Response and Tolerance of Sorghum to Temperature Stress

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Before attempting to address this subject it is important to define what is understood by temperature stress. It is a complex subject which has recently been reviewed in three books (Lyons et al. 1979; Levitt 1980; Turner and Kramer 1980) therefore definitions and details of the physiological and biochemical processes associated with temperature stress will not be given here. In brief, however, a quantitative definition of temperature stress in sorghum, as in any crop, is difficult to provide since it will depend on a number of factors which will include the duration of exposure of either high or low temperature, the activity or stage of growth of the exposed tissue and finally the thermal adaptation of the particular sorghum cultivar.

The productivity and adaptation of a sorghum crop will be most affected when temperature stress coincides with *critical* stages of growth so it is proposed to examine the effects of temperature stress on each critical stage of development (Wilson and Eastin 1982), starting with the newly sown seed, to the grain on the panicle at the hard dough stage. Consideration will be given to what is currently understood about the plants' response and adaptation to low and high temperatures, but more emphasis will be given to describing current screening techniques and how our present understanding of the problem can enable sorghum scientists to develop more efficient screening procedures for the future.

In addition, because it has been suggested that acclimation and adaptation should be examined within distinct geographical regions (House 1981 a), I propose to deal with high and low temperature stress separately.

At the outset it is important to establish two points: (1) the need to obtain a clearer picture of the temperature conditions of the sorghum-growing areas of the world and the probabilities of lethal and stress inducing temperatures occurring at any time during the growing season. An example of this is given by Rosenthal and Hammer (1979) but, as discussed by Sivakumar and Virmani (1982), this is an area where an increased research thrust is required in the future. (2) that to interpret the effects of temperature per se on plant growth in the field is often difficult because temperatures in the crop canopy vary both with time and space (Fig. 1).

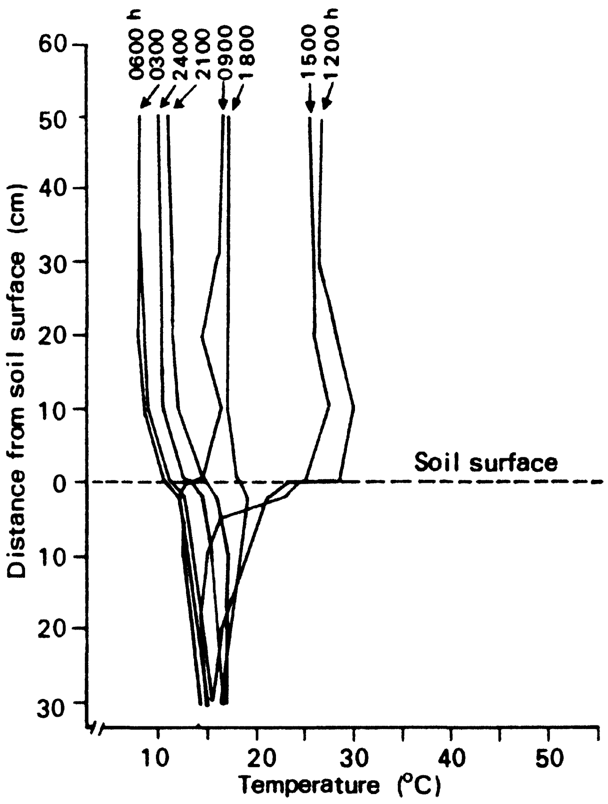

Figure 1. A series of soil and air temperature profiles measured during a 24-hr period (10 April 1976) in a sorghum crop cv 65 D, Sebele, Botswana.

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High Temperature (Heat Stress)

Introduction

Heat stress is a major factor influencing the productivity and adaptation of many wild and cultivated plants and many crop species of tropical and subtropical origin are sensitive to high temperatures in the range 30 – 55°C.

