-2 period was a more critical (sensitive) period than the first half. The lowest means for panicle dry weight, grain yield per plant, number of seeds per panicle and harvest index were obtained from temperature treatment at floret differentiation through bloom (Table 9). Downes (1972) similarly found adverse effects on floret number when sorghum plants were exposed to high temperatures at about when floret differentiation is in progress or completed. In the present experiment, the responses from temperature treatments imposed during FD to bloom were as great as those from treatments during the entire GS-2 period (from panicle initiation through bloom).

Plant growth and development

The effects of growth stage on grain sorghum's response to temperature treatments were better defined for plant growth and development than they were for yield and yield components. When the average numbers of days to heading, bloom and physiological maturity and the lengths of GS-2 and GS-3 periods along with grams of grain/GS-3 day/plant were considered, the period during and immediately after floret differentiation stage (PI_{16} to PI_{20}) was found to be the most critical growth stage

(Table 10). One of the least sensitive growth stages was that period just preceding floret differentiation (PI_{11} to PI_{15}). Also with regard to plant growth and development, the latter half of the GS-2 period was still the more sensitive half to temperature treatments, and the entire GS-2 period was about the average of the two halves. This observation could be due to the fact that plants treated from PI could have gradually developed some form of preconditioning such that they could tolerate the elevated night temperatures reasonably well at later stages. Whereas, plants whose temperature treatment commenced later, at floret differentiation, lacked such prior temperature conditioning.

Correlations

Just as observed in Experiment I, significant positive correlations were observed between grain yield and panicle dry weight (r= 0.99), seed number (r= 0.57), seed weight (r= 0.58) and harvest index (r= 0.80). Similarly, significant positive correlations were observed between grams of grain/GS-3 day/plant and various yield-related attributes (Table A21). As usual, a significant negative correlation was observed between seed number and seed weight (r= -0.28). Similar relationships had been reported by Miller et al (1976) and Muchow and Wilson (1976).

Experiment III

The main objectives of this field experiment were the same as those for Experiment I discussed earlier.

Table 10. Numbers of days to heading, bloom, and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3), and grams of grain per GS-3 day of RS 671 grain sorghum exposed to two night temperatures at various growth stages during panicle development (averaged over temperature treatments): Greenhouse Experiment II, 1978.

Treatment (Growth stage)[1]	Heading (days)[2]	Bloom (days)[2]	Physiological maturity (days)[2]	GS-3 (days)[2]	GS-3 (days)[2]	Grams grain/GS-3 day /plant (g/day^{-1})[2]
PI_1 -PI_5	52.0 ab	57.3 bc	87.3 ab	27.3 bc	30.0 ab	1.60 bc
PI_6 -PI_{10}	51.9 ab	57.7 ab	87.6 ab	27.7 ab	29.7 abc	1.60 bc
PI_{11}-PI_{15}	53.0 a	58.1 ab	88.2 a	28.1 ab	30.1 a	1.82 a
PI_{16}-PI_{20}	51.6 b	56.4 c	86.1 c	26.4 c	29.8 abc	1.62 abc
PI_{21}-PI_{25}	53.3 a	57.8 ab	86.7 bc	27.8 ab	28.9 c	1.82 a
PI_{26}-PI_{30}	53.3 a	58.3 ab	87.4 ab	28.3 ab	29.1 bc	1.64 abc
PI_1 -FD_1	52.9 ab	58.6 a	88.0 a	28.6 a	29.4 abc	1.71 ab
FD_1 -$Bloom_1$	52.6 ab	56.5 c	85.9 c	26.5 c	29.4 abc	1.46 c
PI_1 -$Bloom_1$	52.9 ab	57.7 ab	87.4 ab	27.7 ab	29.7 abc	1.48 c

[1]Numbers in subscripts are the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[2]Means followed by the same letter within a column are not significantly different at P=0.05.

Temperature Effects

Results from this experiment indicated a lack of significant differences between the effects of the two elevated night temperatures (26.5 and 32 C) with respect to panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight, harvest index and panicle length (Table A22), but temperature treatments differed from those of the control (ambient). The significant differences observed between the ambient and the temperature treatments could be credited to the relatively low night and ambient average temperature differences that prevailed during experimentation. The average ambient temperature during experimentation was 20.5 C. The lack of significant differences between the two temperature treatments (26.5 and 32 C) with regard to yield and yield components could partly be explained by the rather brief (4-day) treatment duration. The ever-changing nature of environmental variables that normally exist in the field could possibly have negated the effects of such brief temperature treatments as opposed to moderately more stable greenhouse climatic conditions. Nonetheless, both elevated night temperatures consistently reduced panicle dry weight, grain yield, seed number and harvest index, while seed weight was increased by only the 32 C temperature treatment. Approximately 13% and 15% reductions in panicle dry weight and grain yield were caused by the 26.5 and 32 C night temperature treatments, respectively (Table 11). Comparable 10% and 14% reductions in seed number occurred from the 26.5 and 32 C treatments, respectively.

Despite the fact that temperature treatments did not differ significantly in their effects on yield and yield components, the 32 C

Table 11. Panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight and harvest index of RS 671 field grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development (means averaged over growth stages): Experiment III, 1977.

	Temperature Treatment			$LSD_{(.05)}$
	Control	26.5 C[1]	32.0 C[1]	
Panicle dry weight (g)	115.6	101.1 (12.6)	98.1 (15.2)	5.48
Grain yield/plant (g)	102.4	88.5 (13.5)	86.5 (15.5)	4.77
Seeds/Panicle	3590	3217 (10.4)	3074 (14.4)	178.9
1000-seed weight (g)	28.76	28.67 (~0)	29.30 (+2.0)	0.92
Harvest index	0.53	0.51 (3.8)	0.51 (3.8)	0.01

[1]Values in parentheses represent percent reductions of mean from that of the control with the exception of one for seed size that was percent increase from the control.

treatment consistently caused greater reductions than the 26.5 C treatment. There were no significant seed weight differences.

The main effects of temperatures, growth stages and temperature x growth stage interactions on plant growth and development were significant in this experiment. Significant effects were observed on numbers of days to heading, bloom and physiological maturity, durations of GS-2 and GS-3 periods and plant height. Similarly, the temperature treatments differed significantly from the control with respect to their effects on these growth and developmental attributes (Table A23).

The general pattern observed was for elevated night temperatures to hasten plant development by shortening phenological growth phases. Although means for each of the two elevated temperature treatments did not differ significantly in a few of the cases, the reductions in numbers of days to bloom and physiological maturity, and the durations of panicle expansion and grain fill periods were significant (Table 12). The reduction in grain fill duration and hastened maturity might have accounted for the yield reduction caused by elevated night temperatures. Results observed on wheat by Hoshikawa (1962), Asana and Williams (1965), Wardlaw (1970) and Warrington et al (1977) suggested that temperatures of 30 C and above could hasten maturity.

Table 13 shows the effects of the two elevated night temperatures on stover dry weight, panicle length and plant height. The relatively lesser effects of temperature treatments on vegetative growth compared to their effects on yield-related attributes were expected. Plant vegetative growth was well advanced by the time temperature treatments were

Table 12. Numbers of days to heading, bloom and physiological maturity, and durations of panicle expansion (GS-2) and grain fill (GS-3) of RS 671 field grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development (means averaged over growth stages): Experiment III, 1977.

	Temperature Treatment			$LSD_{(.05)}$
	Control	26.5 C	32.0 C	
Heading (days)	70.5	69.9	69.9	0.33
Bloom (days)	76.9	75.7	75.2	0.43
Physiological maturity (days)[1]	118.3	115.9	114.4	0.68
GS-2 (days)	28.9	27.7	27.2	0.42
GS-3 (days)	41.4	40.1	39.2	0.59

[1]Dark layer appearance at tip of basal panicle branches.

initiated at floret initiation stage. About 3-5% average reductions in growth relative to the ambient were caused by both elevated temperatures (Table 13).

Growth Stage Effects

The various growth stages during which the two elevated night temperatures were imposed differed significantly with regard to their respective sensitivities to these temperature treatments. When the various 4-day growth stages were compared, it was observed that the period about 8 days preceding the bloom stage was the most critical with respect to the responses of yield and yield components of 'RS 671' grain sorghum to these elevated night temperatures (Table 14). The two growth stages in this experiment that composed this critical period within the GS-2 period were FD_{13} to FD_{16} and FD_{17} to FD_{20}. The mid-point between floret differentiation and bloom, here designated as FD_9 to FD_{12}, was relatively the least sensitive to temperature treatments. Another growth stage that seemed to be critical with regard to night temperature effects on yield and yield components was the period from floret initiation through floret differentiation (FI_1 to FD_1). Panicle dry weight, grain yield, seed number and harvest index were significantly reduced by the temperature treatments at this growth stage (Table 14). Because of the great reduction in seed number, seed weight was significantly increased under this treatment. The above results reinforce results from previous experiments suggesting somewhere about floret differentiation as a rather sensitive growth stage, when elevated night temperatures can have considerable effects on yield and yield components.

Table 13. Dry weight of stover, panicle length and plant height of RS 671 field grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development (means averaged over growth stages): Experiment III, 1977.

	Temperature Treatment			$LSD_{(.05)}$
	Control	26.5 C[1]	32.0 C[1]	
Stover dry weight (g)	76.2	71.9 (5.5)	72.4 (4.9)	2.88
Panicle length (cm)	23.8	22.8 (4.2)	22.7 (4.7)	0.49
Plant height (cm)	107.9	104.5 (3.2)	102.4 (5.1)	1.33

[1]Values in parentheses represent percent reductions of mean from that of the control.

Table 14. Panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight and harvest index of RS 671 field grain sorghum when exposed to two night temperatures at various growth stages during panicle development (means averaged over temperature treatments):[1] Experiment III, 1977.

Treatment (Growth stage)[2]	Panicle dry weight (g)	Grain yield/ plant (g)	Seeds/Panicle	1000-seed weight (g)	Harvest index
FI_1 -FD_1	91.0 d	80.8 c	2490 e	34.05 a	0.48 c
FI_1 -$Bloom_1$	96.9 cd	85.4 bc	3116 bc	27.81 de	0.52 a
FD_1 -$Bloom_1$	103.5 abc	88.9 abc	3480 ab	26.43 e	0.52 a
FD_1 -FD_4	108.4 ab	94.6 ab	3447 ab	28.71 cd	0.52 a
FD_5 -FD_8	99.3 abcd	87.2 bc	3395 ab	26.28 e	0.51 ab
FD_9 -FD_{12}	110.7 a	97.9 a	3638 a	27.11 de	0.52 a
FD_{13}-FD_{16}	94.5 cd	83.5 c	2722 de	31.27 b	0.50 bc
FD_{17}-FD_{20}	92.3 cd	81.9 c	2874 cd	30.24 bc	0.49 c

[1]Means followed by the same letter within a column are not significantly different at P=0.05.

[2]Numbers in subscripts represent the numbers of days after floret initiation (FI), floret differentiation (FD) or bloom when temperature treatments were either initiated or terminated.

The three growth stages that seemingly were the most critical, namely, FI_1 to FD_1, FD_{13} to FD_{16} and FD_{17} to FD_{20}, were also the most sensitive to temperature treatments with regard to the numbers of days to heading and bloom and the length of GS-2 period (Table 15).

Correlations

Table A24 contains partial correlation coefficients determined among yield and development attributes for 'RS 671' grain sorghum. As previously observed, highly significant positive correlations were observed between grain yield and panicle dry weight (r= 0.99), seed number (r= 0.82) and much less significantly with seed weight (r= 0.19). Significant negative correlation was found between seed number and seed weight (r= -0.35).

Experiment IV

Plants received severe hail damage during this experiment, prior to panicle initiation, but plants were able to recover afterwards.

The primary objectives of this experiment included the determination of the effects of elevated night temperatures (5 and 10 C above ambient) occurring at various growth stages during panicle development on the yield and growth of a grain sorghum hybrid ('RS 671') under field conditions and assessment of the influence of artificial preconditioning ('hardening') on the response of this grain sorghum genotype to subsequent night temperature elevations. Of major importance in this experiment was the determination of the specific growth stage(s) within the

Table 15. Numbers of days to heading, bloom, and physiological maturity, and durations of panicle expansion (GS-2), and grain fill (GS-3) of RS 671 field grain sorghum when exposed to two night temperatures at various growth stages during panicle development (means averaged over temperature treatments):[1] Experiment III, 1977.

Treatment (Growth stage)[2]	Days to heading	Days to bloom	Days to physiological maturity	GS-2 duration (days)	GS-3 duration (days)
FI_1 -FD_1	69.8 bc	76.1 a	113.8 c	28.1 a	37.7 d
FI_1 -$Bloom_1$	69.4 c	74.8 bc	115.3 b	26.8 bc	40.5 bc
FD_1 -$Bloom_1$	70.2 ab	75.6 ab	117.3 a	27.6 ab	41.2 ab
FD_1 -FD_4	70.7 a	76.2 a	117.0 a	28.2 a	40.8 abc
FD_5 -FD_8	70.2 ab	75.6 ab	115.4 b	27.6 ab	39.8 c
FD_9 -FD_{12}	70.2 ab	76.2 a	118.1 a	28.2 a	41.9 a
FD_{13}-FD_{16}	69.5 c	74.6 c	112.4 cd	26.6 c	37.8 d
FD_{17}-FD_{20}	69.4 c	74.5 c	112.2 d	26.5 c	37.7 d

[1]Means followed by the same letter within a column are not significantly different at P=0.05.

[2]Numbers in subscripts are numbers of days after floret initiation (FI), floret differentiation (FD), or bloom when temperature treatments were either initiated or terminated.

GS-2 period at which grain sorghum would be most vulnerable to elevated night temperatures.

The justification for using a treatment design that provided a known degree of temperature elevation above the prevailing ambient temperatures came from the dynamic nature of ambient air temperatures under natural field conditions. This was a major aspect by which this experiment differed from the three earlier experiments, involving the use of constant temperature levels.

Temperature Effects

Yield and yield components

Analyses of variance were conducted for grain yield and yield components in this experiment (Table A25). Highly significant effects of elevated night temperatures and growth stages were observed on panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight, grams of grain/GS-3 day/plant. However, the effects of pretreatment (preconditioning) and the temperature x growth stage interactions were not significant. The response of RS 671 grain sorghum to these two levels of night temperature (5 and 10 C above ambient) when imposed at various growth stages followed a pattern that was independent of the temperature levels; that is, the ranking of the various growth stages with respect to their relative sensitiveness to temperature treatment remained unaltered for either the upper or lower temperature level.

Compared with the ambient, means for each variable for the two elevated night temperatures were very consistently lower than those for the ambient, and also, the higher temperature elevation (10 C above

ambient) produced much greater and highly significant reductions in yield and yield components than the lower temperature elevation (5 C above ambient) (Table 16). Conversely, however, the two elevated night temperatures produced greater seed weights than the ambient temperature, with 5 and 10 C above ambient temperature treatments resulting in about 6% and 25% greater seed weights, respectively. Wattal (1965) and Spiertz (1977) similarly reported increased wheat grain weight with increase in temperature. Wattal speculated that the higher temperatures probably increased the rate of cell division and other development processes in the grain. Increase in grain size with decreasing number of grains had been reported for rice (Sato et al., 1973), wheat (Spiertz, 1974; Muchow and Wilson, 1976) and sorghum (Chowdhury and Wardlaw, 1978).

When the ambient and the 10 C temperature elevation were compared, it was observed that approximately 18%, 19%, 30% and 17% reductions in panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant, respectively, occurred as a result of the 10 C air temperature difference. The reductions caused by 5 C above ambient treatment were not statistically significant (Table 16). Reduction in grain yield caused by elevated night temperature was in accord with similar observations reported for various cereals by Palis (1971), Peters et al (1971), Downes (1972), Eastin (1976) and Gipson et al (1979). Yoshida (1973) claimed that grain number limits yield more than any yield component, and evidence indicates that temperature during rice panicle development determines grain yield by influencing the number of spikelets.

Table 16. Panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight, grams of grain per GS-3 day and panicle length of RS 671 grain sorghum as affected by two elevated night temperatures (5 and 10 C above ambient):[1] Field Experiment IV, 1978.

	Temperature Treatment			$LSD_{(.05)}$
	Ambient	Ambient[2] + 5 C	Ambient[2] + 10 C	$LSD_{(.01)}$
Panicle dry weight (g)	61.4	59.6 (2.9)	50.2 (18.3)	4.40 6.00
Grain yield/plant (g)	47.4	46.02 (2.87)	38.3 (19.1)	3.29 4.48
Seeds/panicle	2104	1948 (7.4)	1459 (30.7)	175.6 239.5
1000-seed weight (g)	24.03	25.52 (+6.2)	30.07 (+25.1)	1.53 2.09
g Grain/GS-3 day /plant	1.35	1.33 (1.1)	1.12 (17.1)	0.10 0.13
Panicle length (cm)	21.0	21.3 (+1.1)	20.1 (4.4)	0.83 1.13

[1]Means averaged over growth stages and pretreatments.

[2]Values in parentheses are percent reductions from those of the ambient except in (+) cases where they are percent increases over the ambient (control).

Plant growth and development

Temperature effects on plant growth and development were not significant as they were on yield and yield components. One of the plausible reasons for this could be that the application of temperature treatments commenced at a stage when most or all of these growth attributes had been well fixed. Pretreatment (preconditioning) and temperature x growth stage interactions also were not significant for growth attributes. However, elevated night temperatures had highly significant effects on bloom, length of GS-2 period and plant height (Table A26).

The magnitudes of all the various attributes of plant growth and development that were measured in this experiment were reduced by elevated night temperatures, even though such reductions were small and not statistically significant. Also, the two elevated night temperatures did not differ in their effects on these attributes. Approximately 1, 1, 5, 1 and 1 days reductions in numbers of days to heading, bloom and physiological maturity and lengths of GS-2 and GS-3 periods, respectively, were caused by temperature elevation (Table 17). Hastened maturity was, therefore, associated with the yield reduction occurring from elevated night temperatures. About 5 cm reduction in plant height that resulted from 10 C temperature elevation was statistically significant. Based upon these results, the elevated temperature treatments were more pronounced on yield and yield components than they were on plant growth and development.

Table 17. Numbers of days to heading, bloom, and physiological maturity durations of panicle expansion (GS-2) and grain fill (GS-3), and plant height of RS 671 grain sorghum as affected by two elevated night temperatures (5 and 10 C above ambient):[1] Field Experiment IV, 1978.

	Temperature Treatment			$LSD_{(.05)}$
	Ambient	Ambient + 5 C	Ambient + 10 C	
Days to heading	54.8	53.9	53.9	0.69
Days to bloom	61.3	60.3	59.6	0.68
Days to physiological maturity[2]	96.5	90.9	91.9	7.20
GS-2 duration (days)	32.3	31.1	30.7	0.72
GS-3 duration (days)	35.2	35.9	34.3	2.00
Plant height (cm)	100.4	98.0	95.6	3.28

[1]Means averaged over growth stages and pretreatments.

[2]Dark layer appearance at tip of basal panicle branches.

Preconditioning Effects

Although no significant effects of preconditioning were observed for the various yield-related attributes measured in this experiment, there was a consistent tendency for the means for grain yield per plant, panicle dry weight, seed number, seed weight and grams of grain/GS-3 day/plant (metabolic efficiency) to be greater for the preconditioned than the non-preconditioned plant (Table 18). The apparent insignificant benefit from preconditioning (averaged over temperature treatments) observed in this experiment could be due to one or more of the following reasons: (1) the preconditioning was ineffective due to the fact that its duration was too brief; (2) the time lag between the time plants were preconditioned and the time the challenge temperatures were imposed could either be too short or too long; and (3) the challenge heat, particularly the 10 C above ambient treatment, might have been severe enough to overcome any positive effects of preconditioning. In the latter regard, note results in Table 19.

While effects of preconditioning were not noticeable for the higher elevated temperature (10 C above ambient), there was a trend toward beneficial effects of preconditioning for the lower temperature level (5 C above ambient) with regard to panicle dry weight, grain yield and seed number. Preconditioning under a 5 C elevation resulted in increases of about 10%, 8% and 9% above the control (non-preconditioned) plant for panicle dry weight, grain yield and seed number, respectively (Table 19). However, the increases were not statistically significant. Significant increases in grain yield and panicle weight of

Table 18. Effect of preconditioning (hardening) on grain yield and its components of RS 671 grain sorghum exposed to two elevated night temperatures: Field Experiment IV, 1978.

	Control[1]	Preconditioned[1]	$LSD_{(.05)}$
Panicle dry weight (g)	53.1	56.6	4.40
Grain yield/plant (g)	41.1	43.2	3.29
Seeds/panicle	1676	1731	175.6
1000-seed weight (g)	27.33	28.26	1.53
g Grain/GS-3 day/plant	1.20	1.25	0.10
Panicle length (cm)	20.5	20.8	0.83

[1]Means averaged over growth stages and temperature treatments.

Table 19. Effect of preconditioning (hardening) on the response of panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight, grams of grain/GS-3 day and panicle length to two elevated night temperatures (means averaged over growth stages): Field Experiment IV, 1978.