In the semi-arid tropics where sorghum is grown, air temperatures often exceed 40°C and leaf temperatures of 55°C have been measured. At the soil surface even higher temperatures (>60°C) can be experienced by the emerging sorghum plumule (Peacock and Ntshole 1976) and temperatures as high as 68°C have been recorded (Peacock 1977). Under such conditions heat stress is often accompanied by drought stress and there are usually interactions within the plant to these two stresses (Sullivan et al. 1977). Despite this, it is argued (Sullivan and Ross 1979) that for plant breeding purposes it is desirable to measure and select for them separately. This has been done in Nebraska and currently is a major research area at ICRISAT (ICRISAT 1981). In addition, a number of scientists have used response to heat stress to select for drought resistance (Hunter et al. 1936; Heyne and Laude 1940; Heyne and Brunson 1940; Kaloyereas 1958; Kilen and Andrew 1969). Also heat stress is easier to induce experimentally than water stress.

It is for these reasons that in sorghum research at ICRISAT more emphasis is being placed on utilizing temperature stress as a means of selection for both heat and drought tolerance. Already it has been shown that there is sufficient variability to select for sorghum genotypes with high temperature tolerance (Sullivan and Blum 1970; Wilson et al. 1982).

High Temperature Effects on Processes and Growth Stages

Germination and Establishment

The ability of a sorghum seedling to emerge and establish rapidly is a vital prerequisite to the adoption of any new cultivar. However this has been largely ignored by crop improvement programs throughout the world. Although many promising sorghum cultivars may have resistance across geographic regions to local pests and diseases, what is their use if under farm or experimental conditions they fail to emerge and establish?

Martin et al. (1935) stated that sorghums are of tropical origin and have long been known to germinate and grow best at relatively high temperatures. The optimum soil temperature in Martin's experiment was between 30°C and 35°C but a review of the literature (Table 1) 46 years after that experiment was conducted shows that optimum germination can occur at soil temperatures ranging from 21°–35°C (Martin et al. 1935; Rosbaco 1958; Stoffer and Van Riper 1963; Bajay and Papp 1969; Kanemasu et al. 1975; Aisien and Ghosh 1978). It would also appear that the supposedly lethal temperature for germination ranges from 40°–48°C (Knapp 1966; Singh and Dhaliwal 1972; Kailasanathan et al. 1976). These two ranges in temperature suggest that there is genetic variation, not only in the optimum temperature for germination but in the temperature at which coleoptiles can survive.

Recent studies at ICRISAT (Wilson et al. 1982) have confirmed that there is genetic variation in the ability of sorghum to emerge at high soil temperatures and the results of this series of experiments will be discussed in the later section on selection for heat tolerance.

Leaf Area Development, Stem Growth, and Tillering

In sorghum, as in any crop plant, the rate of dry

Table 1. Summary of data on optimum and lethal germination temperatures in sorghum.

	°C	Reference
Optimum temperature	30–35	Martin et al, 1935
	30–35	Rosbaco, 1958
	21	Stickler et al, 1962
	22	Bajay and Papp, 1969
	26	Pavlov, 1969
	23	Kanemasu et al, 1975
	22	Aisien and Ghosh, 1978
	22–25	Kusewa, 1978
Lethal temperature	> 40	Singh and Dhaliwal, 1972
	40	Kailasanathan et al, 1976
	47	Kusewa, 1978
	48	Knapp, 1966

matter production is strongly affected by leaf area especially during GS1 when the canopy is developing (McCree and Davis 1974). The components affecting leaf area development include the time to panicle initiation, (through its influence on leaf number) the rates of leaf appearance, leaf expansion and leaf senescence, and the combined effects of canopy structure. In the Poaceae, in the absence of water and nutrient stress, these developmental rates have been shown to be largely governed by temperature (Watts 1974, for maize; Peacock 1975a, b, and 1976a, for temperate grasses; and Gallagher 1979, for temperate cereals). In sorghum, few quantitative data are available (Troughton et al. 1974; McCree and Davis 1974; Johnson 1967) about the effects of temperature on leaf area development although Johnson's (1967) data suggest that leaf extension closely parallels air temperature particularly at night. More recent data of Baker (1981 unpublished) show that final leaf number and leaf area were increased when temperatures were varied from 25°/20°C to 35°/25°C.

The effect of temperature on the rate of leaf appearance has been examined by Downes (1968) who showed that in sorghum, leaf appearance increased linearly with air temperature from 13° to 23°C.

Genetic variation in leaf growth in relation to temperature has been shown to be large (Quinby et al. 1973; Wade et al. unpublished). Some data from ICRISAT on the effects of temperature on leaf extension are shown in Figure 2. The continuous line represents the best fit of the data and it can be seen that the rate of leaf extension is markedly reduced above temperatures of 34°C. The dotted line, fitted by eye suggests that the base temperature (T_o) for leaf extension is around 15.5°C. In most field situations however, water stress, which usually accompanies high temperatures, will have had an earlier and more drastic effect on the rate of leaf extension.

Tillering will also affect the final leaf area and although it is affected by many environmental variables, Downes (1968) showed that the rate of tiller production in the cv Combine Kafir ceased if the average daily mean temperature exceeded a threshold value of about 18°C. However Escalada and Plucknett (1975) show that there is a considerable interaction between temperature and photoperiod; when temperatures were increased (from 23.9°/15.5°C to 32.2°/23.9°C) with a simultaneous increase in daylength (10–14h) increases in tiller number per plant resulted.

There is clearly a dearth of information on the effects of temperature on leaf area development and almost none on the effects of high temperature. Studies were initiated at ICRISAT in 1980 to examine the effects of temperature on leaf area development over a wide range of temperatures

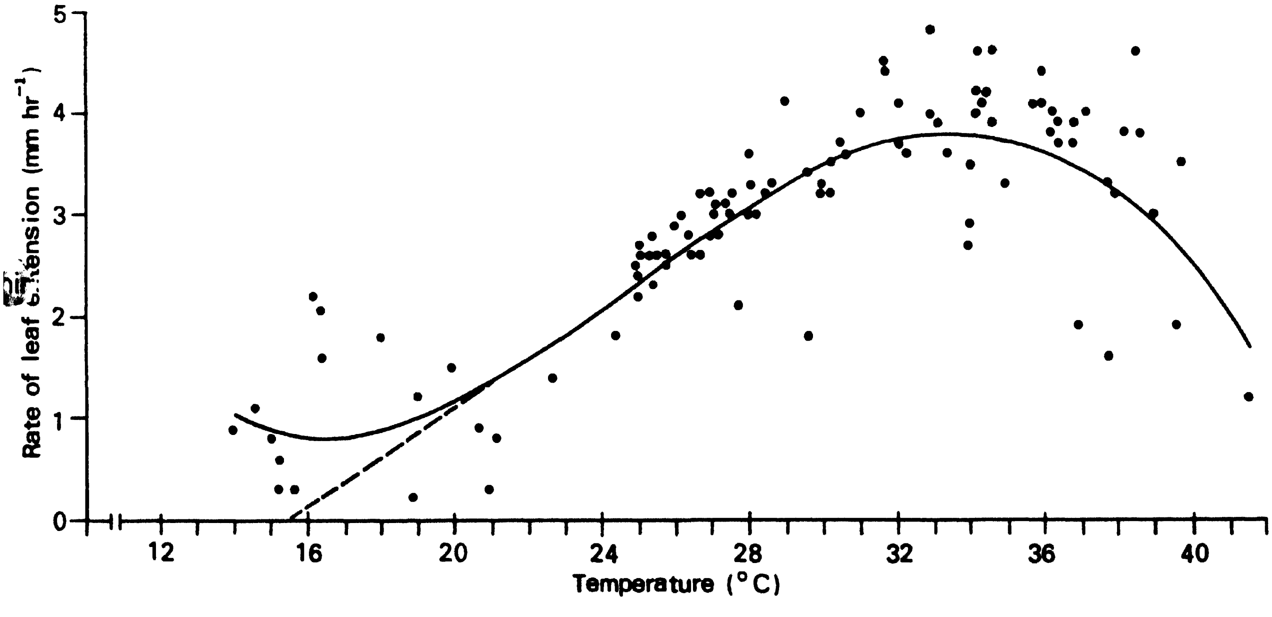

Figure 2. Relationship between leaf extension and temperature in sorghum cv CSH 8 (adapted from Wade et al. unpublished).

with emphasis on the summer season where the effects of high temperature in the absence of water and nutrient stress are being examined. Of particular interest is the effect of high temperature per se not on cell expansion, division or the resultant growth, but on cell and leaf tissue survival. (See later section on selection for heat tolerance.)