	Pretreatment				$LSD_{(.05)}$
	Control		Preconditioned		
	Ambient + 5 C	Ambient + 10 C	Ambient + 5 C	Ambient + 10 C	
Panicle dry weight (g)	56.6	49.7	62.6	50.7	6.22
Grain yield/plant (g)	44.2	38.0	47.8	38.6	4.65
Seeds/panicle	1860	1492	2035	1426	2.48
1000-seed weight (g)	25.34	29.32	25.69	30.82	2.17
g Grain/GS-3 day/plant	1.29	1.11	1.37	1.13	0.13
Panicle length (cm)	21.0	20.0	21.5	20.2	1.18

early and medium maturity sorghum hybrids were reported by Sullivan et al (1977a) and in yield of soybean (Specht et al, 1977).

Preconditioning did not have significant effects on the responses of plant growth and development to elevated night temperatures (Table 20). On the whole, preconditioning was less beneficial on plant growth and development than it was for yield and yield components.

Growth Stage Effects

Yield and yield components

Significant differences were observed among the various growth stages within the GS-2 period, when the two elevated night temperatures were imposed, with respect to effects on 'RS 671' grain sorghum's yield and yield components measured in this experiment (Table 21). In other words, the various growth stages differed significantly in their respective sensitivities to the temperature treatments. For each of these variables, namely, grain yield, panicle dry weight, seed number and grams of grain/GS-3 day/plant, the greatest reductions occurred when temperature treatments were imposed during the first 7 days after floret differentiation (FD_1 to FD_7). The magnitudes of the effects on these variables were approximately 43%, 44%, 57% and 42% reductions, respectively, as against the least critical growth stage ($bloom_1$ to $bloom_7$). The high degree of consistency in these results helps to establish convincingly that the most critical growth stage during the GS-2 period is about the first 7 days after floret differentiation begins. However, the greatest seed weight or size was obtained for that particular growth stage (FD_1 to FD_7), possibly because seed number was reduced considerably

Table 20. Effect of preconditioning (hardening) on the response of some attributes of plant growth and development of RS 671 grain sorghum to two elevated night temperatures: Field Experiment IV, 1978.

	Control[1]	Preconditioned[1]	$LSD_{(.05)}$
Days to heading	53.8	53.9	0.69
Days to bloom	59.9	60.0	0.68
Days to physiological maturity	90.2	92.6	7.20
GS-2 duration (days)	30.9	31.0	0.72
GS-3 duration (days)	35.5	34.7	2.00
Plant height (cm)	96.6	97.0	3.28

[1]Means averaged over growth stages and temperature treatments.

Table 21. Effect of plant growth stage on the response of grain yield and its components of RS 671 grain sorghum to two elevated night temperatures (means averaged over temperatures and pretreatment):[1] Field Experiment IV, 1978.

Growth stage[2]	Panicle dry weight (g)[3]	Grain yield/ plant (g)	Seeds/ Panicle	1000-Seed weight (g)	Grams grain/GS-3 day/plant
PI_1-PI_7	60.4 ab (7.2)	46.7 ab (6.4)	1889 ab (11.7)	26.58 b (+5.4)	1.38 a (2.1)
PI_8-FD_1	56.8 b (12.8)	44.3 b (11.2)	1854 ab (13.4)	26.74 b (+6.0)	1.28 ab (9.2)
FD_1-FD_7	37.0 c (43.2)	27.9 c (44.1)	932 c (56.5)	33.42 a (+32.5)	0.82 c (41.8)
FD_8-$Bloom_1$	55.1 b (15.4)	42.0 b (15.8)	1703 b (20.4)	27.00 b (+7.0)	1.22 b (13.5)
$Bloom_1$-$Bloom_7$	65.1 a (0)	49.9 a (0)	2140 a (0)	25.23 b (0)	1.41 a (0)

[1]Values in parentheses are percent reductions from maximum or percent increases (+) from minimum.

[2]Numbers in subscripts represent the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[3]Means followed by the same letter within a column are not significantly different at P=0.05.

here. For about 57% reduction in seed number, there was about 30% increase in seed weight representing a mechanism by which cereals attempt to compensate for losses in one or more earlier-determined yield components through one or more later-determined yield components. This compensation in this case was not adequate to completely offset grain yield reduction.

Figures 1, 2, 3 and 4 show the responses of grain yield and the various yield components to the two elevated night temperatures when imposed at the various growth stages. The separate responses of grain yield per plant, seed number and grams of grain/GS-3 day/plant at the respective growth stages followed remarkably similar trends, while seed weight (size) responses followed a complete reversal of those trends. It could be said with a reasonable degree of confidence that as 'RS 671' goes from panicle initiation toward floret differentiations, its vulnerability to elevated night temperatures increases until beyond about 7 days after floret differentiation when its tolerance starts to increase.

The responses of the various yield-related variables to each of the two elevated night temperatures were quite identical with regard to their trends across the GS-2 period (that is, lack of significant temperature x growth stage interactions).

Figure 5 shows the effect of preconditioning on the response of grain sorghum yield to each of the two imposed elevated night temperatures considered separately. Note that the response of 'RS 671' grain sorghum to elevated night temperatures with respect to the various growth stages followed similar trends whether preconditioned or not. Preconditioning did not influence the ranking order of the various growth stages

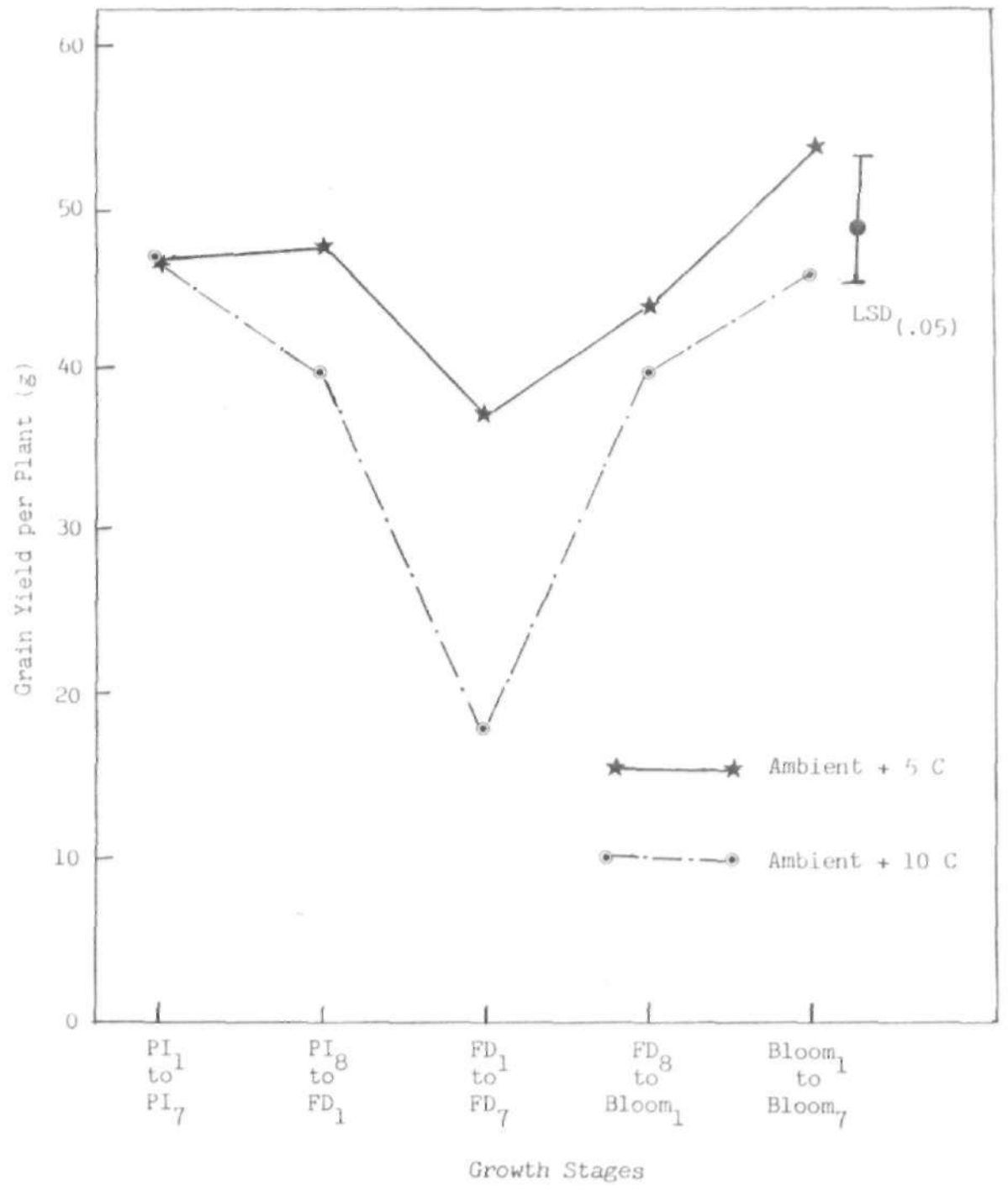


Fig. 1. The effect of 5 and 10 C ambient night temperature elevations at various growth stages on grain yield of RS 671 grain sorghum: Field Experiment IV, 1978.

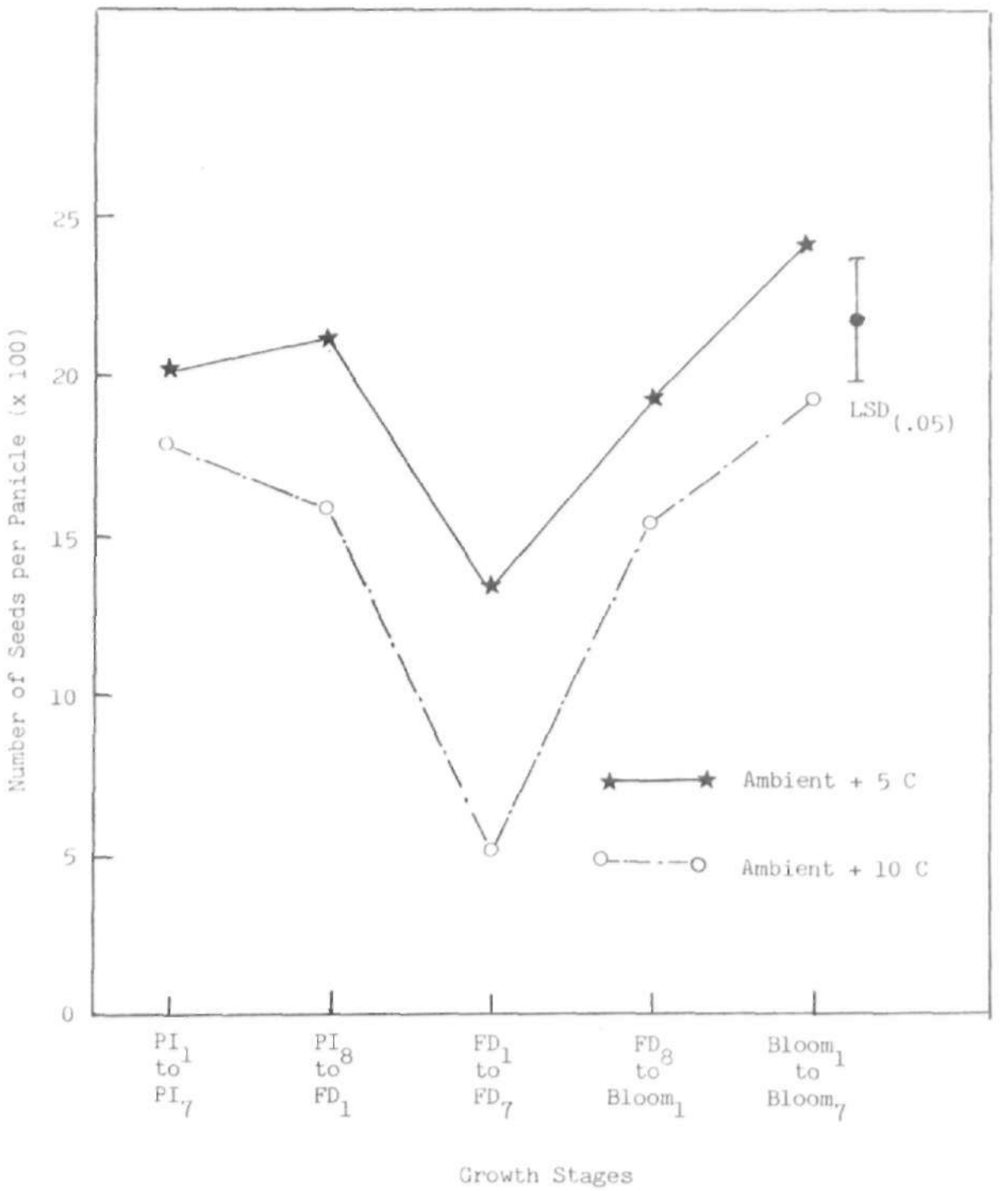


Fig. 2. The effect of 5 and 10 C ambient night temperature elevations at various growth stages on number of seeds per panicle of RS 671 grain sorghum: Field Experiment IV, 1978.

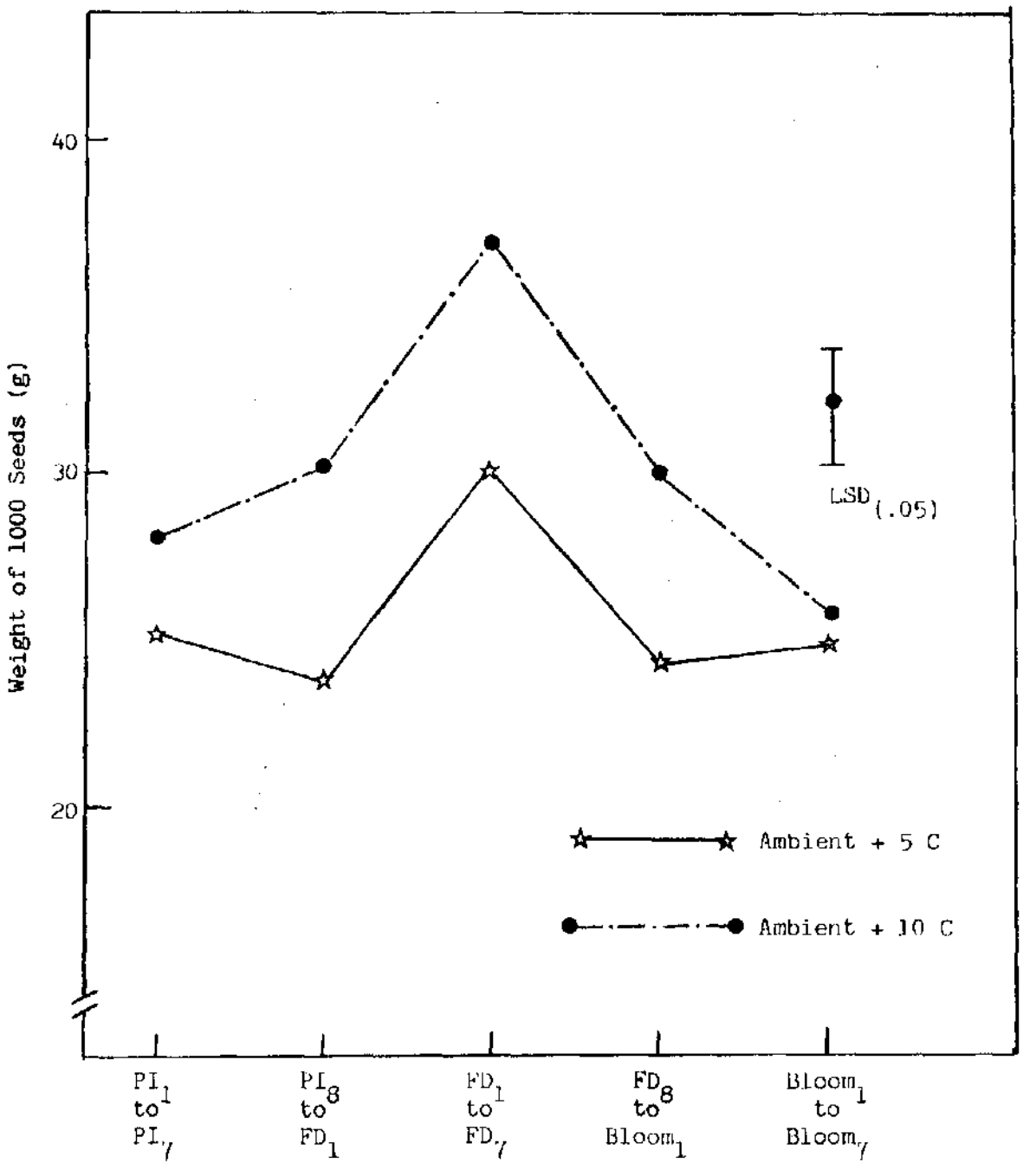


Fig. 3. The effect of 5 and 10 C ambient night temperature elevations at various growth stages on 1000-seed weight of RS 671 grain sorghum: Field Experiment IV, 1978.

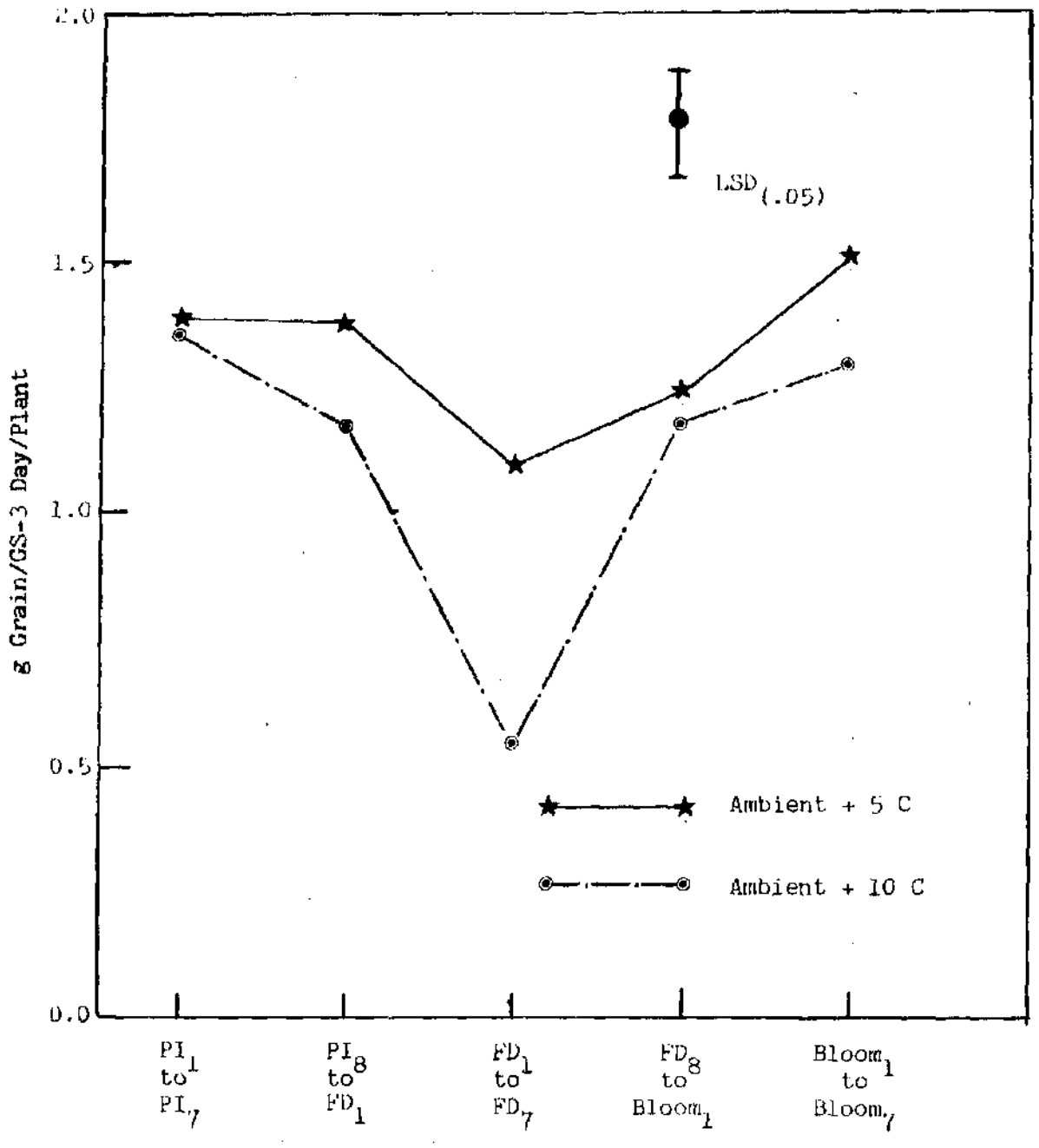


Fig. 4. The effect of 5 and 10 C ambient night temperature elevations at various growth stages on metabolic efficiency (g grain/GS-3 day/plant) of RS 671 grain sorghum: Field Experiment IV, 1978.

on the basis of their vulnerability to each of the two elevated night temperatures. With the exception of PI_1 to PI_7 for both temperatures and FD_8 to bloom for the higher temperature level, positive but non-significant trend effects of preconditioning were reflected in the grain yield for each temperature and for each growth stage (Fig. 5).