In my opinion, studies on the relationships between (high) temperature and the rates of leaf extension, appearance and senescence and the interactions with water and nutrient stress are vital both in the areas of improved crop establishment and drought resistance. This should be marked as an area for a major research thrust in the 80s.

Root Growth and Nutrient Uptake

There appears to be a complete dearth of information on the effects of high temperature on root development and nutrient uptake in sorghum. This is an important area and should perhaps be examined in the 80s.

Panicle Initiation and Development—The Components of Yield

The onset of the reproductive phase commences with the initiation of the panicle meristem marking the end of the vegetative growth phase. This usually occurs between 30 and 40 days after emergence but the timing which may vary from 19 to 70 days (House 1981 b) is largely controlled by photoperiod and temperature (Caddel and Weibel 1971; Downes 1972; Quinby et al. 1973). How temperature affects floral initiation is still not clear. Recent work by Baker (1981 unpublished) shows that increasing day/night temperatures from 25°/20° to 35°/25°C hastened floral initiation. However earlier work by Downes (1972) and Quinby et al. (1973) indicated that higher temperatures (day/night 32°/28° and 32°/29°C) delayed initiation. It is possible that the higher night temperatures are delaying initiation. The length of the reproductive phase (GS3) is also markedly reduced by temperature (Baker 1981 unpublished) and day temperatures were shown by Caddel and Weibel (1971) to be most important. There is no information about very high (45°–55°C) temperatures on either the onset or the length of the floral period.

Some information is available though on the effects of high temperature on floret development. Downes (1972) and Baker (1981 [illegible]lished) showed that high temperature (day/night 33°/28° and 35°/28°C) late in panicle development induced floret abortion, a result which was, in general, consistent with the findings of Pasternak and Wilson (1969) using artificially produced heat waves (5 days at 42°/32°C day/night) at the boot stage. However they showed that there was no floret damage if the panicle was fully emerged. In a study using 6 sorghum cultivars grown in 14 different environments, it was found that tolerance to high temperatures contributed more to yied stability than did tolerance of low moisture conditions. Specifically, where high temperatures occurred during panicle development, the capacity of a genotype to produce greater seed numbers per head (and hence greater yield) was important (Heinrich 1981).

It is now well documented that heat hardening occurs when plants are exposed to subinjurio[illegible] high temperatures (Sullivan and Kinbacher 19[illegible]. Coffman 1957; Levitt 1980); however, as concluded from the above results the ability of genotypes to heat harden, varies. Some genotypes may fail to harden appreciably, while others harden very noticeably. Table 2 shows the heat tolerance of four sorghum lines before and after heat hardening in growth chambers at about 3 weeks of age. The relative ranking of heat tolerance changed when they were exposed to high temperatures. In this experiment (Sullivan et al. 1977), sorghum CK-60 did not heat-harden to the same extent as the others, and its relative tolerance was lower than the other sorghums after the high temperature treatment. However it was found that as the plants aged and neared the boot and bloom stage in the field, only the yellow

Table 2. Effect of heat hardening on the relative heat tolerance of four sorghum genotypes.[a]

Day/night, temperature (°C)	
31/27	42/27
CK 60	9084
9084	RS 610
RS 610	C 7078
C 7078	CK 60

a. The sorghums are ranked from highest to lowest in heat tolerance (from Sullivan et al. 1977).

endosperm sorghum 9084 remained high in heat tolerance and that there were no evident differences in the heat tolerance of the remaining three. The effect of high temperatures at the time of panicle development may not be that critical but it is obviously an area which needs further research in an attempt to establish whether heat hardening carried out in the seedling stage can confer tolerance in the later stages.

The effects of temperature on the components of yield are well documented (Tateno and Ojima 1976; Eastin 1976; Chowdhury and Wardlaw 1978). Grain number per head itself was not significantly altered by temperatures over the range (day/night) 21°/16° to 36°/31°C and 30°/25° to 35°/25°C (Chowdhury and Wardlaw . 1978; Downes 1972; Baker 1981 unpublished); however, yields were markedly reduced at higher temperatures (30°/25°, 35°/25°C) due to a reduction [illegible] grain weight (Tateno and Ojima 1976; Baker 1981 unpublished). There is evidence that high temperatures during panicle development may reduce seed number per head, and yield, in some sorghum cultivars (Heinrich 1981; Ogunlela 1979).

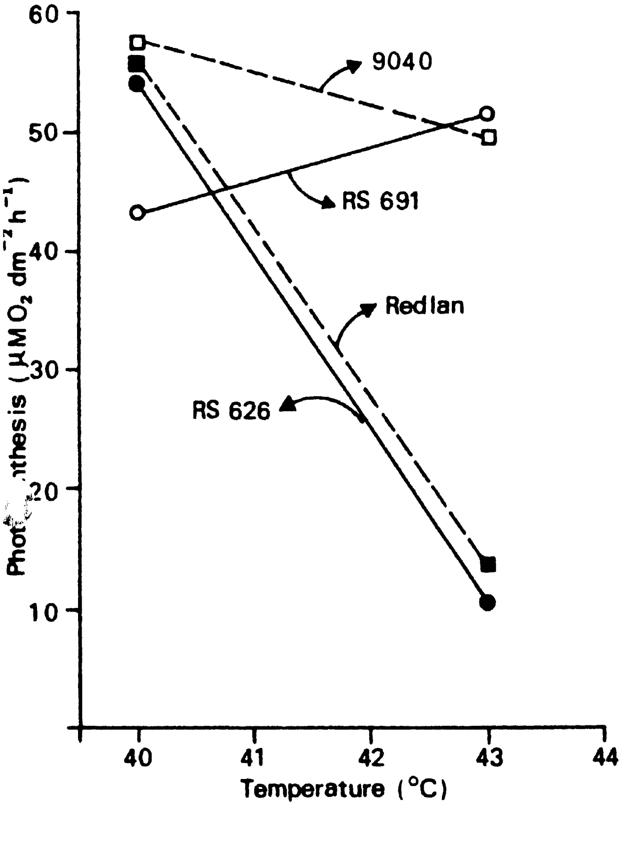

Figure 3. High temperature effects on photosynthesis of four sorghum cultivars (from Norcio 1976).

Photosynthesis and Respiration

Genetically based variation in photosynthetic capacity has always been of interest in crop plants. In C_4 species, like sorghum, high rates of photosynthesis occur only at high temperatures and at high light intensities. The optimum temperature has been shown to range from 30° to 42°C (Norcio 1976; Vong and Murata 1977). Sumayao et al. (1977) concluded however that photosynthetic rates declined when leaf temperatures exceeded 33°C. Chesnokov et al. (1974) found that photosynthesis was reduced by 70% at 44°C and 95% at 48°C. Genotype differences in the maintenance of photosynthesis at high temperatures (43°C) obviously occur (Norcio 1976). Figure 3 shows that the hybrid RS 691 and its male parent 9040 maintained high levels of photosynthesis compared with Redlan and RS 626. Norcio (1976) also found a positive correlation between high photosynthesis rates at high temperatures and cellular heat tolerance of sorghums determined by the "electro-conductivity" method (Sullivan 1972). However, selection for high photosynthetic rates per se in other crops has generally not been a productive approach to increasing yields. However when heat stress is involved, an ability to maintain relatively high rates of photosynthesis may very well contribute to yield. This should be examined further. The high correlation between heat tolerance and high photosynthesis as shown by Norcio (1976) is encouraging but it is unlikely that the measurement of photosynthesis per se will ever become a practical screening method.