Plant growth and development

None of the five growth stages differed significantly from the rest in their respective sensitivities to the two elevated temperatures with respect to either the number of days to physiological maturity or the length of grain fill (GS-3) period (Table 22). During the period of about 14 days after floret differentiation, FD_1 to FD_7 and FD_8 to bloom, seemed to be identical in being the two most vulnerable growth stages with respect to the numbers of days to heading and bloom and the length of panicle expansion period. The three remaining growth stages were the least vulnerable to elevated night temperatures (Table 22). The relative ranking of the various growth stages with respect to their vulnerability to elevated night temperature was less clear for plant growth and development than it was for yield and yield components.

Correlations

As usual, highly significant positive correlations were observed between grain yield and panicle dry weight ($r= 0.95$), seed number ($r= 0.75$), grams of grain/GS-3 day/plant ($r= 0.98$), while a highly significant negative correlation between seed number and seed weight ($r= -0.60$) was observed (Table A27).

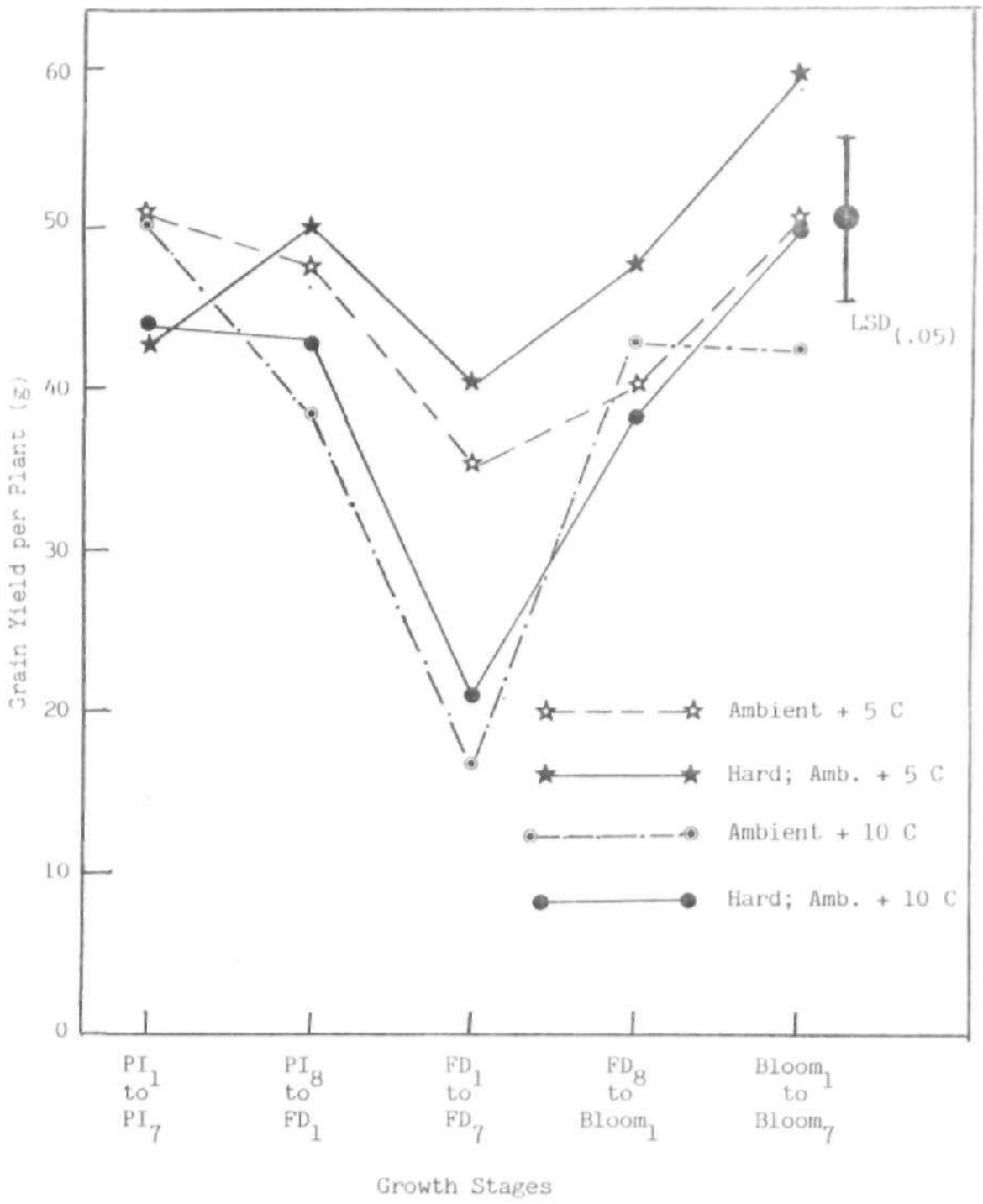


Fig. 5. The effect of preconditioning on the response of RS 671 grain sorghum yield to elevated night temperatures imposed at various growth stages: Field Experiment IV, 1978.

Table 22. Effect of plant growth stage on the response of numbers of days to heading, bloom, and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3) of RS 671 grain sorghum to two elevated night temperatures:[1] Field Experiment IV, 1978.

Growth stage[2]	Days to heading[3]	Days to bloom	Days to physiological maturity	GS-2 duration (days)	GS-3 duration (days)
PI_1-PI_7	53.7 ab	60.7 a	95.3 a	31.3 ab	34.8 a
PI_8-FD_1	54.2 a	60.7 a	90.0 a	81.7 a	37.0 a
FD_1-FD_7	53.0 b	58.4 b	92.4 a	29.4 c	33.8 a
FD_8-$Bloom_1$	53.7 ab	59.0 b	83.5 a	30.2 bc	34.6 a
$Bloom_1$-$Bloom_1$	54.6 a	60.8 a	95.7 a	32.0 a	35.4 a

[1]Means averaged over temperatures and pretreatments.

[2]Numbers in subscripts represent the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

[3]Means followed by the same letter within a column are not significantly different at P=0.05.

Experiment V

The main objectives of this field experiment were essentially the same as those for Experiment IV discussed earlier on. A further expansion made here over the preceding field experiment was to undertake some measurement of a few physiological processes and parameters with a view of gaining some understanding into how plant processes and parameters responded to elevated night temperatures and/or preconditioning. Such information, hopefully, will afford us a better comprehension of the responses of plant growth and yield to elevated night temperatures imposed at various growth stages during panicle development.

Physiological Studies

Leaf heat tolerance (cell membrane thermostability)

The analysis of variance for the combined data for all five leaf-disc heat tolerance tests conducted at various growth stages (dates) indicated that pretreatment (preconditioning) had no significant effects on heat tolerance level (Table A28). Lack of significant date x pretreatment interactions was indicative of the fact that preconditioning did not influence the heat tolerance level of 'RS 671' grain sorghum leaves at the various growth stages. However, heat tolerance levels of sorghum leaves determined on various dates differed quite significantly.

On the first test date (at 7 days after panicle initiation), leaves of preconditioned plants displayed greater heat tolerance (less heat injury) than leaves from non-hardened plants (Table 23), but that relationship was reversed on the second test date (at floret initiation).

Table 23. Heat tolerance levels of preconditioned and nonpreconditioned RS 671 field grain sorghum leaves determined by electrical conductivity tests at various growth stages: Experiment V, 1979.

Pretreatment	Growth Stage				
	Panicle initiation + 7 days	Floret differentiation	FD + 7 days	Bloom	Bloom + 7 days
	----------% Heat Injury[1]----------				
Unhardened	65.2	60.0	31.6	56.1	73.4
Hardened	59.0	65.1	33.1	56.0	73.7
$LDS_{(.05)}$	10.04	11.04	3.79	8.25	4.02
Mean[2]	62.1 b	62.6 b	32.4 a	56.1 c	73.6 a

[1]Heat treatment of 53.5 C for 15 min (means of 12 reps).

[2]Means followed by the same letter are not significantly different at P=0.05.

On the subsequent three test dates (that is, at 7 days after floret differentiation, at bloom and at 7 days after bloom), no significant differences were observed between the heat tolerance levels of preconditioned and non-preconditioned plants. Sullivan et al (1977a) reported that higher heat tolerance of preconditioned early and medium maturity sorghum hybrids persisted up to 26 days after heat hardening, but Specht et al (1977) claimed that higher membrane stability in soybean induced by temperature hardening persisted throughout the growing season.

By means of Duncan's multiple range test, the average heat injury levels on various test dates (growth stages) were compared, and it was observed that while heat injury levels on the first two test dates did not differ, the least heat tolerance (highest heat injury) occurred from test conducted on the 7th day after bloom (Table 23). The highest level of heat tolerance (lowest heat injury) occurred on the 7th day after floret differentiation, followed by heat tolerance at 7th day after panicle initiation and then at floret differentiation, both of which did not differ. Prevailing weather conditions seemed to have a significant impact on the average heat tolerance level obtained on any given test date. In this experiment, the lowest leaf heat injury occurred on a very hot day, August 5, while the highest injury level was obtained on a very cool, overcast wet day, August 19. The rest of the test dates were on bright, warm days. It is, therefore, important to take note of the strong association of leaf heat injury level with prevailing weather conditions. Such strong associations between leaf heat tolerance and weather conditions have earlier been demonstrated by Smith (1973) and Ogunlela (1974) on field-grown sorghums.

Leaf carbon dioxide exchange

Analyses of variance for the various dates during panicle development when leaf photosynthetic rates were measured indicated significant effects of temperature treatments on photosynthetic rates for only three of the five various dates (Table A29). There were, however, no significant effects of pretreatment (preconditioning) on photosynthetic rates. The average leaf photosynthetic rates obtained on the five various dates differed highly significantly (Table A30).

Table 24 contains leaf photosynthetic rates of 'RS 671' grain sorghum on various dates as affected by earlier imposed two elevated night temperatures (5 and 10 C above ambient). Each date of measurement was about the 3rd day after the termination of temperature treatment. On the first date (July 25), when plants were at about the 10th day after panicle initiation, the average leaf photosynthetic rate for the ambient +5C treatment (45.5 mg CO_2 dm^{-2} hr^{-1}) was significantly higher than that for the ambient (35.7 mg CO_2 dm^{-2} hr^{-1}), while that for the ambient +10 C treatment (28.4 mg CO_2 dm^{-2} hr^{-1}) was considerably lower than either one. Photosynthetic rates measured on the second date (August 1), when plants were at the 3rd day after floret differentiation, followed the same relative ranking as the first date. On another two consecutive dates (August 8 and 9), when plants were at about the 10th and 11th days after floret differentiation, respectively, the highest photosynthetic rates were measured from plants under the ambient, followed by the ambient +5 C and last was the ambient +10 C treatment. On the fifth and last test date (August 17), plants at 5th day after bloom, there were no significant differences among leaf photosynthetic rates

Table 24. Photosynthetic rates of RS 671 field grain sorghum leaves exposed to two elevated night temperatures measured on various dates: Experiment V, 1979.

Temperature Treatment	Date				
	July 25	Aug. 1	Aug. 8	Aug. 9	Aug. 17
	Leaf Photosynthetic Rate[1] ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)				
Ambient	35.65	41.12	30.53	34.09	25.96
Ambient +5 C	45.39	48.51	28.17	25.02	26.32
Ambient +10 C	28.38	37.63	23.43	17.36	24.62
Mean[2]	36.47	42.42	27.38	25.49	25.64

$LSD_{(.05)}$ for temperature treatment means within dates (averaged over pretreatments) = 8.10.

$LSD_{(.05)}$ for date means within temperature treatments = 8.10.

[1]Values are means for 18 plants from three replications averaged over pretreatments. Photosynthesis measurements at 26, 29, 34, 32 and 33 C mean ambient field temperatures, respectively.

[2]$LSD_{(.05)}$ for overall date means = 4.68.

measured for the three different temperature conditions (Fig. 6). Leaf photosynthetic rates were measured on bright, clear days under photosynthetically active radiation of approximately 2.0 x 10^3 μ Ei m^{-2} s^{-1}.

The ambient +10 C treatment consistently reduced leaf photosynthetic rate throughout the measurement period. When summarized for all five dates, the average photosynthetic rates for the ambient and ambient +5 C treatment did not differ significantly, but that for the ambient +10 C treatment was considerably lower, having average rates of 33.5, 34.7 and 26.3 mg CO_2 dm^{-2} hr^{-1}, respectively (Table 26). When leaf photosynthetic rates were averaged over temperature treatments across the measurement period, only the rates measured on the first two dates differed significantly from the rest (Table 24). Three distinct groups into which photosynthetic rates seemed to fall were: (1) the second date, with approximately 42.4 mg CO_2 dm^{-2} hr^{-1}; (2) the first date, with approximately 36.5 mg CO_2 dm^{-2} hr^{-1}; and (3) the last three dates, with approximately 26.2 mg CO_2 dm^{-2} hr^{-1} (Table 24).

The effects of preconditioning were not significant on leaf photosynthetic rate under any of the temperature treatments (Table 26, Figs. 7 and 8) or on any of the measurement dates (Table 25).

These results suggest that mild night temperature elevations can be beneficial to sorghum leaf photosynthesis, and that very high night temperature elevations (10 C) above ambient can be detrimental to leaf photosynthesis. Artificial preconditioning was beneficial only when the challenge temperature (heat) was high enough to considerably reduce leaf photosynthetic rates of non-hardened plants.

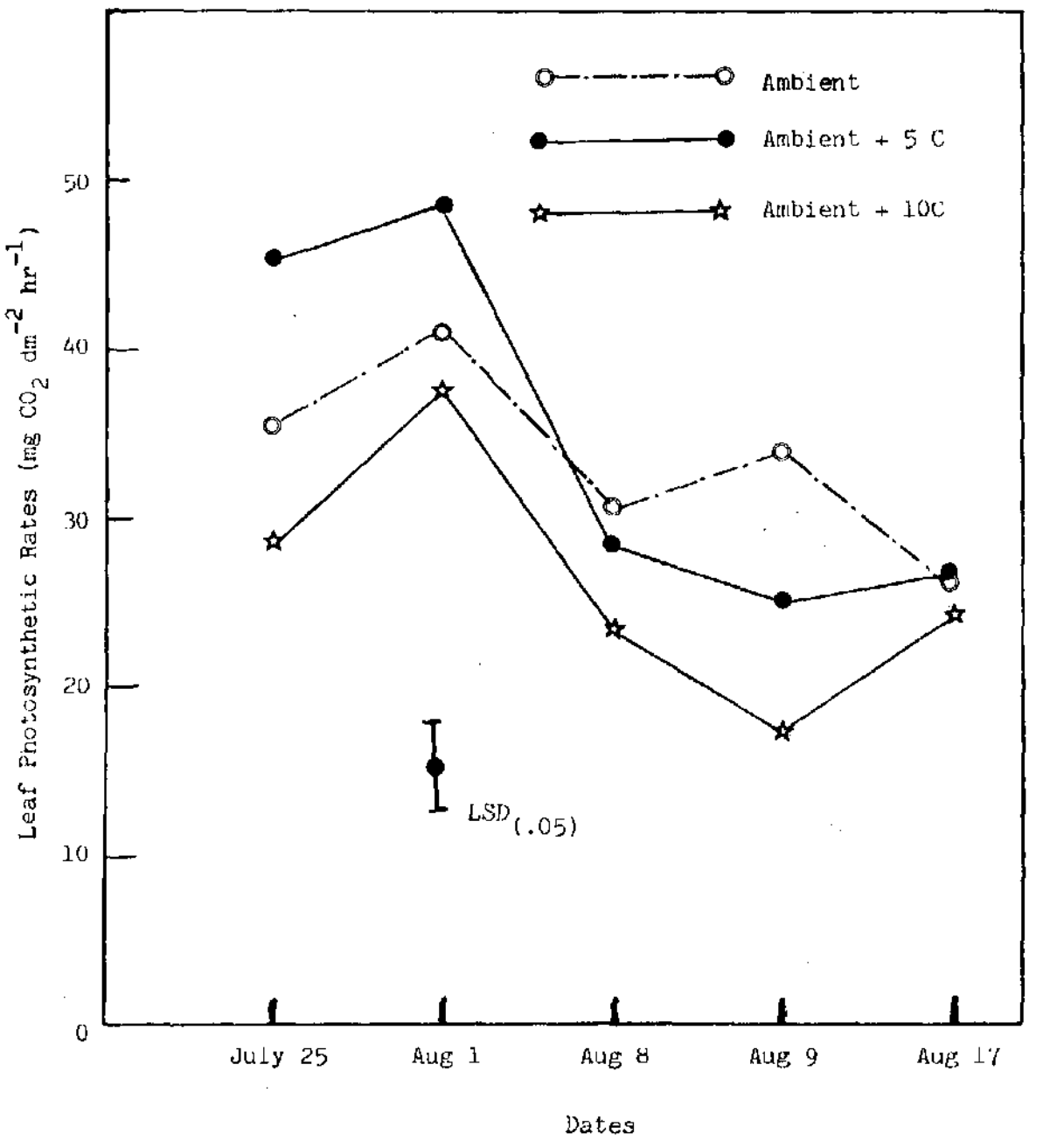


Fig. 6. The after-effect of two elevated night temperatures on the leaf photosynthetic rates of RS 671 grain sorghum at various dates during panicle development: Field Experiment V, 1979.

Table 25. Effect of preconditioning on the response of leaf photosynthetic rates of RS 671 field grain sorghum to elevated night temperatures imposed during panicle development (means averaged over temperature treatments):[1] Experiment V, 1979.

Date	Pretreatment		$LSD_{(.05)}$
	Unhardened	Hardened	
	Leaf Photosynthetic Rate ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)		
July 25	35.63	37.31	8.95
Aug. 1	43.40	41.44	7.74
Aug. 8	27.42	27.33	4.32
Aug. 9	23.48	27.50	6.19
Aug. 17	25.16	26.11	4.49
Mean	31.02	31.94	

[1]Measured at 26, 29, 34, 32 and 33 C average air temperatures, respectively.

Table 26. Photosynthetic rates of RS 671 field grain sorghum leaves exposed to two elevated night temperatures averaged over all measurement dates: Experiment V, 1979.

Temperature Treatment	Pretreatment		Mean[2]
	Unhardened	Hardened	
	Leaf Photosynthetic Rate[1] ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)		
Ambient (check)	33.57	33.37	33.47
Ambient + 5 C	34.29	35.08	34.68
Ambient + 10 C	25.20	27.37	26.29
Mean[3]	31.02	31.94	31.48

[1]Values are means for 45 plants from three replications on five dates.

[2]$LSD_{(.05)}$ = 3.62

[3]$LSD_{(.05)}$ = 2.96

$LSD_{(.05)}$ for temperature treatment means within pretreatments = 5.12.

$LSD_{(.05)}$ for pretreatment means within temperature treatments = 5.12.

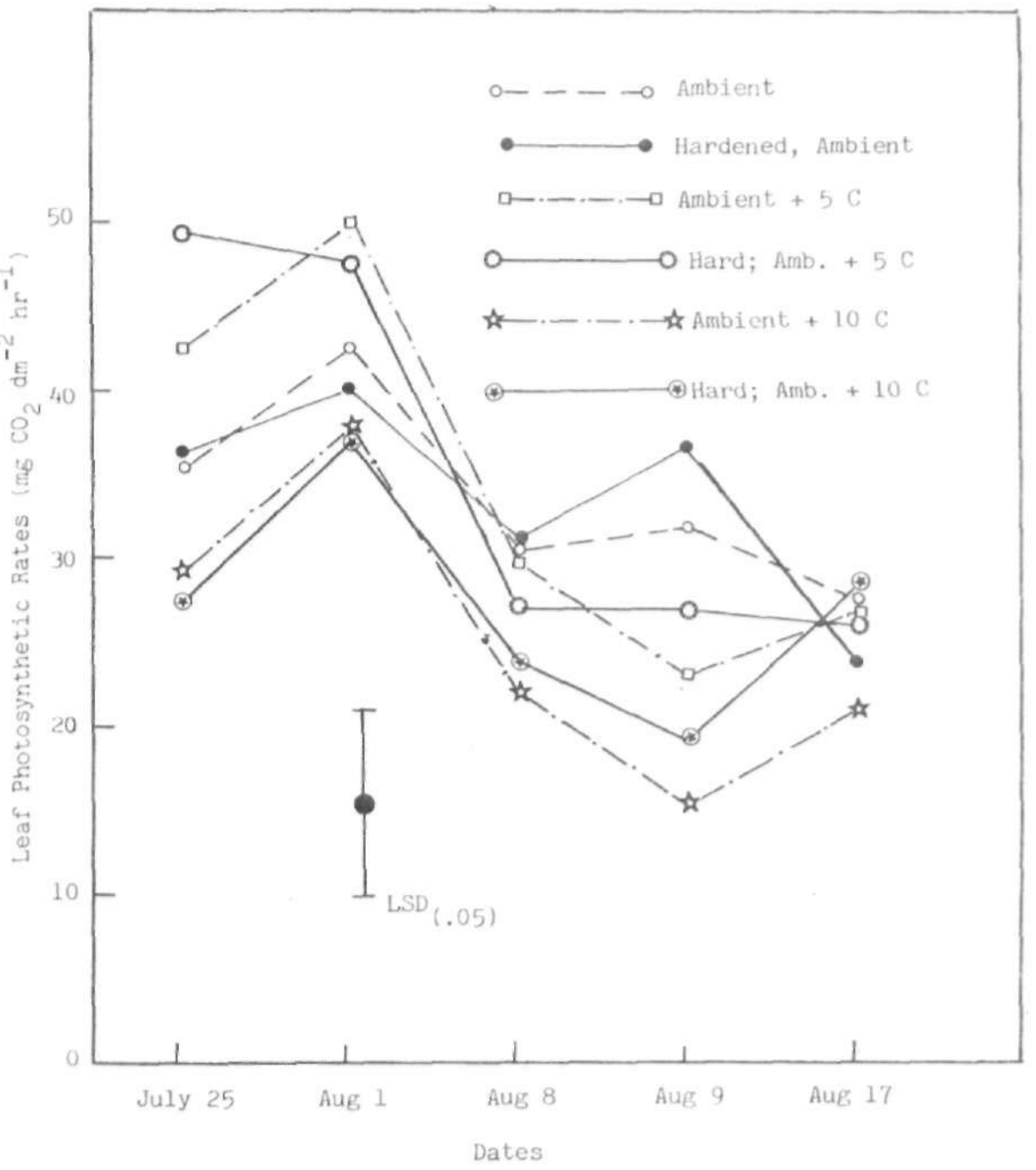


Fig. 7. The effect of preconditioning on the response of RS 671 grain sorghum's leaf photosynthetic rates to elevated night temperatures measured at various dates during panicle development: Field Experiment V, 1979.

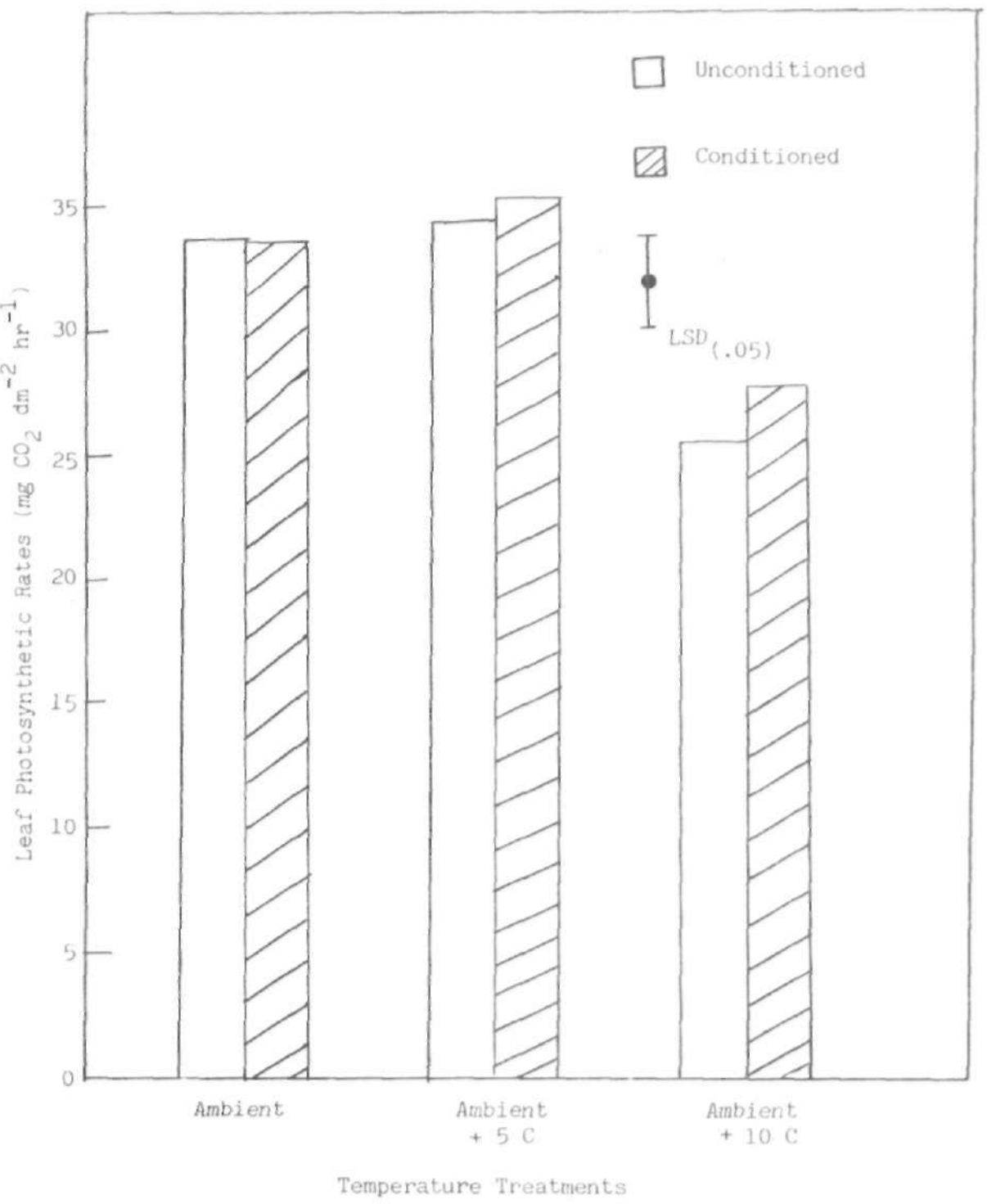


Fig. 8. The effect of preconditioning on the after-effect of two elevated night temperatures (5 and 10 C above ambient) on leaf photosynthetic rate of RS 671 grain sorghum (averaged over measurement dates): Field Experiment V, 1979.

Results were in accord with findings of Raschke (1970) who showed that carbon dioxide assimilation of maize (Zea mays) at 25 C was not affected by previous temperatures between 10 and 35 C, but exposure to higher temperature sharply diminished subsequent CO_2 fixation. Bauer et al (1973) later expressed a similar view, claiming that extreme temperatures may have aftereffects which could inhibit subsequent photosynthesis even at optimal temperatures.

Results from this experiment support the views of Murata (1964) who claimed that reduced yield by high night temperature was partly due to increased respiration and decreased photosynthesis but refute those of Moss et al (1961) who believed that high night temperature increases respiration in the night but increased photosynthesis in the daytime.

Results obtained here were also in accord with a report by Norcio and Sullivan (1976a) who had earlier claimed that based on their findings from a study of some corn and sorghum genotypes, the flowering stage was the more sensitive to elevated night temperatures than panicle initiation was.

Grain dry matter accumulation

Kernel dry weight, kernel growth rate and relative kernel growth rate of 'RS 671' grain sorghum were determined at various weekly intervals during grain fill (GS-3) period with a view of estimating the aftereffect of elevated night temperatures imposed during the panicle development period.

Kernel dry weight. The effects of elevated night temperatures on kernel dry weight were significant only at the initial and latter points

during grain fill, while the effects at the various growth stages were significant only at the latter part of grain fill (Table A31). In no instance were temperature x growth stage interactions significant. Throughout the linear grain growth phase, kernel dry weight increased with increasing night temperature, but in the lag phase (about 2 weeks after bloom), no differences in kernel dry weight were observed among temperature treatments (Fig. 9). The ambient +10 C treatment consistently produced the greatest kernel dry weight, followed by the ambient +5 C treatment, and least was that of the ambient. The differences in kernel dry weight among the three temperature levels widened as the grain fill period advanced until a point was reached when such differences began to diminish. These results were in accord with reports made on corn by Duncan et al (1965) and on wheat by Wattal (1965) and Spiertz (1977). Wattal thought that the higher temperature conditions probably increased the rate of cell division and other development processes in the grain and hence the greater movement of assimilate to the developing grains. He found that wheat grain weight increased with increase in temperature from 27.9 to 31.4 C. Duncan et al (1965) and Wattal (1965) suggested that grain development was compensated by supply of sugars from the stem, while Spiertz (1977) believed that redistribution of carbohydrate was greater at high temperatures.

Grain fill curves for a total panicle are usually more linear than noted in the Figure 9 curve which is for kernels all the same maturity (i.e., selected from the same bloom date in a panicle in this case). Apparently, the dynamics of grain fill for a whole panicle where

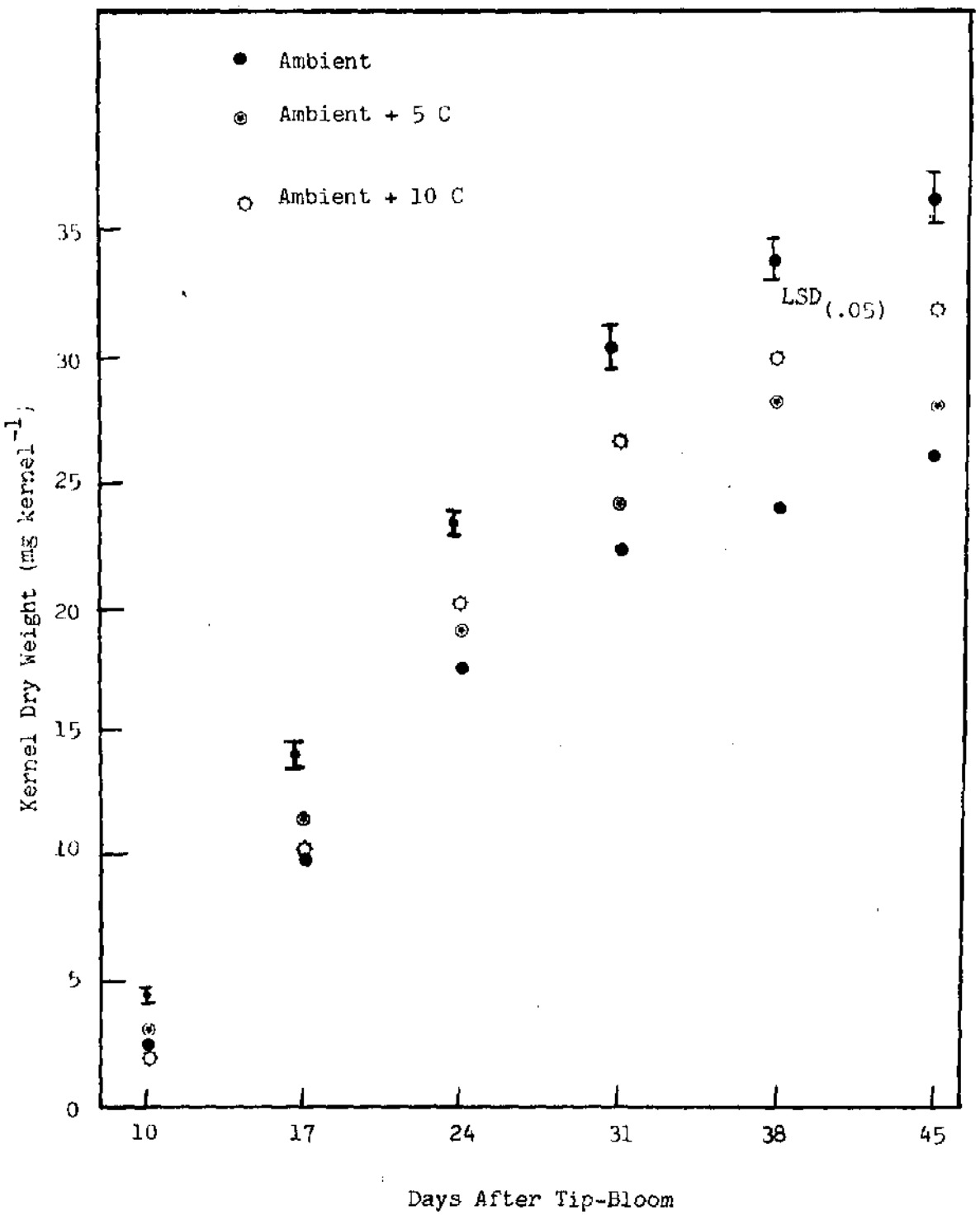


Fig. 9. The effect of elevated night temperatures (5 and 10 C above ambient) on kernel dry weight of RS 671 grain sorghum determined at weekly intervals after tip bloom: Field Experiment V, 1979.

kernels differ in maturity by 5 to 10 days is different than for an individual kernel.

The various 7-day growth stages during which the two elevated temperatures were imposed differed significantly with respect to kernel dry weights. Considerably greater kernel dry weights were observed when either of the two elevated night temperatures was imposed during 7 days preceding or 7 days after floret differentiation (PI_8 to FD_1 or FD_1 to FD_7) as shown in Table 27. The lowest kernel dry weights were obtained when temperature treatments were imposed during the first or last growth stage (PI_1 to PI_7 or $bloom_1$ to $bloom_7$). The average kernel dry weights determined after physiological maturity for the five growth stages (when temperature treatments were imposed) and the control were 25.9, 33.9, 33.4, 29.3, 26.2 and about 25 mg $kernel^{-1}$, respectively (Table 27). This indicates that the closer the elevated night temperature occurrence is to floret differentiation stage, the greater will be the kernel dry weight, probably because of an associated reduction in seed number.

Kernel growth rate. Kernel growth rates did not differ among the temperature levels until after about 2 weeks following bloom when kernel growth rate was significantly higher for plants that had been exposed to the ambient +10 C treatment than for plants that were exposed to either the ambient or the ambient +5 C treatment (Fig. 10). This observation conformed with earlier reports on rice (Nagato and Ebata, 1966), wheat (Wardlaw, 1970; Spiertz, 1977) and sorghum (Chowdhury and Wardlaw, 1978). They reported that higher temperatures resulted in a greater rate of kernel development. As much as 45% increase in sorghum kernel growth

Table 27. Kernel dry weights of RS 671 field grain sorghum exposed to two elevated night temperatures during five different growth stages as determined after physiological maturity:[1] Experiment V, 1979.

Temperature Treatment	Growth Stage				
	PI_1 to PI_7	PI_8 to FD_1	FD_1 to FD_7	FD_8 to $Bloom_1$	$Bloom_1$ to $Bloom_7$
	Kernel Dry Weight[2] (mg/kernel)				
Ambient + 5 C	25.04 c	32.35 a	29.56 ab	26.65 bc	24.81 c
Ambient + 10 C	26.77 c	35.35 ab	37.28 a	31.84 b	27.49 c
Mean[2]	25.91 c	33.85 a	33.42 a	29.25 b	26.15 c

[1]Values are means of two replications.

[2]Values followed by the same letter within a row are not significant different at the 5% probability level.

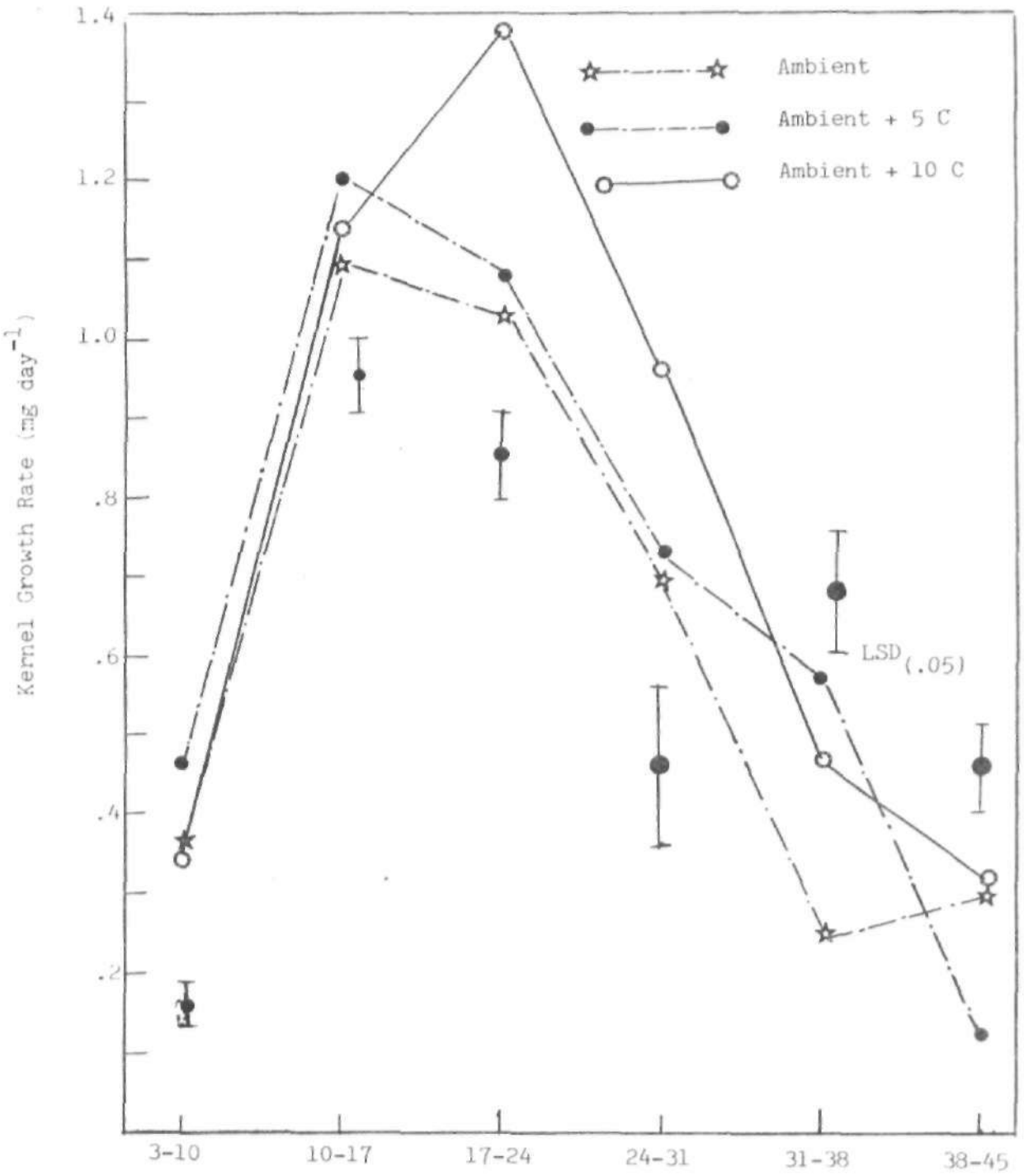


Fig. 10. The effect of two elevated night temperatures (5 C and 10 C above ambient) on kernel growth rate of RS 671 grain sorghum at various weekly intervals after tip-bloom: Field Experiment V, 1979.

rates with a 24/19 C to 30/25 C day/night temperature rise was observed by Chowdhury and Wardlaw (1978). Wattal (1965) and Wardlaw (1970) associated this with a corresponding increase in the rate of cell division in the endosperm tissue of the grain.

Average kernel growth rates across the grain fill period increased sharply during about the first 2 weeks after bloom and thereafter, declined gradually until it dropped sharply to its lowest ebb, at close to physiological maturity. The relative ranking of the various growth stages followed a pattern similar to the one for kernel dry weights (Tables 27 and 28). The highest kernel growth rates occurred in plants temperature treated during either 7 days preceding or 7 days after floret differentiation, while plants treated during either 7 days after panicle initiation or 7 days after bloom stage had the lowest growth rates.

Relative kernel growth rate. Relative kernel growth rates (sink strength estimates) during the earlier part of grain fill were significantly influenced by the different temperature levels but not during the latter part of that period (Table A32). Also, growth stage consistently influenced it at certain points during GS-3 period, but significant temperature x growth stage interactions did not occur. Relative kernel growth rates during the first 3 weeks after bloom were enhanced by the ambient +10 C temperature treatment, but thereafter, there were no tangible differences among the different temperature levels (Fig. 11). This reflects that after grain fill was well advanced in the growing season, the temperatures to which plants had earlier been exposed became

Table 28. Kernel growth rates of RS 671 field grain sorghum exposed to two elevated night temperatures during five different growth stages (averaged over sampling dates and pretreatments):[1] Experiment V, 1979.

Temperature Treatment	Growth Stages				
	PI_1 to PI_7	PI_8 to FD_1	FD_1 to FD_7	FD_8 to $Bloom_1$	$Bloom_1$ to $Bloom_7$
	Kernel Growth Rate (mg x 10^{-1}/day)				
Ambient + 5 C	6.13	8.10	7.53	6.51	5.95
Ambient + 10 C	6.38	8.57	8.93	7.58	6.59
Mean	6.26	8.34	8.23	7.05	6.27

[1]Values are means of two replications.