That respiration rates in sorghum (like any crop) are influenced by temperature is well established (Norcio 1976; Vong and Murata 1977; McCree 1974; Eastin 1981). Wilson and Eastin (These Proceedings) have thoroughly reviewed this subject and concluded that there is a great deal of genetic variability in respiration response to temperature. Of particular interest is the recent work of Gerik (1979) and Mahalakshmi (1978); the former showing that whole plant dark respiration varied from 4 to 10 mg Co_2 g^{-1} hr^{-1} at 30°C. More recent work by Eastin (1981) shows that respiration in sorghum at panicle initiation increased 12–14% for every degree C over the range from 12°-27°C.

Selection Methods for Heat Tolerance

It has been established that genetic variation to

Table 3. Rank order of percent emergence for some genotypes of different surface treatments, showing (a) no interaction with temperature and (b) interaction.

Surface treatment	Genotype serial number											
	(a) 3	7	16	18	19	22	30	(b) 23	24	26	13	25
Bare soil	1	27	18	26	17	29	6	3	5	4	11	30
Light kaolin	4	25	18	27	16	30	1	5	8	14	15	23
Heavy kaolin	4	26	18	29	15	30	7	13	25	16	1	12

heat stress in sorghum exists. It is vital therefore that in the 80s breeders and physiologists concentrate on developing screening and breeding methods to generate heat tolerant material. It is equally important that the selection methods are simple, repeatable and inexpensive, and capable of screening a wide range of germplasm and breeders lines.

Improved Emergence and Establishment

A series of experiments were conducted, at ICRISAT, in the laboratory, glasshouse and field studying the emergence of a number of sorghum genotypes over a range of high temperatures. The work demonstrated that some lines have an ability to emerge even when soil surface temperatures were as high as 55°C. In the laboratory experiments, the temperature of the soil surface in pots was controlled using a band of heating elements positioned above a water bath (Soman 1981). The surface temperature could be varied between 35° and 65°C either by a thermostat or varying the height of the heat source above the soil. The significance of this technique is that the effect of heat stress can be examined in the absence of either water shortage or soil crusting. In the glasshouse similar experiments were conducted but different surface treatments were used to manipulate temperature. Charcoal dust (black) and kaolin (white) were used to modify surface temperatures (Wilson et al. 1982) with the bare soil surface (no surface cover) providing a medium treatment. In the field (in this case large brick chambers) (Wilson et al. 1982) the same surface covers were used to modify soil temperature independently of soil water and crusting. The results show that there is considerable genotypic variation and tolerance. Genotype x temperature interactions were also observed and this requires further investigation (Table 3).

The effect of temperature on the rate of plumule extension was also examined (Soman 1981, Fig. 4). It is argued that the quicker the plumule reaches the surface the more chance it has for emerging before a surface crust develops. The rates were shown to vary among genotypes (e.g., at 41°C the hybrid CSH 6, grew at a rate of less than 0.5 mm hr^{-1} while the variety SPV [illegible] grew at a rate of 1.3 mm hr^{-1}).*

The development of the plumule in the soil is now being examined more closely. Visual observations indicate (Plate 1) that on reaching the surface (in many instances where there is no crust) the plumule bends over. In some instances the leaves curled around themselves and could not emerge. In collaboration with the production economists at ICRISAT, a survey into the specific problems relating to crop establishment in farmer's fields has been initiated together with on-farm experiments. The problems of crop establishment in sorghum cannot be overemphasized. Along with drought it is the major limiting factor to sorghum production in the SAT (Peacock 1980). Temperature clearly plays an important role and I regard this as one of the key areas for research in the 80s.

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* It is worth noting that throughout this series of experiments on factors affecting crop establishment (temperature, water and crusting effects) the Indian varieties performed significantly better than the hybrids CSH 1, CSH 5, CSH 6. Only CSH 8 appeared to have the tolerance of the varieties (Soman 1981). This is perhaps important because numerous reports have been received this year about poor crop establishment of CSH 5 in farmers' fields in Central India and until now the dominance of sorghum hybrids in nonstress, and to some extent in stress conditions has gone unchallenged.