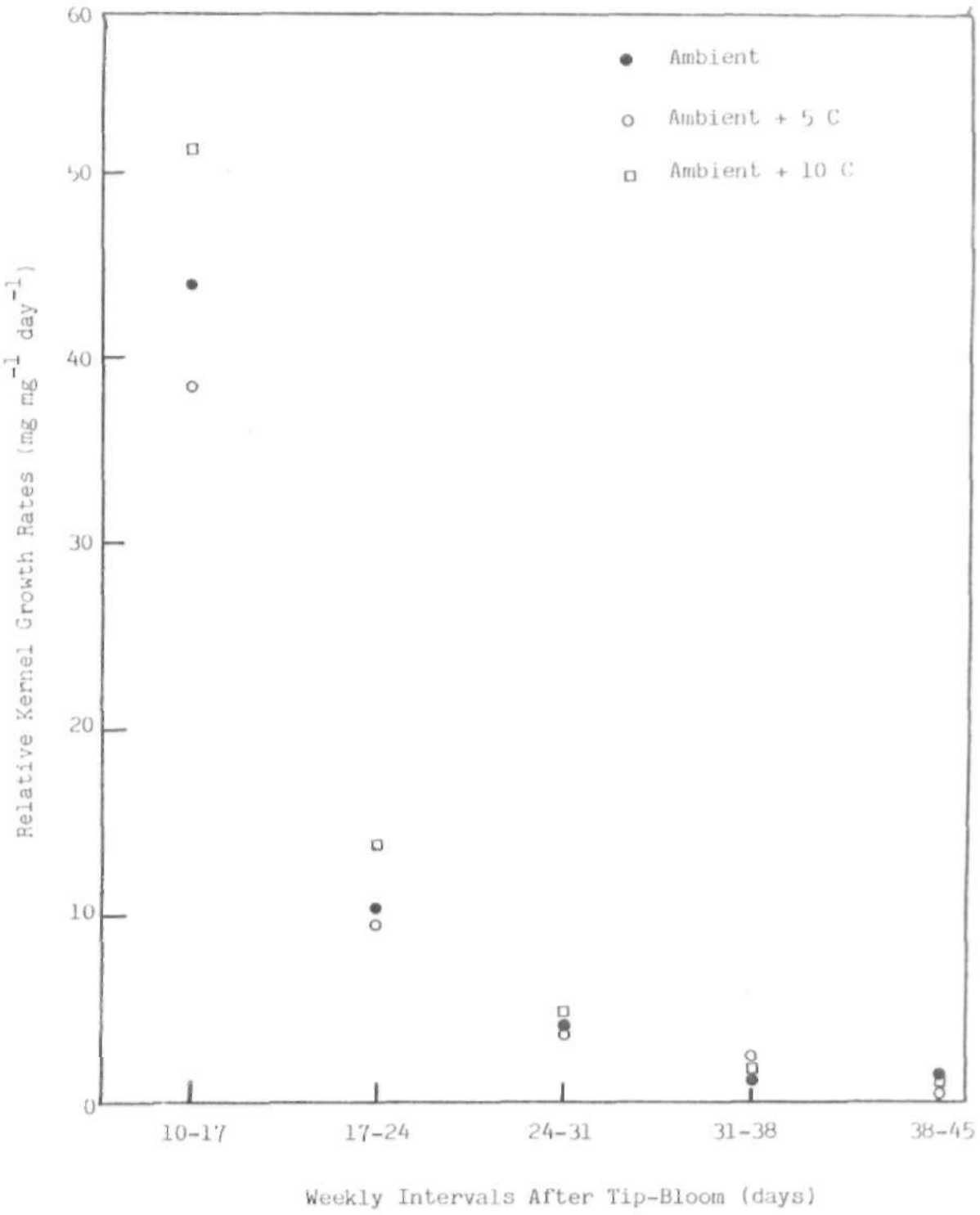


Fig. 11. The effect of two elevated night temperatures (5 and 10 C above ambient) on relative kernel growth rate of RS 671 grain sorghum at various weekly intervals after tip-bloom: Field Experiment V, 1979.

less significant in their effects to sink strength. Relative kernel growth rates were quite high during the first 2 weeks after bloom, dropped sharply during the week that followed, and began to drop gradually thereafter until about physiological maturity when rates were lowest (Fig. 11). Exposure of 'RS 671' grain sorghum plants to ambient +10 C night temperature during the first three-fourths of GS-2 period resulted in significantly higher relative kernel growth rates than during the last one-fourth of that period (Table 29), but significant differences among growth stages did not occur for the ambient +5 C night temperature treatment.

Agronomic Studies

Table A33 contains mean squares for grain yield and yield components extracted from separate analyses of variance. Effects of temperature treatments for the various growth stages during which they were imposed were highly significant for panicle dry weight, grain yield per plant, seed number per panicle, 1000-seed weight and grams grain/GS-3 day/plant, but temperature x growth stage interactions were significant only for panicle dry weight and seed number. These results were similar to those obtained from Experiment IV reported earlier.

Temperature Effects

Yield and yield components

Both the ambient +5 C and the ambient +10C night temperature treatments caused significant reductions in panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant (metabolic efficiency

Table 29. Relative kernel growth rates of RS 671 field grain sorghum exposed to two elevated night temperatures during five different growth stages (averaged over sampling dates and pretreatments): Experiment V, 1979.

Temperature[3] Treatment	Growth Stage				
	PI_1 to PI_7	PI_8 to FD_1	FD_1 to FD_7	FD_8 to $Bloom_1$	$Bloom_1$ to $Bloom_7$
	Relative Kernel Growth Rate[2] (mg x 10^{-2}/mg kernel/day)				
Ambient + 5 C	10.91 a	12.12 a	10.85 a	10.03 a	10.23 a
Ambient + 10 C	17.45 a	15.84 a	16.86 a	12.15 b	10.20 b
Mean[2]	14.18 a	13.98 a	13.85 a	10.09 b	10.22 b

[1]Values are means of two replications.

[2]Values followed by the same letter within a row are not significantly different at P=0.05.

[3]$LSD_{(.05)}$ for temperature treatment means within growth stages = 2.94.

estimate), while the higher temperature level (ambient +10 C) also caused a significant increase (about 15%) in 1000-seed weight (Table 30). Reductions in yield and yield components by 5 and 10 C temperature elevations were about 19% and 26% for panicle dry weight, 19% and 28% for grain yield, 19% and 34% for seed number and 19% and 28% for grams of grain/GS-3 day/plant, respectively. The considerable increase (approximately 15%) in seed weight caused by the higher temperature level could be associated rather strongly with the substantial decrease in seed number that resulted from that same treatment. This can be considered as an attempt by the plant to compensate for the decrease in seed number by increasing seed size; however, the degree of compensation was not sufficient to completely offset yield loss.

Dry matter partitioning to the grain during the GS-3 period was possibly a major limiting factor of grain yield under these temperature conditions. The differences in grain yield under the different temperature levels may, therefore, at least to some extent, be attributable to differences in grain (sink) size. Efficiency of dry matter partitioning or distribution *per se* may very well be the key factor, too, and may relate to number of sinks (seeds) attracting assimilate.

Plant growth and development

Temperature effects were significant for most of the attributes of plant growth and development measured in this experiment, namely, numbers of days to bloom and physiological maturity, length of GS-2 period and plant height but not on the length of GS-3 period (Table A34). The pretreatment and temperature x growth stage interactions

Table 30. Yield and yield components of RS 671 field grain sorghum as affected by two elevated night temperatures (5 and 10 C above ambient):[1] Experiment V, 1979.

	Temperature Treatment			$LSD_{(.05)}$
	Ambient	Ambient[2] + 5 C	Ambient[2] + 10 C	
Panicle dry weight (g)	83.1	67.1 (19.3)	61.7 (25.8)	4.85
Grain yield/plant (g)	66.9	53.9 (19.4)	48.2 (28.0)	3.64
Seeds/panicle	2659	2152 (19.1)	1764 (33.7)	154.4
1000-seed weight (g)	26.58	27.61 (+3.9)	30.42 (+14.5)	0.80
g Grain/GS-3 day per plant	2.09	1.70 (18.7)	1.51 (27.8)	0.12

[1]Means averaged over growth stages and pretreatments.

[2]Values in parentheses are percent reductions or percent increases (+) over the ambient (control).

were significant only for the number of days to bloom and length of GS-2 period.

Similar to observations made on Experiment IV, the degrees of reductions in the various attributes of plant growth and development were much more modest than those reductions caused in yield-related attributes. Surprisingly though, the numbers of days to bloom and physiological maturity and the length of GS-2 were higher or greater under the ambient +10 C treatment than under the ambient or ambient +5 C treatment (Table 31). A similar finding was reported on rice by Yoshida (1973) who claimed that heat caused delayed flowering. Perhaps the severe temperature treatment caused plants to go into some kind of dormancy, at least for a brief period. This explanation becomes more tenable if one considers the fact that the ambient +5 C treatment caused reductions in the numbers of days to bloom and physiological maturity and the length of GS-2 period. Friend et al (1963) found that increasing temperature between 10 and 30 C resulted in earlier anthesis in wheat, while acceleration of anthesis in grain sorghum by higher temperatures was also reported by Pasternak and Wilson (1969). With respect to plant height, the ambient +10 C treatment very significantly reduced it more than did the ambient +5 C treatment.

Preconditioning Effects

There were consistent positive effects of preconditioning on the various yield-related attributes, but such increases were significant only for panicle dry weight, seed number and grams of grain/GS-3 day/plant (Table 32). Preconditioning (averaged over temperature treatments)

Table 31. Effect of two elevated night temperatures (5 and 10 C above ambient) on some growth and developmental attributes of RS 671 field grain sorghum:[1] Experiment V, 1979.

	Temperature Treatment			LSD(.05)
	Ambient	Ambient + 5 C	Ambient + 10 C	
Days to bloom	59.2	58.7	60.3	0.39
Days to physiological maturity[2]	91.2	90.3	92.3	0.38
GS-2 duration (days)	28.2	27.7	29.3	0.39
GS-3 duration (days)	32.0	31.6	32.0	0.54
Plant height (cm)	116.2	113.0	106.2	1.45

[1]Means averaged over growth stages and pretreatments.

[2]Dark layer appearance at tip of middle panicle branches.

Table 32. *Effect of preconditioning (hardening) on grain yield and its components of RS 671 grain sorghum exposed to two elevated night temperatures: Field Experiment V, 1979.*

	Pretreatment[1]		LSD (.05)
	Control	Preconditioned[2]	
Panicle dry weight (g)	63.6	68.5 (7.7)	4.6
Grain yield/plant (g)	50.9	54.0 (6.1)	3.47
Seeds/panicle	1930	2115 (9.6)	147.2
1000-seed weight (g)	29.04	28.55 (-1.7)	0.76
g Grain/GS-3 day per plant	1.59	1.71 (6.4)	0.12

[1]Means averaged over growth stages and temperature treatments.

[2]Values in parentheses are percent increases or percent decrease (-) over the control (non-preconditioned).

resulted in about 8%, 6%, 10% and 6% increases in panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant, respectively. The effects of preconditioning on seed size were, for all practical purposes, negligible.

By comparing control and preconditioned plants under each of the two elevated night temperature treatments, it became more apparent that the degree of benefit from preconditioning for yield and yield components of 'RS 671' grain sorghum was a function of temperature treatment. Greater benefits from preconditioning were observed under the ambient +10 C treatment than under the ambient +5 C treatment (Table 33). That type of relationship was consistent for all the yield-related attributes measured in this experiment. The observation of greater benefits from preconditioning for the ambient +10 C treatment rather than for the ambient +5 C treatment was contrary to the observation made in Experiment IV. In that experiment, greater benefits from preconditioning were realized for the ambient +5 C treatment than for the ambient +10 C treatment (Table 19). This could, at least in part, be attributable to the significantly higher day ambient (37.5 C) and night ambient (20.4 C) temperatures that prevailed during Experiment IV in 1978 (Table A7) as against the lower day ambient (31.6 C) and the night ambient (18.5 C) temperatures that occurred during the experiment in 1979 (Table A11). This implies that the ambient +10 C treatment in 1979 (Experiment V) was less severe than the same treatment in 1978 (Experiment IV) as temperature treatments in both experiments were relative to prevailing ambient temperatures. Common to both experiments, however, was the fact that for either the lower or the higher temperature treatment, the

Table 33. Effect of preconditioning on the response of yield and yield components of RS 671 grain sorghum to two elevated night temperatures (means averaged over growth stages): Field Experiment V, 1979.

	Ambient	Pretreatment				$LSD_{(.05)}$
		Control		Preconditioned		
		Ambient + 5 C	Ambient + 10 C	Ambient + 5 C	Ambient + 10 C	
Panicle dry weight (g)	83.1	64.7	58.8	69.5	64.6	6.86
Grain yield/plant (g)	66.9	52.3	46.3	55.4	50.1	5.15
Seeds/panicle	2659	2130	1588	2174	1942	218.3
1000-seed weight (g)	26.58	27.12	31.30	28.09	29.55	1.13
g Grain/GS-3 day per plant	2.09	1.65	1.44	1.76	1.59	0.18

presence of some benefit from preconditioning was apparent and consistent, and substantial reductions in yield-related attributes always occurred from elevated night temperatures irrespective of preconditioning as against the ambient (Table 33).

Similar to observations made on Experiment IV, the effects of preconditioning on attributes of plant growth and development in this experiment were fairly negligible and of much less significance than on yield-related attributes (Table 34). There were virtually no significant effects of preconditioning on plant growth and development despite a tendency for these to be slightly enhanced by preconditioning.

Growth Stage Effects

Yield and yield components

Table 35 contains the rankings of the various growth stages for yield and yield components. The most critical growth stage was found to be a period of 7 days after floret differentiation (FD_1 to FD_7). This was consistently the case for every yield-related attribute considered in this experiment. The least sensitive growth stages were found to be during the first 7 days after panicle initiation and during 7 days after bloom (PI_1 to PI_7 and $bloom_1$ to $bloom_7$). It is interesting and noteworthy that the rankings of these growth stages were strikingly similar to those observed in Experiment IV the previous year (Tables 21 and 35). The magnitudes of reductions that were observed when elevated temperatures occurred during the most critical growth stage (FD_1 to FD_7) were approximately 21%, 25%, 38% and 26% for panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant, respectively. It is

Table 34. Effect of preconditioning on growth and developmental attributes of RS 671 grain sorghum exposed to two elevated night temperatures: Field Experiment V, 1979.

	Pretreatment[1]		$LSD_{(.05)}$
	Control	Preconditioned	
Days to bloom	59.2	59.8	0.37
Days to physiological maturity	91.2	91.4	0.36
GS-2 duration (days)	28.2	28.8	0.37
GS-3 duration (days)	32.0	31.6	0.52
Plant height (cm)	110.5	109.9	1.47

[1]Means averaged over growth stages and temperature treatments.

Table 35. Effect of plant growth stage on the response of yield and yield components of RS 671 grain sorghum to two elevated night temperatures (means averaged over temperatures and pretreatments):[1] Field Experiment V, 1979.

Growth Stage[2]	Panicle dry[3] weight (g)	Grain yield/ plant (g)	Seeds/ panicle	1000-seed weight (g)	g Grain/GS-3 day/plant
PI_1-PI_7	70.9 a (0)	55.9 a (0)	2142 ab (6.7)	27.56 c (+7.4)	1.76 a (0)
PI_8-FD_1	60.6 bc (14.5)	49.3 b (11.8)	1932 b (15.9)	29.85 b (+16.3)	1.58 a (10.2)
FD_1-FD_7	55.8 c (21.3)	41.9 c (25.0)	1430 c (37.7)	33.10 a (+29.0)	1.30 b (26.1)
FD_8-$Bloom_1$	66.6 ab (6.1)	53.1 ab (5.0)	1993 b (13.2)	28.92 b (+12.7)	1.64a (6.8)
$Bloom_1$-$Bloom_7$	68.1 ab (4.0)	55.1 ab (1.4)	2296 a (0)	25.66 d (0)	1.75 a (~0)

[1]Values in parentheses are percent reductions from the maximum or percent increases (+) from the minimum.

[2]Numbers in subscripts represent the number of days after panicle initiation (PI), floret differentiation (FD) or bloom when treatment commenced or terminated.

[3]Means followed by the same letter within a column are not significantly different at P=0.05.

probably safe to conclude that a period of 7 days preceding and 7 days after floret differentiation was the most vulnerable to elevated night temperatures. As usual, the most sensitive growth stage(s) produced the greatest seed weight, with as much as 29% increase occurring at FD_1 to FD_7. This observation further confirmed the hypothesis that a mechanism for compensation operates in cereals when under some form of environmental stress such as elevated temperatures.

Plant growth and development

The various growth stages differed significantly with respect to number of days to bloom, length of GS-2 period and plant height (Table A34).

When attributes of plant growth and development were considered and the various growth stages were ranked with respect to their respective vulnerability to elevated temperatures, a pattern identical to that for yield-related attributes emerged. As usual, a period of 7 days after floret differentiation (FD_1 to FD_7) consistently proved to be the most critical growth stage for all the growth attributes, while about 7 days after panicle initiation (PI_1 to PI_7) and 7 days after bloom ($bloom_1$ to $bloom_7$) proved to be the least sensitive growth stages in this experiment (Table 36). With respect to length of grain fill (GS-3) and plant height, PI_8 to FD_1 was the second most sensitive growth stage stage, while FD_8 to $bloom_1$ was in that category for numbers of days to bloom and physiological maturity and length of panicle expansion (GS-2).

Table 36. Effect of plant growth stage on the response of growth and developmental attributes of RS 671 grain sorghum to two elevated night temperatures (means averaged over temperatures and pretreatments):[1] Field Experiment V, 1979.

Growth stage[2]	Days to bloom	Days to physiol. maturity	GS-2 (days)	GS-3 (days)	Plant height (cm)
PI_1-PI_7	60.1 a	91.8 ab	29.1 a	31.8 a	115.0 a
PI_8-FD_1	60.7 a	92.0 a	29.7 a	31.3 b	106.1 c
FD_1-FD_7	57.6 c	89.8 c	26.6 c	32.3 ab	103.7 c
FD_8-$Bloom_1$	58.9 b	91.3 b	27.9 b	32.4 a	109.5 b
$Bloom_1$-$Bloom_7$	60.3 a	91.8 ab	29.3 a	31.4 ab	113.8 a

[1]Means followed by the same letter within a column are not significantly different at P=0.05.

[2]Numbers in subscripts present the numbers of days after panicle initiation (PI), floret differentiation (FD) or bloom when temperature treatments were either commenced or terminated.

Correlations

Grain yield had significant positive correlations with panicle dry weight (r= 0.98), seed number (r= 0.71) and grams of grain/GS-3 day/ plant (r= 0.79). The correlation between seed number and seed weight (r= -0.46) was negative and significant (Table A35). The correlations observed between grain yield and each of the various yield components and between seed number and seed size consistently followed trends common to all the experiments in the investigations reported here.

SUMMARY

Two greenhouse and three field experiments were conducted to study the effects of elevated night temperatures on the yield and growth of a grain sorghum (Sorghum bicolor (L.) Moench) hybrid. The genotype used in these investigations was the 'RS 671' (Redlan x Tx 415), an open-pedigree temperate-adapted grain sorghum. The phenological growth phase during which temperature treatments were imposed was the panicle development (GS-2) period.

Experiments I, II (greenhouse) and III (field) were designed to determine the response of grain sorghum to two elevated night temperatures and the growth stage during GS-2 period when the plant is most sensitive to elevated temperatures. Experiments IV and V (field) were conducted with the same objectives as those for Experiments I, II and III and also to determine the effect of artificial preconditioning on the plant's response to elevated night temperatures.

Experiment I

Plants were exposed to 26.5 and 32 C night temperatures at 4-day durations commencing from floret differentiation through bloom. The two elevated night temperatures caused significant reductions in grain yield and yield components except seed size that was enhanced (12%) by the 32 C treatment. Approximately 19%, 21%, 24% and 20% reductions in panicle dry weight, grain yield per plant, number of seeds per panicle and grams of grain/GS-3 day/plant, respectively, were caused by the 32 C treatment. The 26.5 C treatment also caused reductions in these

variables but to much lesser degrees. Numbers of days to physiological maturity, length of grain fill (GS-3), plant height and panicle exertion were significantly reduced by elevated temperatures.

Highly significant positive correlations were observed between grain yield and panicle dry weight (r= 0.98), seed number (r= 0.64) and seed weight (r= 0.30), while a significant negative correlation occurred between seed number and seed size (r= -0.44). Some degree of compensation by increased seed size for loss in seed number was apparent in this experiment.

Only in terms of seed number and seed size did the various 4-day growth stages differ significantly in their respective sensitivities to temperatures. Growth stages closer to floret differentiation were more sensitive to elevated temperatures than those closer to the bloom stage.

Experiment II

The main objectives of this greenhouse experiment were the same as those for Experiment I, differing only in that temperature treatments spanned the entire panicle development period (from panicle initiation through bloom) and sequential growth stages were of 5-day durations in Experiment II.

The ambient and the 26.5 C treatment did not differ in their effects on the variables measured as the average ambient night temperature during that period was 26.3 C. The 26.5 C treatment, in this case, can be considered ineffective. The 32 C treatment caused moderate reductions in panicle dry weight (7%), grain yield (7%), seed number

(18%) and harvest index (6%), but it caused about 23% increase in seed size. Temperature treatment reduced the length of grain fill (GS-3) period, grams of grain/GS-3 day/plant, plant height and panicle exertion significantly. The 32 C treatment decreased specific leaf area (SLA) and increased leaf weight ratio (LWR) and had no effect on total leaf area.

It was somewhat difficult to discern the most sensitive among the 5-day growth stages in this experiment. This might be conditioned by the higher-than-optimum ambient temperatures that prevailed during part of that period. However, the last growth stage of panicle development (PI_{26} to PI_{30}) seemed to be the least sensitive, at least with respect to seed number. It was, however, apparent that the second half of GS-2 period was more sensitive to elevated night temperatures than the first half was. The highest degrees of reductions in panicle dry weight, grain yield, seed number and harvest index occurred during that second half. Plants that were temperature treated throughout the GS-2 period were even less responsive than the second half. This could be suggestive of some degree of temperature preconditioning early in the GS-2 period. With regard to the effects of temperature treatments on plant growth and development, the growth stage immediately after floret differentiation (PI_{16} to PI_{20}) was the most sensitive.

Significant positive correlations were observed between grain yield and each yield component. As usual, seed number negatively correlated with seed size.

Experiment III

This field experiment was conducted with the same objectives as Experiment I with night temperature treatments being 26.5 C and 32 C as well. Six 4-day growth stages within floret differentiation through bloom were used in addition to three longer-duration growth stages in GS-2.

The lack of significant differences between the two temperature treatments for panicle dry weight, grain yield, seed number, 1000-seed weight and harvest index could be a result of brevity of treatment duration compounded by the dynamic nature of field conditions. However, each temperature treatment differed significantly from the control (ambient) in its effects on these variables, both temperatures having caused significant reductions with the exception of seed weight that was increased by the 32 C treatment. Approximately 13% and 15% reductions in panicle dry weight and grain yield were caused by the 26.5 C and the 32 C treatments, respectively, with seed number being reduced 10% by the 26.5 C and 14% by the 32 C treatments.

Even though the two night temperature levels did not differ significantly in their effects, they caused reductions in the numbers of days to bloom and physiological maturity and the lengths of panicle expansion and grain fill. There was a general tendency for elevated night temperatures to hasten plant development by shortening developmental growth stages. These reductions in panicle expansion and grain fill apparently accounted for the observed yield reduction.

The various growth stages differed significantly with regard to their respective sensitivities to the elevated night temperatures. The most sensitive growth stages were about 8 days preceding bloom stage (FD_{13} to FD_{16} and FD_{17} to FD_{20}). The greatest reduction in yield and yield components occurred when plants were treated during either of these growth stages.

Seed number and seed size were inversely related in this experiment, having a significant negative correlation (r= -0.35) between them. Grain yield had significant positive correlation with each of the yield components.

Experiment IV

This field experiment was conducted with the same objectives as Experiment I, but in addition, it was to determine the effect of artificial preconditioning ("heat hardening") on the response of grain sorghum to two levels of ambient night temperature elevations (5 C and 10 C above ambient). Night temperature treatments involved treating plants for 7-day periods (growth stages) from panicle initiation until 7 days after bloom.

The two elevated night temperatures caused considerable reductions in yield and yield components except seed weight that was increased. The 10 C above ambient treatment consistently caused greater reductions than the 5 C above ambient treatment. Approximately 18%, 19%, 30% and 17% reductions in panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant occurred under the ambient +10C treatment. Reductions in lengths of growth stages were not significant.

Although there were no significant effects of preconditioning on yield and yield components, there was a consistent tendency for preconditioning to increase these variables. Such preconditioning effects were much more apparent under the ambient +5 C treatment than under the ambient +10 C treatment. No effect of preconditioning was apparent for plant growth and development in this experiment.

The various growth stages (during which temperature treatments were imposed) differed quite significantly with regard to their respective temperature sensitivities. The greatest reductions in grain yield and yield components occurred during the first 7 days after floret differentiation (FD_1 to FD_7), compared with the least sensitive growth stage (7 days after bloom). Imposing temperature treatments during FD_1 to FD_7, the most sensitive growth stage, caused about 43%, 44%, 57% and 42% reductions for grain yield, panicle dry weight, seed number and grams of grain/GS-3 day/plant, respectively. This growth stage (FD_1 to FD_7) and about 7 days prior to bloom (FD_8 to bloom) were the most sensitive growth stages with respect to plant growth and development, at least for the numbers of days to heading and bloom and the length of panicle expansion period.

Apparently, as the plant develops from panicle initiation toward floret differentiation, its vulnerability to elevated night temperature increases until beyond 7 days after floret differentiation, when its tolerance starts to increase.

Significant positive correlations were observed between grain yield and each component of yield, while a significant negative correlation occurred between seed number and seed size ($r = -0.60$).

Experiment V

This field experiment was a repeat of Experiment IV with the exception of measurements of leaf heat tolerance, leaf carbon dioxide exchange and grain dry matter accumulation that were included in this experiment.

Preconditioning had no significant effects on leaf heat tolerance determined by the leaf-disc electrical conductivity method at various growth stages during the panicle development period. Leaf discs were heat treated at 53.5 C for 15 min on all test dates. Prevailing field weather conditions had significant impact on the levels of heat tolerance obtained on each test date, high heat injury occurring on cool, overcast days.

Previously imposed elevated night temperatures (5 C and 10 C above ambient treatments) had significant effects on leaf photosynthetic rates measured by a portable plexiglas chamber infrared gas analysis technique. On the first two dates, leaf photosynthetic rates were higher for plants treated with the ambient +5 C than for control (ambient) plants, but that relationship was reversed on three subsequent measurement dates. However, photosynthetic rates of plants treated with ambient +10 C temperature were consistently much lower than those of the control (ambient) and the ambient +5 C plants. Summarized for all measurement dates, the control (ambient) and the ambient +5 C treatment did not differ significantly, but the ambient +10 C treatment reduced leaf photosynthetic rates considerably. The overall mean photosynthetic rates for plants under the control, the ambient +5 C and the ambient

+10 C treatments were 33.5, 34.7 and 26.3 mg CO_2 dm^{-2} hr^{-1}, respectively.

Kernel dry weights, kernel growth rates and relative kernel growth rates measured at weekly intervals from 10 days after tip-bloom were significantly influenced by night temperature treatments. Kernel dry weight and kernel growth rate significantly increased with increasing night temperature during the linear grain growth phase but not close to physiological maturity stage. Relative kernel growth rates were enhanced by the ambient +10 C treatment during the first 3 weeks after bloom but not thereafter.

Both the ambient +5 C and the ambient +10 C treatments caused significant reductions in panicle dry weight, grain yield, seed number and grams of grain/GS-3 day/plant, but the higher temperature caused a significant 15% seed size increase. The ambient +5 C and the ambient +10 C treatments caused reductions of 19% and 26% in panicle dry weight; 19% and 28% in grain yield; 19% and 34% in seed number and 19% and 28% in grams of grain/GS-3 day/plant, respectively. The considerable increase in seed size can be associated with the considerable reduction in seed number by the higher temperature level.

Consistent positive effects of preconditioning were observed for panicle dry weight, seed number and grams of grain/GS-3 day/plant but not for grain yield.

The most sensitive growth stage was found to be a period of 7 days after floret differentiation (FD_1 to FD_7) and that was consistently the case for all yield-related attributes. The least sensitive growth stages were the first 7 days after panicle initiation (PI_1 to PI_7) and the first 7 days after bloom ($bloom_1$ to $bloom_7$). These conditions were

true for both yield and growth attributes and quite similar to those results obtained in Experiment IV.

Significant positive correlations were observed between grain yield and each yield component, while seed number negatively correlated with seed size ($r = -0.46$).

Based upon the results of this series of experiments, the following conclusions are in order:

1. Brief periods (a week or less) of elevated night temperatures are capable of causing yield reduction in grain sorghum.
2. Elevated night temperatures occurring during GS-2 period are more detrimental to yield than plant growth.
3. The plant's response to elevated temperatures is dependent on the growth stage at which they are imposed.
4. Artificial heat preconditioning provided only limited beneficial effects on the plant's response to elevated temperatures.
5. A period of up to about one week after floret differentiation (appearance of stamen and pistil primordia) appears to be the most sensitive growth stage during panicle development to elevated night temperatures in grain sorghum.

LITERATURE CITED

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Alexandrov, V. Ya. 1964. Cytophysiological and cytoecological investigations of heat resistance of plant cells toward the action of high and low temperature. Quart. Rev. Biol. 39: 35-37

Alofe, C. O., L. E. Schrader, and R. R. Smith. 1973. Influence of high day and variable night temperatures on nitrate reductase activity of young corn (Zea mays L.) plants. Crop Sci. 13: 625-629.

Amos, J. A., and R. L. Scholl. 1977. Effect of growth temperature on leaf nitrate reductase, glutamine synthetase, and NADH-glutamate dehydrogenase of juvenile maize genotypes. Crop Sci. 17: 445-448.

Asana, R. D., and A. D. Saini. 1962. Studies in the physiological analysis of yield. V. Grain development in relation to temperature, soil moisture, and changes with age in the sugar content of the stem and in the photosynthetic surface. Indian J. Plant Physiol. 5: 128-171.

Asana, R. D., and R. F. Williams. 1965. The effect of temperature stress on grain development in wheat. Aust. J. Agric. Res. 16: 1-13.

Baker, B. S. 1969. Growth and some metabolic responses of four perennial grass influenced by temperature. Ph.D. Thesis, West Virginia University. 89pp. (Diss. Abstr. 30: 2986-B. 1970).

Baker, B. S., and G. A. Jung. 1970a. Effect of environmental conditions on the growth of four perennial grasses. III. Nucleic acid concentration as influenced by day-night temperature combinations. Crop Sci. 10: 376-378.

Baker, B. S., and G. A. Jung. 1970b. Response of four perennial grasses to high temperature stress. Proc. 11th Grassld. Congr. pp. 499-502.

Baker, B. S., and G. A. Jung. 1972. Growth and metabolic changes in orchard grass during acclimation. Bot. Gaz. 133: 120-126.

Bauer, H., W. Larcher, and R. B. Walker. 1973. Influence of temperature stress on CO_2 gas exchange. pp. 557-586. In J. P. Cooper (ed.) Photosynthesis and Productivity in Different Environments. Cambridge Univ. Press, Cambridge.

Berry, J. 1975. Adaptation of photosynthetic processes to stress. Science 188: 644-650.

Bierhuizen, J. F. 1973. The effect of temperature on plant growth, development, and yield. pp. 89-98. In R. Slatyer (ed.) Plant Response to Climatic Factors. Proc. Uppsala Sympo. UNESCO, Paris.

Bjorkman, Olle. 1975. Photosynthetic responses of plants from habitats with contrasting thermal environments. II. Thermal stability of the photosynthetic apparatus in intact leaves. Carnegie Inst. Wash. Yearbook 74: 748-751.

Bjorkman, Olle, and J. Berry. 1973. High efficiency photosynthesis. Scientific Amer. 229: 80-93.

Bjorkman, Olle, and R. W. Pearcy. 1971. Effect of growth temperature on the temperature dependence of photosynthesis in vivo and on CO_2 fixation by carboxydismutase in vitro in C_3 and C_4 species. Carnegie Inst. Wash. Yearbook 70: 511-520.

Bjorkman, Olle, R. W. Pearcy, A. T. Harrison, and H. Mooney. 1972. Photosynthetic adaptation to high temperatures: A field study in Death Valley, California. Science 175: 786-789.

Bjorkman, Olle, J. Boynton, and J. Berry. 1976. Comparison of the heat stability of photosynthesis, chloroplast membrane reactions, photosynthetic enzymes, and soluble protein in leaves of heat-adapted and cold-adapted C_4 species. Carnegie Inst. Wash. Yearbook 75: 400-407.

Brouwer, R. A., A. Kleinendorst, and J. Th. Locher. 1973. Growth responses of maize plants to temperature. pp. 169-174. In R. O. Slatyer (ed.) Plant Responses to Climatic Factors. Proc. Uppsala Sympo. UNESCO, Paris.

Caddel, J. L., and D. E. Weibel. 1971. Effect of photoperiod and temperature on the development of sorghum. Agron. J. 63: 799-803.

Campbell, I. S., and D. E. McCloud. 1977. Growth and development of peanuts under sixteen temperature regimes. Agron. Abstr. p. 81

Chabot, B. F., and A. R. Lewis. 1976. Thermal acclimation of photosynthesis in northern red oak. Photosynthetica 10: 130-135.

Chinoy, J. J. 1947. Correlation between yield of wheat and temperature during ripening of grain. Nature 159: 442-444.

Chowdhury, S. I., and I. F. Wardlaw. 1978. The effect of temperature on kernel development in cereals. Aust. J. Agric. Res. 29: 205-223.

Clegg, M. D., and C. Y. Sullivan. 1976. A rapid method for measuring carbon dioxide concentrations. Agron. Abstr. p. 70.

Clegg, M. D., C. Y. Sullivan, and J. D. Eastin. 1978. A sensitive technique for the rapid measurement of carbon dioxide concentrations. Plant Physiol. 62: 924-926.

Cochran, W. G., and G. M. Cox. 1957. Experimental Designs (2nd edition). John Wiley and Sons, Inc., New York. 611pp.

Coffman, F. A. 1957. Factors influencing heat resistance in oats. Agron. J. 49: 368-373.

Cooper, J. P. 1973. Control of photosynthetic production in terrestrial system. pp. 593-621. In J. P. Cooper (ed.) Photosynthesis and Productivity in Different Environments. Cambridge Univ. Press, Cambridge.

Dexter, T., W. E. Tottingham, and L. F. Graber. 1932. Investigations of the hardiness of plants by measurement of electrical conductivity. Plant Physiol. 7: 63-78.

Downes, R. W. 1970. Effect of light intensity and leaf temperature on photosynthesis and transpiration in wheat and sorghum. Aust. J. Biol. Sci. 23: 775-782.

Downes, R. W. 1972. Effect of temperature on the phenology and grain yield of Sorghum bicolor. Aust. J. Agric. Sci. 23: 585-594.

Downs, R. J., and H. Hellmers. 1977. Environment and the Environmental Control of Plant Growth. Academic Press, New York. 145pp.

Duncan, W. G., and A. L. Hatfield. 1964. A method for measuring the daily growth of corn kernels. Crop Sci. 4: 550-551.

Duncan, W. G., D. L. Shaver, and W. A. Williams. 1973. Insolation and temperature effects on maize growth and yield. Crop Sci. 13: 187-191.

Eastin, J. D. 1972. Photosynthesis and translocation in relation to plant development. pp. 214-246. In N. G. P. Rao and L. R. House (eds.) Proc. Sorghum in Seventies Sympo., Hyderabad. Oxford and IBH Publishing Co., New Delhi.

Eastin, J. D. 1976. Temperature influence on sorghum yield. pp. 19-23. In H. D. Loden and D. Wilkinson (eds.) Proc. Thirty-first Ann. Corn and Sorghum Res. Conf., Amer. Seed Trade Assoc., Washington, D.C.

Eastin, J. D., Ian Brooking, and A. O. Taylor. 1976. Influence of temperature on sorghum respiration and yield. Agron. Abstr. p. 71.

Eastin, J. D., J. H. Hulquist, and C. Y. Sullivan. 1973. Physiologic maturity in grain sorghum. Crop Sci. 13: 176-178.

Eastin, J. D., and C. Y. Sullivan. 1969. Carbon dioxide exchange in compact and semi-open sorghum inflorescences. Crop Sci. 9: 165-166.

Emmerikh, F. D. 1973. Effect of adenine on heat resistance of tomatoes. Soviet Plant Physiol. 10: 1096-1098.

Federer, W. 1955. Experimental Design. The Macmillan Book Co., New York. 544pp.

Feldman, N. L. 1968. The effect of heat hardening on the heat resistance of some enzymes from plant leaves. Planta (Berl.) 78: 213-225.

Fischer, K. S., and G. L. Wilson. 1971. Studies of grain production in Sorghum vulgare. I. The contribution of pre-flowering photosynthesis to grain yield. Aust. J. Agric. Res. 22: 33-37.

Ford, M. A., and G. N. Thorne. 1975. Effects of variation in temperature and light intensity at different times on growth and yield of spring wheat. Ann. Appl. Biol. 80: 283-299.

Friend, D. J. C. 1965. Ear length and spikelet number of wheat grown at different temperatures and light intensities. Can. J. Bot. 43: 345-353.

Friend, D. J. C., J. E. Fisher, and V. A. Helson. 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. Can. J. Bot. 41: 1663-1674.

Friend, D. J. C., V. A. Helson, and J. E. Fisher. 1965. Changes in the leaf area ratio during growth of Marquis wheat as affected by temperature and light intensity. Can. J. Bot. 43: 15-28.

Fryer, H. C., A. W. Pauli, and F. C. Stickler. 1966. Temperature influence on anthesis date in grain sorghum, Sorghum vulgare Pers. Agron. J. 58: 9-12.

Gaastra, P. 1962. Photosynthesis of leaves and field crop. Neth. J. Agric. Sci. 10: 311-324.

Gallagher, J. N., P. V. Biscoe, and B. Hunter. 1976. Effects of drought on grain growth. Nature 264: 541-542.

Gipson, J. R., J. W. Johnson, and D. T. Rosenow. 1979. Effect of night temperature on phenotypic periods and yield components of grain sorghum. Agron. Abstr. p. 88.

Halse, N. J., and R. N. Weir. 1974. Effects of temperature on spikelet number of wheat. Aust. J. Agric. Res. 25: 687-695.

Henderson, K. E. 1969. Some effects of night temperature and photoperiod on growth and nitrogen constituents of alfalfa (Medicago sativa L.) roots and crowns. Ph.D. Thesis, University of Arizona. 130pp (Diss. Abstr. 30: 3948-B, 1970).

Heyne, E. G., and H. H. Laude. 1940. Resistance of corn seedlings to high temperatures in laboratory tests. J. Amer. Soc. Agron. 32: 116-126.

Hoshikawa, K. 1962. Studies on the ripening of wheat grain. 4. Influence of temperature upon the development of the endosperm. Proc. Crop Sci. Soc. Japan 30: 228-231.

Huxley, P. A., and R. J. Summerfield. 1976. Effects of daylength and day/night temperatures on growth and yield of cowpea cv 2809 grown in controlled environments. Ann. Appl. Biol. 83: 259-271.

Itai, C., and A. Benzioni. 1974. Regulation of plant response to high temperature. pp. 477-482. In R. L. Bielski, A. R. Ferguson, and M. M. Cresswell (eds.) Mechanisms of Regulation of Plant Growth. The Royal Soc. of New Zealand, Wellington, NZ. Bull. 12.

Ivory, D. A., and P. C. Whiteman. 1978. Effect of temperature on growth of five subtropical grasses. I. Effect of day and night temperature on growth and morphological development. Aust. J. Plant Physiol. 5: 139-147.

Jones, D. F. 1947. Effect of temperature on the growth and sterility of maize. Science 105: 390-391.

Karr, E. J., A. J. Linck, and C. A. Swanson. 1959. The effect of short periods of high temperature during day and night periods on pea yields. Amer. J. Bot. 46: 91-93.

Kinbacher, E. J., C. Y. Sullivan, and H. R. Knull. 1967. Thermal stability of malic dehydrogenase from heat-hardened Phaseolus acutifolius 'Tepary Buff.' Crop Sci. 7: 148-151.

Koffler, H., and G. O. Gale. 1957. The relative thermostability of cytoplasmic proteins from thermophilic bacteria. Arch. Biochem. Biophys. 67: 249-251.

Koffler, H., G. E. Mallett, and J. Adye. 1957. Molecular basis of biological stability to high temperatures. Proc. National Acad. Sci., USA 43: 464-477.

Lambert, R. G., and A. J. Linck. 1958. Effects of high temperature on yield of peas. Plant Physiol. 33: 347-350.

Lange, O. L. 1965. Leaf temperatures and methods of measurement. pp. 203-209. In F. E. Eckardt (ed.) Methodology of Plant Eco-physiology. Proc. Montpellier Sympo., UNESCO, Paris.

Langridge, J. 1963a. The genetic bases of climatic response. pp. 367-379. In L. T. Evans (ed.) Environmental Control of Plant Growth. Academic Press, New York.

Langridge, J. 1963b. Biochemical aspects of temperature response. Ann. Rev. Plant Physiol. 14: 441-462.

Langridge, J., and J. R. McWilliam. 1967. Heat response of higher plants. pp. 231-292. In A. H. Rose (ed.) Thermobiology. Academic Press, New York.

Laude, H. H. 1939. Diurnal cycle of heat resistance in plants. Science 89: 556-557.

Laude, H. M. 1964. Plant response to high temperatures. pp. 15-31. In M. Stelley and H. L. Hamilton (eds.) Forage Plant Physiology and Soil-Range Relationship. Amer. Soc. Agron., Madison, WI.

Laude, H. M., and B. A. Chaugule. 1953. Effect of stage of seedling development upon heat tolerance in bromegrass. J. Range Management 6: 320-324.

Lee, Kit-wah, R. C. Lommasson, and J. D. Eastin. 1974. Developmental studies on panicle initiation in sorghum. Crop Sci. 14: 80-84.

Leopold, A. C., and P. E. Kriedemann. 1976. Plant Growth Development. McGraw-Hill Book Co., New York. 545pp.

Levitt, J. 1956. The Hardiness of Plants. Academic Press, New York. 278pp.

Levitt, J. 1972. Responses of Plants to Environmental Stresses. Academic Press, New York. 697pp.

Levitt, J., C. Y. Sullivan, and E. Krull. 1960. Some problems in drought resistance. Bull. Res. Council, Israel 8D: 173-180.

Lomagin, A. G., T. A. Antropova, and A. Ilemete. 1963. Effect of heat hardening on the resistance of plant cells to various injurious agents. Tsitologiya 5: 142-150 (Biol. Abstr. 45: 106185, 1964).

Lundergardh, H. 1925. Cited by Brown, E. M. 1939. Some effects of temperature on the growth and chemical composition of certain pasture grasses. Missouri Agric. Exp. Sta. Res. Bull. 299. 76pp.

Maranville, J. W., and C. Y. Sullivan. 1976. Studies of nitrate reductase activity in sorghum in relation to heat stress. In The Development of Improved High-Yielding Sorghum Cultivars. Univ. of Nebraska, Lincoln. Ann. Report No. 9: 87-95.

Maun, M. A., C. L. Canode, and I. D. Teare. 1969. Influence of temperature during anthesis on seed set of Poa pratensis L. Crop Sci. 9: 210-212.

McWhorter, C. G., and T. N. Jordan. 1976. The effect of light and temperature on the growth and development of johnsongrass. Weed Sci. 24: 88-91.

Miller, F. R., J. W. Collier, and J. D. Smith. 1976. Relationship of seed size and seed number to yield of Sorghum bicolor L. Agron. Abstr. p. 57.

Mooney, H. A., and M. West. 1964. Photosynthetic acclimation of plants of diverse origin. Amer. J. Bot. 51: 825-827.

Moss, D. N., R. B. Musgrave, and R. E. Lemon. 1962. Photosynthesis under field conditions. III. Some effects of light, CO_2, temperature and soil moisture on photosynthesis, respiration and transpiration of corn. Crop Sci. 1: 83-87.

Muchow, R. C., and G. L. Wilson. 1976. Photosynthetic and storage limitations to yield in Sorghum bicolor (L. Moench). Aust. J. Agric. Res. 27: 489-200.

Munakata, K. 1976. Effects of temperature and light on the reproductive growth and ripening of rice. pp. 187-207. In Climate and Rice. Inter Rice Res. Instit. Sympo., 1974, Los Banos, Philippines.

Murata, Y. 1964. On the influence of solar radiation and air temperature upon the local differences in the productivity of paddy rice in Japan. Proc. Crop Sci. Soc., Japan 33: 59-63.

Nagato, K., and M. Ebata. 1965. Effects of high temperature during ripening period on the development and the quality of rice kernels. Proc. Crop Sci. Soc., Japan 34: 59-66.

Nel, P. C., and J. G. C. Small. 1973. Photoperiod and temperature effects on yield of four South African wheat cultivars. Agroplantae 5: 25-32.

Norcio, N. V., and C. Y. Sullivan. 1965. Effect of high temperature on the rate of photosynthesis and respiration of some sorghum and corn genotypes. In The Physiology of Yield and Management of Sorghum in Relation to Genetic Improvement. Univ. of Nebraska-Lincoln. Ann. Report No. 8: 113-117.

Norcio, N. V., and C. Y. Sullivan. 1976a. Effect of high temperature on photosynthesis rate of sorghum and corn genotypes. In The Development of Improved High-Yielding Sorghum Cultivars. Univ. of Nebraska-Lincoln. Ann. Report No. 9: 61-63.

Norcio, N. V., and C. Y. Sullivan. 1976b. Stomatal and non-stomatal inhibition of photosynthesis at high temperatures in sorghum. In The Development of Improved High-Yielding Sorghum Cultivars. Univ. of Nebraska-Lincoln. Ann. Report No. 9: 69-86.

Ogunlela, V. B. 1974. A field study of the heat and drought tolerance of grain sorghum (Sorghum bicolor (L) Moench) as an approach to genetic improvement. M.S. Thesis, The University of Nebraska, Lincoln. 93pp.

Onwueme, I. C. 1979. Rapid, plant-conserving estimation of heat tolerance in plants. J. Agric. Sci. 92: 527-536.

Onwueme, I. C., H. M. Laude, and R. C. Huffaker. 1971. Nitrate reductase activity in relation to heat stress in barley. Crop Sci. 11: 195-200.

Owen, P. C. 1971. Responses of a semi-dwarf wheat to temperatures representing a tropical dry season. II. Extreme temperatures. Expl. Agric. 7: 43-47.

Palis, R. K. 1971. Diurnal effects of high temperature stress on grain development in wheat. Ph.D. Thesis, Kansas State University, Manhattan. 70pp.

Palmer, A. F. E. 1973. Photoperiod and temperature effects on a number of plant characters in several races of maize grown in the field. pp. 113-119. In R. C. Slatyer (ed.) Plant Response to Climatic Factors. Proc. Uppsala Sympo., UNESCO, Paris.

Pasternak, D., and G. L. Wilson. 1969. Effects of heat waves on grain sorghum at the stage of head emergence. Aust. J. Expl. Agric. Anim. Husb. 9: 636-638.

Pearcy, R. W., J. A. Berry, and D. C. Fork. 1977. Effects of growth temperature on the thermal stability of the photosynthetic apparatus of Atriplex lentiformis (Torr.) Wats. Plant Physiol. 59: 873-878.

Pearson, C. J. 1975. Thermal adaptation of Pennisetum: Seedling development. Aust. J. Plant Physiol. 2: 413-424.

Pearson, C. J., and G. A. Derrick. 1977. Thermal adaptation of Pennisetum: Leaf photosynthesis and photosynthate translocation. Aust. J. Plant Physiol. 4: 763-769.

Peters, D. B., J. W. Pendleton, R. H. Hageman, and C. M. Brown. 1971. Effect of night air temperature on grain yield of corn, wheat, and soybeans. Agron. J. 63: 309.

Petinov, N. W., and U. G. Molotkovsky. 1959. The protective processes of heat-resistant plants. pp. 275-283. In Arid Zone Res. XVI. Plant-Water Relationships in Arid and Semi-arid Conditions. Proc. Madrid Sympo., UNESCO, Paris.

Potter, J. R. 1975. The effect of temperature on growth and partitioning of photosynthate. Plant Physiol. 56: suppl. 79.

Quinby, J. R., J. D. Hesketh, and R. L. Voight. 1973. Influence of temperature and photoperiod on floral initiation and leaf number in sorghum. Crop Sci. 13: 243-246.

Rathnam, C. K. M. 1978. Heat inactivation of leaf phosphoenolpyruvate carboxylase: protection of aspartate and malate in C_4 plants. Planta 14: 289-295.

Rascke, K. 1970. Temperature dependence of CO_2-assimilation and stomatal aperture in leaf sections of Zea mays L. Planta (Berl.) 91: 336-363.

Robson, M. J. 1973. The effect of temperature on the growth of S. 170 tall fescue (Festuca arundinacea). II. Independent variation of day and night temperatures. J. Appl. Ecology 10: 93-105.

Ruegg, J., and J. Nosberger. 1977. Influence of temperature on the phenological development, dry matter distribution, total non-structural carbohydrates and crude protein of Festuca pratensis Huds. Angew Botanik 51: 167-177.

Said, H., T. Hegazy, and R. M. Imam. 1967. Growth, productivity and compositional contents of bean (Vicia faba) seeds as affected by different night temperatures. Flora Abt. A, 158: 569-576.

Salmon, S. C. 1941. Climate and small grains. pp. 321-342. In Climate and Man. Yearbook of Agriculture, USDA. U.S. Government Printing Office, Washington, D.C.

Sato, K., K. Inaba, and M. Tozawa. 1973. High temperature injury of ripening in rice plant. I. The effects of high temperature treatments at different stages of development on the ripening. Proc. Crop Sci. Soc., Japan 42: 207-213.

Schroeder, C. A. 1963. Induced temperature tolerance of plant tissue in vitro. Nature 200: 1301-1302.

Schuster, W., and F. Okuyucu. 1976. The response of various sorghum cultivars to different daylengths and temperatures. Angew Botanik 50: 149-168.

Skerman, P. J. 1956. Heatwaves and their significance in Queensland's primary industries. Arid Zone Res. XI: 195-197.

Smith, D. H. 1973. Selected studies of heat tolerance in grain sorghum (Sorghum bicolor (L.) Moench). MS Thesis, Univ. of Nebraska-Lincoln. 46pp.

Specht, J. E., J. H. Williams, and J. R. Martineau. 1977. Temperature tolerance in soybeans—Artificial hardening effects. Agron. Abstr. p. 93.

Spiertz, J. H. J. 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. Neth. J. Agric. Sci. 22: 207-220.

Spiertz, J. H. J. 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant. Neth. J. Agric. Sci. 25: 182-197.

Steel, R. G., and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481pp.

Stoy, V. 1965. Photosynthesis, respiration and carbohydrate accumulation in spring wheat in relation to yield. Physiol. Plant Suppl. IV: 125pp.

Sullivan, C. Y. 1972. Mechanisms of heat and drought resistance in grain sorghums and methods of measurement. pp. 247-264. In N. G. P. Rao and L. R. House (eds.) Sorghum in Seventies. Oxford and IBH Publishing Co., New Delhi.

Sullivan, C. Y., and E. J. Kinbacher. 1967. Thermal stability of Fraction I protein from heat-hardened Phaseolus acutifolius Gray 'Tepary Buff.' Crop Sci. 7: 241-244.

Sullivan, C. Y., M. D. Clegg, and J. M. Bennett. 1976. A new portable method for measuring photosynthesis. Agron. Abstr. p. 77.

Sullivan, C. Y., D. H. Smith, and J. M. Bennett. 1977a. Effects of a short duration seedling heat stress on yield of grain sorghum. Proc. Tenth Grain Sorghum Res. and Utilization Conf. p 15.

Sullivan, C. Y., N. V. Norcio, and J. D. Eastin. 1977b. Plant responses to high temperatures. pp. 301-317. In A. Muhammed, R. Aksel, and R. C. von Borstel (eds.) Genetic Diversity in Plants. Plenum Publishing Corp., New York.

Taylor, G. A., and K. J. Frey. 1972. Influence of temperature at various growth stages of oat cultivars. I. Utilization of controlled environment chambers, climatological data and developmental growth stages. Crop Sci. 12: 450-453.

Threshow, M. 1970. Environment and Plant Response. McGraw-Hill Book Co., New York. pp. 51-76.

Wardlaw, I. F. 1970. The early stages of grain development in wheat: Response to light and temperature in a single variety. Aust. J. Biol. Sci. 23: 765-774.

Wardlaw, I. F. 1974. Temperature control of translocation. pp. 533-538. In R. L. Bieleski, A. R. Ferguson, and M. M. Cresswell (eds.) Mechanisms of Regulation of Plant Growth. The Royal Soc. of New Zealand, Wellington, NZ. Bull. 12

Warrington, I. J., R. L. Dunstone, and L. M. Green. 1977. Temperature effects at three development stages on the yield of the wheat ear. Aust. J. Agric. Res. 28: 11-27.

Warrington, I., M. Peet, D. Patterson, J. Bunce, and H. Hellmers. 1976. Physiological response of soybean to thermoperiod in relation to growth. Plant Physiol. 57: Suppl. 105.

Watson, D. J. 1963. Climate, weather and plant yield. pp. 337-350. In L. T. Evans (ed.) Environmental Control of Plant Growth. Academic Press, New York.

Wattal, P. N. 1965. Effect of temperature on the development of the wheat grain. Indian J. Plant Physiol. 8: 145-149.

Went, F. W. 1944. Plant growth under controlled conditions. III. Correlation between various physiological processes and growth in the tomato plant. Amer. J. Bot. 31: 597-618.

Went, F. W. 1948. Thermoperiodicity. pp. 145-157. In A. E. Murneek and R. O. Whyte (eds.) Vernalization and Photoperiodism. Chronica Botanica, Waltham, MA.

Went, F. W. 1950. The response of plants to climate. Science 112: 489-494.

Wilsie, C. P. 1962. Crop Adaptation and Distribution. W. H. Freeman, San Francisco. 448pp.

Wilson, J. W. 1966. Effect of temperature on net assimilation rate. Ann. Bot. 30: 753-761.

Wilson, J. H., M. St. Cloves, and J. C. S. Allison. 1973. Growth and yield of maize at different altitudes in Rhodesia. Ann. Appl. Biol. 73: 77-84.

Winter, S. R., and J. W. Pendleton. 1970. Results of changing light and temperature effects on the apparent photosynthesis of individual leaves. Agron. J. 62: 181-184.

Yamamoto, K. 1954. Cited by S. Yoshida. 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23: 437-464.

Yarwood, C. E. 1961a. Acquired tolerance of leaves to heat. Science 134: 941-942.

Yarwood, C. E. 1961b. Translocated heat injury in plants. Nature 192: 887.

Yarwood, C. E. 1962. Acquired sensitivity of (Phaseolus vulgaris var. Pinto) leaves to heat. Plant Physiol. Suppl. 37: 70.

Yarwood, C. E. 1967. Adaptation of plants and plant pathogens to heat. pp. 75-92. In C. L. Prosser (ed.) Molecular Mechanisms of Temperature Adaptation. Publication No. 84. Amer. Assoc. Advance. Science, Washington, D.C.

Yoshida, S. 1973. Effects of temperature on growth of the rice plant (Oryza sativa L.) in a controlled environment. Soil Sci. Plant Nutr. 19: 299-310.

APPENDIX

Table A1. Composition of the modified Hoagland-Arnon nutrient solution.[a]

Compound	Amount (g/l)	Nutrient Element Supplied
KNO_3	0.706	K
$Ca(NO_3)_2$	0.950	Ca
45% P_2O_5	0.325	P
$MgSO_4$	0.120	Mg
NH_4SO_4	0.084	N
KCl	0.004	Cl
Iron Chelate (10% Fe) (Sequestrene 330 Fe; Ciba-Geigy)	0.060	Fe
H_3BO_3	0.00155	B
$MnSO_4 \cdot H_2O$	0.00085	Mn
$ZnSO_4 \cdot H_2O$	0.00058	Zn
$CuSO_4 \cdot 5H_2O$	0.00013	Cu
$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.00016	Mo

[a]C. Y. Sullivan, personal communication.

Table A2. Greenhouse ambient temperatures during Experiment I (1977) summarized by growth periods (stages).

Growth Period	Ambient Temperature (C)		
	Maximum	Minimum	Mean
FD_1 to FD_4	38.4	20.4	29.4
FD_5 to FD_8	35.8	21.4	28.6
FD_9 to FD_{12}	35.6	21.2	28.4
FD_{13} to FD_{16}	34.0	27.0	30.5
FD_1 to Bloom	36.0	22.3	29.2
Mean	36.0	22.5	29.2

Table A3. Greenhouse ambient temperatures during Experiment II (1978) summarized by growth periods (stages).

Growth Period	Ambient Temperature (C)		
	Maximum	Minimum	Mean
PI_1 to PI_5	32.6	22.6	27.6
PI_6 to PI_{10}	33.4	23.0	28.2
PI_{11} to PI_{15}	37.2	32.0	34.6
PI_{16} to PI_{20}	39.6	27.5	33.6
PI_{21} to PI_{25}	33.0	31.6	32.3
PI_{26} to PI_{30}	39.0	26.3	32.6
PI_1 to FD_1	33.8	23.3	28.5
FD_1 to Bloom	37.0	25.8	31.4
PI_1 to Bloom	35.4	24.6	30.0
Mean	35.7	26.3	31.0

Table A4. Field ambient temperatures during Experiment III (1977) summarized by growth periods (stages).

Growth Period	Ambient Temperature (C)		
	Maximum	Minimum	Mean
FI_1 to FD_1	35.7	17.7	26.7
FI_1 to Bloom	36.2	21.2	28.7
FD_1 to Bloom	36.0	20.8	28.4
FD_1 to FD_4	34.5	22.2	28.4
FD_5 to FD_8	37.2	26.4	31.8
FD_9 to FD_{12}	36.5	23.3	29.9
FD_{13} to FD_{16}	35.3	16.3	25.8
FD_{17} to FD_{20}	35.6	16.2	25.9
Mean	35.9	20.5	28.2

Table A5. Climatic data for 1977 for the University of Nebraska farm at Lincoln.[1]

Month	% RH	Ambient Temperature (C)				
		Ave. Max.	Ave. Min.	Mean	Highest (date)	Lowest (date)[2]
May	76-82	26.2	15.4	20.8	31 (17)	10 (10)
June	71-79	30.1	18.6	24.3	37 (6)	13 (7)
July	66-74	33.2	21.7	27.4	38 (18)	14 (1)
August	79-85	28.3	18.0	23.2	34 (27)	13 (11)
September	84-87	25.6	15.2	20.4	31 (9)	10 (26)
October	84-87	17.4	7.6	12.5	26 (27)	0 (12)

[1]Nebraska Climatological Data, Vol. 82, 1977. National Climatic Center, Asheville, North Carolina.

[2]Figures in parentheses are dates of the month the highest or lowest ambient temperatures occurred.

Table A6. Maximum and minimum daily ambient air temperatures (C) at the University of Nebraska-Lincoln for May through September, 1977.[1]

Day of Month	May		June		July		August		September	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	18	14	26	16	27	14	29	16	28	18
2	26	13	29	13	32	22	33	18	27	17
3	26	16	28	19	33	23	31	20	23	18
4	25	18	29	22	37	25	33	19	27	21
5	28	14	36	23	36	25	32	20	27	20
6	26	16	37	18	37	26	27	18	27	17
7	26	11	26	13	37	21	31	18	31	18
8	24	16	29	18	32	21	34	26	31	21
9	23	13	36	15	32	17	30	19	31	13
10	24	10	25	19	31	19	27	19	24	13
11	22	11	37	22	32	17	24	13	26	13
12	25	13	32	20	28	20	26	15	27	18
13	28	15	24	18	32	24	28	19	23	16
14	27	17	23	16	37	24	27	18	22	11
15	29	16	30	20	37	22	21	16	23	10
16	29	16	34	21	32	24	33	19	21	14
17	31	16	32	20	36	26	22	16	28	17
18	27	19	29	18	38	27	27	16	27	19
19	29	16	29	17	37	27	25	17	26	10
20	24	16	31	19	37	26	30	17	21	12
21	25	15	29	16	37	22	30	18	23	13
22	23	13	22	16	27	21	26	17	27	14
23	25	14	27	20	30	23	23	16	24	14
24	28	18	30	21	34	24	27	14	27	16
25	29	19	31	19	37	22	26	18	27	16
26	29	21	32	19	29	15	29	19	25	10
27	29	18	34	22	26	17	34	24	27	11
28	23	15	35	22	30	19	30	17	22	14
29	29	17	27	14	31	18	26	14	21	16
30	28	18	31	20	34	21	27	21	25	16
31	22	14	--	--	36	17	31	18	--	--
$\bar{X}$	26.2	15.4	30.1	18.6	33.2	21.7	28.3	18.0	25.6	15.2

[1]Nebraska Climatological Data, Vol. 82, 1977. National Climatic Center, Asheville, North Carolina.

Table A7. Ambient field temperatures during Experiment IV (1978) summarized by growth periods.

Growth Period	Ambient Temperature (C)		
	Maximum	Minimum	Mean
PI_1 to PI_7	32.7	24.0	28.3
PI_8 to FD_1	42.0	23.0	32.5
FD_1 to FD_7	35.6	19.7	25.7
FD_8 to $Bloom_1$	38.3	18.7	28.5
$Bloom_1$ to $Bloom_7$	39.0	16.6	27.8
Mean	37.5	20.4	28.6

Table A8. Climatic data for 1978 for the University of Nebraska farm at Lincoln.[1]

Month	% RH	Ambient Temperature (C)				
		Ave. Max.	Ave. Min.	Mean	Highest (date)	Lowest (date)[2]
May	81-88	21.5	11.6	16.6	33 (25)	2 (2)
June	79-88	29.0	17.8	23.4	39 (17)	8 (8)
July	79-86	30.8	20.1	25.4	38 (6)	14 (23)
August	77-84	31.0	19.1	25.1	38 (14)	11 (4)
September	80-86	27.6	15.9	21.8	36 (8)	7 (21)
October	72-78	19.2	5.8	12.5	29 (21)	0 (28)

[1]Nebraska Climatological Data, Vol. 83, 1978. National Climatic Center, Asheville, North Carolina.

[2]Figures in parentheses are dates of the month the highest or lowest ambient temperatures occurred.

Table A9. Maximum and minimum daily ambient air temperatures (C) at the University of Nebraska, Lincoln, for May through September, 1978.

Day of Month	May		June		July		August		September	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	14	7	18	12	36	22	29	19	33	18
2	14	2	19	10	32	21	28	20	31	17
3	16	4	26	14	34	21	28	16	32	19
4	14	8	26	13	35	24	24	11	33	20
5	13	7	27	13	38	27	26	14	33	19
6	17	6	28	17	38	20	28	19	35	19
7	10	7	26	16	27	19	31	18	35	18
8	14	8	22	8	29	18	33	21	33	19
9	15	8	26	14	29	22	35	19	32	17
10	22	11	31	20	24	16	32	19	32	17
11	27	17	33	21	24	16	30	19	33	23
12	25	16	33	16	26	19	31	18	31	21
13	18	9	27	14	36	21	33	22	23	12
14	22	8	31	20	28	20	38	26	26	11
15	24	9	34	23	30	19	36	19	28	16
16	23	9	37	24	32	22	26	16	29	14
17	21	11	39	25	35	25	32	21	18	12
18	22	13	30	17	36	22	36	21	31	18
19	25	17	30	18	32	21	24	13	26	13
20	28	13	32	16	33	21	27	16	14	9
21	21	10	24	13	29	21	29	21	21	4
22	25	14	28	18	27	19	35	24	22	7
23	18	17	22	18	23	14	36	25	24	7
24	24	17	28	21	27	16	37	24	28	11
25	33	19	33	24	29	22	37	22	26	10
26	32	19	35	21	35	21	36	24	26	10
27	28	16	31	19	31	19	32	21	23	9
28	23	16	29	21	30	18	31	18	25	8
29	27	13	35	24	35	22	27	14	18	11
30	22	13	35	25	27	17	24	14	20	9
31	28	13	--	--	27	19	28	17	--	--
$\bar{X}$	21.5	11.6	29.0	17.8	30.8	20.1	31.0	19.1	27.3	13.8

[1]Nebraska Climatological Data, Vol. 83, 1978. National Climatic Center, Asheville, North Carolina.

Table A10. Percent relative humidities recorded at the experimental site during various treatment periods (growth stages) in 1979, Experiment V.

Treatment Period	% Relative Humidity[1]		
	08:00 am	20:00 pm	Mean
PI_1 to PI_7	72	79	76
PI_8 to FD_1	90	85	88
FD_1 to FD_7	87	78	83
FD_8 to $Bloom_1$	69	70	70
$Bloom_1$ to $Bloom_7$	69	81	75

[1]Values are averages for seven-day periods.

Table A11. Field ambient temperatures during Experiment V in 1979 summarized by growth periods.

Growth Period	Ambient Temperature (C)		
	Maximum	Minimum	Mean
PI_1 to PI_7	31.0	15.6	23.3
PI_8 to FD_1	33.9	19.1	26.5
FD_1 to FD_7	31.9	19.1	25.5
FD_8 to $Bloom_1$	37.4	24.1	30.8
$Bloom_1$ to $Bloom_7$	24.0	14.8	19.4
Mean	31.6	18.5	25.1

Table A12. Mean squares for panicle dry weight, grain yield per plant, number of seeds per panicle, 1000-seed weight, number of primary panicle branches, and threshing percent of RS 671 grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development: Greenhouse Experiment I, 1977.

Source of variation	d.f.	Dry weight of panicle	Grain yield per plant	Seeds per panicle	1000-seed weight	No. of pan. branches	Threshing %
Check vs others	1	453.26**	321.75**	1,037,475.93**	7.15	12.02	61.28**
Temperature (T)	1	1037.81**	692.60**	800,309.16**	14.89	1069.29**	0.88
Stage (S)	4	587.06**	334.64**	3,089,996.64**	332.74**	1290.33**	48.70**
T x S	4	894.04**	711.02**	959,221.41**	38.75*	773.67**	57.82**
Residual	90	60.10	51.06	81,331.65	11.76	29.58	8.72
Total	109	133.12	105.02	239,777.94	25.90	112.44	13.27
CV %		16.09	19.07	16.26	15.28	9.52	3.62

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A13. Mean squares for panicle length, panicle exertion, grams of grain per GS-3 day, days to physiological maturity, duration of grain fill (GS-3) and plant height of RS 671 grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development: Greenhouse Experiment I, 1977.

Source of variation	d.f.	Panicle length	Panicle exertion	Grams grain/ GS-3 day/plant	Days to maturity	Duration of grain fill	Plant height
Check vs others	1	33.51**	175.20**	0.281*	29.45**	10.80	1579.20**
Temperature (T)	1	20.25**	56.44**	0.416**	88.36**	56.25**	1398.76**
Stage (S)	4	67.11**	73.95**	0.254**	78.83**	47.31**	1019.12**
T x S	4	26.73**	91.95**	0.670**	14.79**	12.95*	404.44**
Residual	90	2.11	8.02	0.052	3.02	4.15	40.15
Total	109	5.81	20.11	0.095	7.41	6.69	115.08
CV %		7.18	23.59	19.33	1.78	6.38	5.66

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A14. Mean squares for dry weights of laminae, sheaths, stem, panicle and aboveground plant total of RS 671 grain sorghum as affected by two night temperatures imposed at certain growth stages during panicle development:[1] Greenhouse Experiment I, 1977.

Source of variation	d.f.	Laminae	Sheaths	Stem	Panicle	Aboveground plant total
Check vs others	1	5.63	0.25	23.59*	172.43	471.65*
Temperature (T)	1	8.62*	7.44**	82.11**	377.73**	970.72**
Stages (S)	4	4.62	2.96*	19.15*	417.30**	932.36**
T x S	4	1.05	3.45**	27.06**	702.26**	962.57**
Residual	30	1.99	0.79	4.90	47.42	71.53
Total	43	2.46	1.38	10.26	158.38	269.84
CV %		9.47	9.51	11.97	13.86	9.19

[1]Dry weights determined after physiological maturity.

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A15. Mean squares for dry weight of roots and shoot:root ratio of RS 671 grain sorghum as affected by two night temperatures imposed at certain growth stages during panicle development: Greenhouse Experiment I, 1977.

Source of variation	d.f.	Root dry weight	Top:root ratio
Check vs others	1	4.015	0.465
Temperature (T)	1	7.944	0.484
Stage (S)	4	70.403**	14.716**
T x S	4	66.358**	26.702**
Residual	38	10.296	2.294
Total	52	19.132	5.035
CV %		31.34	31.19

** denotes significance at P=0.01.

Table A16. Partial correlation coefficients determined among grams of grain per GS-3 day, panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight, and threshing percent of RS 671 grain sorghum hybrid: Greenhouse Experiment I, 1977.

	Panicle dry weight	Grain yield/ plant	Seeds/panicle	1000-seed weight	Threshing %
Grain dry weight/GS-3 day	0.941**	0.933**	0.642**	0.247*	0.600**
Panicle dry weight	---	0.983**	0.683**	0.244*	0.598**
Grain yield/plant		---	0.636**	0.295**	0.674**
Seeds/panicle			---	-0.442**	0.331**
1000-seed weight				---	0.263*

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A17. Mean squares for panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight, number of primary panicle branches, and harvest index of RS 671 grain sorghum as affected by two night temperatures imposed during various growth stages during panicle development: Greenhouse Experiment II, 1978.

Source of variation	d.f.	Dry weight of panicle	Grain yield per plant	Seeds per panicle	1000-seed weight	Panicle branches	Harvest index
Check vs others	1	18.29	22.99	233341	83.17*	91.37	0.0036
Temperature (T)	1	690.99**	423.88**	4932471**	665.43**	46.69	0.0120**
Stage (S)	8	305.81**	255.69**	915413**	129.05**	92.94	0.0069**
T x S	8	274.22**	244.72**	32110**	48.38**	39.99	0.0080**
Residual	126	68.69	7759.60	59847	13.70	47.94	0.0010
Total	151	98.04	85.83	152905	26.42	48.45	0.0019
CV %		15.11	16.25	13.54	13.60	10.81	6.81

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A18. Mean squares for panicle length, panicle exertion, grams of grain per GS-3 day, threshing percent, and plant height of RS 671 grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development: Greenhouse Experiment II, 1978.

Source of variation	d.f.	Panicle length	Panicle exertion	Grams grain/ GS-3 day/plant	Threshing %	Plant height
Check vs others	1	3.58	348.95**	0.0014	3.54	722**
Temperature (T)	1	2.20	421.28**	0.3203*	29.94**	459**
Stage (S)	8	31.39**	352.75**	0.2585**	33.95**	1440**
T x S	8	20.62**	45.36**	0.2465**	12.58**	92*
Residual	126	2.36	11.21	0.0769	523.30	5370
Total	151	4.88	36.06	0.1008	6.42	128
CV %		6.62	31.15	16.92	2.32	5.71

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A19. Mean squares for durations of panicle expansion (GS-2) and grain fill (GS-3), and numbers of days to heading, bloom and physiological maturity as affected by two night temperatures imposed at various growth stages during panicle development: Greenhouse Experiment II, 1978.

Source of variation	d.f.	GS-2	GS-3	Heading	Bloom	Physiological maturity
Check vs others	1	5.26	5.09	3.95	5.26	0.01
Temperature (T)	1	21.78**	14.69**	26.69**	21.77**	1.17
Stage (S)	8	9.03**	2.44	5.81*	9.03**	9.94*
T x S	8	11.62**	5.38**	9.18**	11.62**	2.10
Residual	126	272.05	166.24	333.09	272.05	194.54
Total	151	3.15	1.93	62.43	3.15	2.03
CV %		5.34	3.88	3.09	2.55	1.43

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A20. Mean squares for total leaf area, specific leaf area, leaf weight ratio, leaf:stem ratio and leaf area ratio of RS 671 grain sorghum as affected by two night temperatures imposed at various growth stages during panicle development: Greenhouse Experiment II, 1978.

Source of variation	d.f.	Total leaf area	Specific leaf area	Leaf weight ratio	Leaf:stem ratio	Leaf area ratio
Check vs others	1	1.77	0.0065	0.00002	2.59	0.0001
Temperature (T)	1	3.16	0.0897**	0.0032**	0.49	0.0005
Stage (S)	8	16.68*	0.0550**	0.0019**	1.47	0.0046**
T x S	8	8.40	0.0175	0.0011*	1.25	0.0026
Residual	54	6.73	0.0098	0.0231	86.31	0.0016
Total	75	7.73	0.0166	0.0005	1.49	0.0020
CV %		10.59	5.61	8.92	18.19	6.67

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A21. Partial correlation coefficients determined among grain dry weight per GS-3 day, panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight, and harvest index of RS 671 grain sorghum hybrid: Greenhouse Experiment II, 1978.

	Panicle dry weight	Grain yield/ plant	Seeds/panicle	1000-seed weight	Harvest index
Grain dry weight/GS-3 day	0.951**	0.955**	0.557**	0.553**	0.747**
Panicle dry weight	---	0.994**	0.631**	0.514**	0.766**
Grain yield/plant		---	0.568**	0.576**	0.796**
Seeds/panicle			---	-0.278**	0.453**
1000-seed weight				---	0.426**

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A22. Mean squares for panicle dry weight, grain yield/plant, number of seeds per panicle, 1000-seed weight, harvest index and panicle length of RS 671 grain sorghum as affected two night temperatures imposed during various growth stages: Field Experiment III, 1977.

Source of variation	d.f.	Panicle dry weight	Grain yield per plant	Seeds per panicle	1000-seed weight	Harvest index	Panicle length
Check vs others	1	2415.53**	2073.46**	1,864,078.8*	0.471	0.0057**	10.31*
Temperature (T)	1	354.71	170.42	818,818.2	15.750	0.0010	0.56
Stage (S)	7	1076.51**	733.58**	3,403,059.2**	146.281*	0.0055**	14.57**
T x S	7	265.53	204.08	482,817.6	67.930*	0.0023*	2.62
Residual	144	305.94	232.36	326,366.2	8.700	0.0008	2.40
Total	169	338.04	255.34	457,109.3	16.149	0.0011	2.91
CV %		17.40	17.25	18.01	10.18	5.67	6.80

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A23. Mean squares for number of days to heading, bloom and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3), and plant height of RS 671 grain sorghum as affected by two night temperatures: Field Experiment III, 1977.

Source of variation	d.f.	Heading	Bloom	Physiological maturity	GS-2	GS-3	Plant height
Check vs others	1	3.459	20.476**	93.388**	20.30**	28.41**	185.85**
Temperature (T)	1	0.306	10.000*	87.025**	9.51*	28.90**	170.16**
Stage (S)	7	4.635**	10.243**	99.014**	10.28**	58.19**	210.76**
T x S	7	5.366**	10.139**	23.428**	10.06**	11.59**	63.63**
Residual	144	1.083	1.851	4.690	1.83	3.56	17.93
Total	169	1.451	2.654	10.260	2.63	6.37	29.27
CV %		1.49	1.80	1.88	4.92	4.75	4.08

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A24. Partial correlation coefficients determined among durations of panicle expansion (GS-2) and grain fill (GS-3), panicle dry weight, grain yield per plant, number of seeds per panicle and 1000-seed weight of RS 671 grain sorghum hybrid: Field Experiment III, 1977.

	GS-3 duration	Panicle dry weight	Grain yield per plant	Seeds per panicle	1000-seed weight
GS-2 duration	-0.085	0.352**	0.373**	0.130	0.329**
GS-3 duration	---	0.387**	0.361**	0.580**	-0.401**
Panicle dry weight		---	0.988**	0.835**	0.161
Grain yield/plant			---	0.816**	0.192*
Seeds/panicle				---	-0.347**

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A25. Mean squares for panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight, grams of grain/GS-3 day, and panicle length of RS 671 grain sorghum as influenced by two night temperatures imposed during various growth stages during panicle development: Field Experiment IV, 1978.

Source of variation	d.f.	Panicle dry weight	Grain yield per plant	Seeds per panicle	1000-seed weight	Grams grain/ GS-3 day/plant	Panicle length
Block	2						
Temperature (T)	1	1332.93**	889.04**	3,576,553**	310.67**	0.691**	20.18*
Stage (S)	4	1373.87**	865.33**	2,525,917**	124.49**	0.668**	13.72*
T x S	4	190.47	151.96	155,444	17.01	0.125	4.72
Pretreatment	1	332.911	162.56	124,193	17.04	0.092	2.29
Residual	20	66.72	37.27	106,288	8.09	0.031	2.38
Total	65	215.01	142.08	373,471	24.04	0.109	4.00
CV %		14.73	16.32	18.74	10.36	14.36	7.46

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A26. Mean squares for number of days to heading, bloom, and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3), and plant height of RS 671 grain sorghum as influenced by two night temperatures imposed at various growth stages during panicle development: Field Experiment IV, 1978.

Source of variation	d.f.	Heading	Bloom	Physiological maturity	GS-2	GS-3	Plant height
Block	2						
Temperature (T)	1	0.1927	6.208	13.16	2.321	36.038	83.54
Stage (S)	4	4.2625	15.541**	296.36	14.350**	16.957	309.87**
T x S	4	1.3610	2.622	73.04	4.189	15.867	54.84
Pretreatment	1	0.2074	0.1364	70.68	0.080	6.244	4.08
Residual	20	1.6561	1.587	178.53	1.808	13.747	37.08
Total	65	1.6223	2.848	167.25	2.539	14.461	65.58
CV %		2.39	2.10	14.55	4.33	10.56	6.27

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A27. Partial correlation coefficients determined among panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight, and grams of grain/GS-3 day of RS 671 grain sorghum hybrid: Field Experiment IV, 1978.

	Grain yield per plant	Seeds per panicle	1000-seed weight	Grams grain/ GS-3 day/plant
Panicle dry weight	0.954**	0.777**	-0.120	0.925**
Grain yield/plant	---	0.752**	-0.033	0.984**
Seeds/panicle		---	-0.596**	0.710**
1000-seed weight			---	-0.023

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A28. Mean squares from ANOVA performed for percent heat injury of RS 671 leaves combined for various test dates: Experiment V, 1979.

Source of variation	d.f.	Mean square
Date	4	5626.11**
Pretreatment	1	0.27 ns
Date x Pretreatment	4	99.51 ns
Residual	99	78.66
Total	119	281.25
CV %		15.47

** denotes significance at P=0.01

ns denotes nonsignificance at P=0.05.

Table A29. Mean squares of the ANOVA's performed for RS 671 leaf photosynthetic rates at five different dates: Experiment V, 1979.

Source of variation	d.f.	July 25	Aug. 1	Aug. 8	Aug. 9	Aug. 17
Temperature	2	437.00*	184.94 ns	78.53*	420.81**	4.82 ns
Pretreatment	1	12.70 ns	17.19 ns	0.03 ns	72.72 ns	4.03 ns
Residual	14	78.35	58.74	18.25	37.42	19.75
Total	17	116.68	71.14	24.27	84.60	17.07
CV %		24.27	18.07	15.60	24.00	17.33

* denotes significance at P=0.05.

** denotes significance at P=0.01.

ns denotes nonsignificance at P=0.05.

Table A30. Mean squares of the ANOVA performed for leaf photosynthetic rates of RS 671 combined by dates: Experiment V, 1979.

Source of variation	d.f.	Mean square
Date	4	1041.84**
Temperature	2	618.22**
Pretreatment	1	19.14 ns
Residual	82	49.74
Total	89	106.76
CV %		22.40

** denotes significance at P=0.01

ns denotes nonsignificance at P=0.05.

Table A31. Mean squares from ANOVA's performed for kernel dry weights determined at various weekly intervals during grain fill (GS-3): Experiment V, 1979.

Source of variation	d.f.	10[1]	17[1]	24[1]	31[1]	38[1]	45[1]
Block	1						
Temperature	1	6.45*	16.38*	8.06 ns	67.18 ns	34.56 ns	165.32 **
Stage	4	1.31 ns	6.61 ns	15.57 ns	64.91*	106.60**	116.20**
Temp x Stage	4	0.64 ns	2.51 ns	5.99 ns	9.65 ns	3.77 ns	11.53 ns
Residual	10	0.71	2.40	11.04	17.57	17.47	19.92
Total	43	0.68	2.60	5.46	15.16	19.15	23.95
CV %		16.98	8.80	5.59	10.00	7.71	8.55

* denotes significance at P=0.05.

** denotes significance at P=0.01

ns denotes nonsignificance at P=0.05.

[1]Number of days after tip-bloom.

Table A32. Mean squares from ANOVA's performed for relative kernel growth rates determined at periodic intervals during GS-3 period: Experiment V, 1979.

Source of variation	d.f.	Weekly Intervals (days after tip-bloom)					
		10-17	17-24	24-31	31-38	38-45	Entire GS-3
Block	1						
Temperature	1	0.162**	0.020**	0.001*	0.0003 ns	0.0004 ns	0.013**
Stage	4	0.040*	0.003 ns	0.001**	0.0004 ns	0.0001 ns	0.003*
Temp x Stage	4	0.028 ns	0.001 ns	0.0001 ns	0.0002 ns	0.0001 ns	0.002 ns
Residual	10	0.010	0.001	0.001	0.001	0.001	0.0006
Total	43	0.018	0.001	0.0002	0.0001	0.0001	0.001
CV %		21.91	19.09	31.99	50.09	74.64	14.80

* denotes significance at P=0.05.

** denotes significance at P=0.01.

ns denotes nonsignificance at P=0.05.

Table A33. Mean squares for panicle dry weight, grain yield/plant, number of seeds/panicle, 1000-seed weight and grams of grain/GS-3 day of RS 671 grain sorghum as influenced by two elevated night temperatures imposed at various growth stages during panicle development: Field Experiment V, 1979.

Source of variation	d.f.	Panicle dry weight	Grain yield /plant	Seeds/panicle	1000-seed weight	Grams grain/ GS-3 day/plant
Block	2					
Temperature	1	43.17*	474.89**	2,251,568.82**	119.00**	0.554**
Stage	4	450.23**	392.83**	1,286,680.81**	92.32**	0.425**
Temp x Stage	1	88.36	80.96	381,169.78*	21.38*	0.056
Pretreatment	1	392.74*	159.19	565,267.64*	3.91	0.232
Residual	20	81.21	45.73	82,136.68	2.21	0.053
Total	65	126.16	94.22	269,981.63	13.46	0.099
CV %		13.64	12.88	14.17	5.16	13.99

* denotes significance at P=0.05.

** denotes significance at P=0.01.

Table A34. Mean squares for numbers of days to bloom and physiological maturity, durations of panicle expansion (GS-2) and grain fill (GS-3) and plant height of RS 671 grain sorghum as influenced by two elevated night temperatures imposed at various growth stages during panicle development: Field Experiment V, 1979.

Source of variation	d.f.	Days to bloom	Days to physiological maturity	GS-2	GS-3	Plant height
Block	2					
Temperature	1	40.02**	60.00**	40.02**	2.02	703.15**
Stage	4	19.23**	9.38	19.23**	2.56	279.81**
Temp x Stage	4	10.31**	5.98	10.31**	1.56	83.18
Pretreatment	1	4.91**	0.38	4.91**	2.56	4.69
Residual	20	0.51	0.48	0.51	1.01	8.21
Total	65	3.55	3.91	3.56	1.49	63.34
CV %		1.20	0.76	2.51	3.16	2.60

** denotes significance at P=0.01.

Table A35. Partial correlation coefficients determined between grain yield and its components for RS 671 grain sorghum: Field Experiment V, 1979.

	Grain yield /plant	Seeds/ panicle	1000-seed weight	Grams grain/ GS-3 day/plant
Panicle dry weight	0.98**	0.70**	-0.18	0.97**
Grain yield/plant	--	0.71**	-0.16	0.79**
Seeds/panicle		--	-0.46*	0.76**
1000-seed weight			--	-0.28

* denotes significance at P=0.05.

** denotes significance at P=0.01.