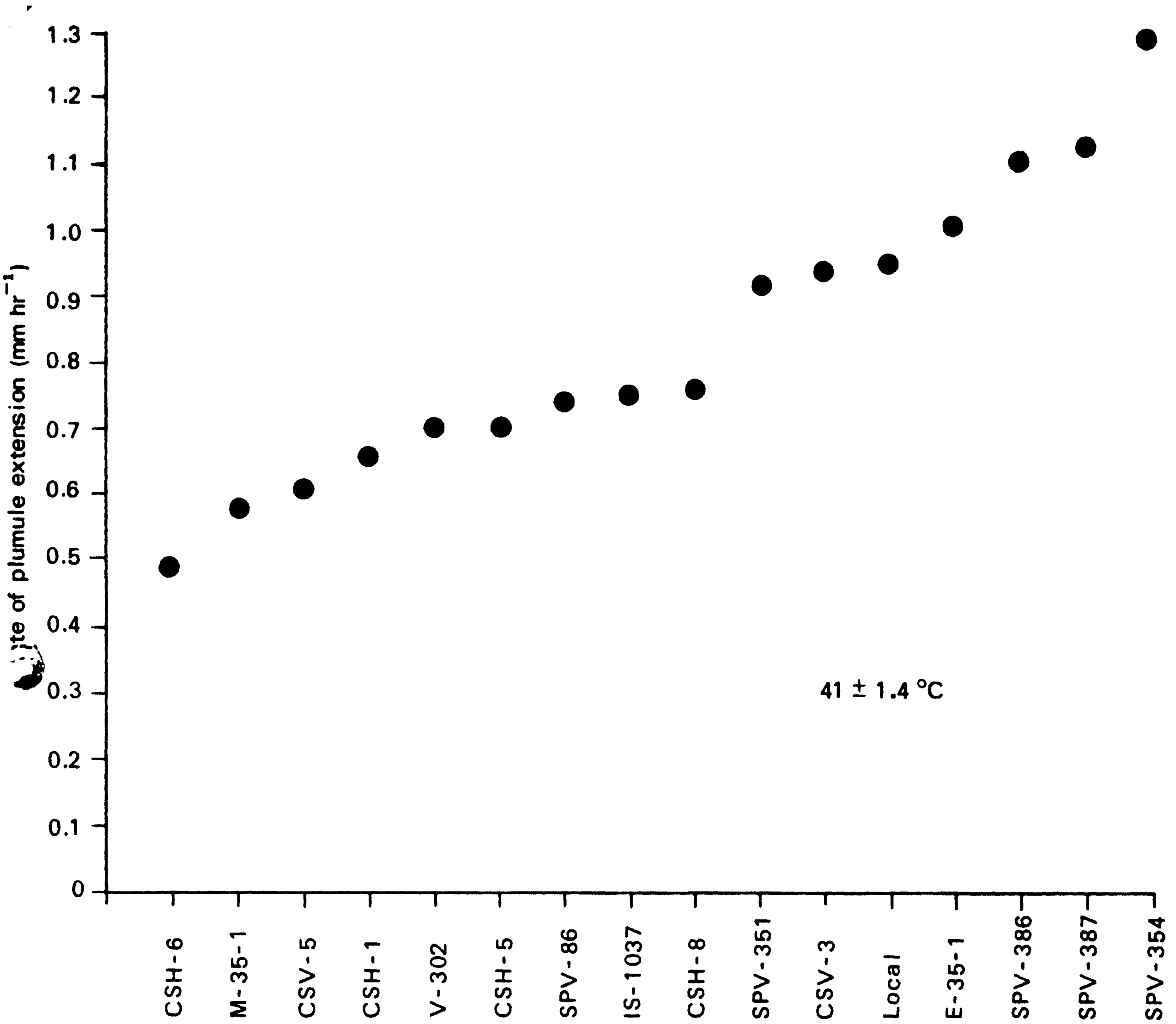

Figure 4. Genotypic differences in the effect of temperature on the rate of plumule extension in a range of sorghum cultivars (adapted from Soman 1981).

Leaf Tissue Survival

Earlier work (Sullivan and Blum 1970; Sullivan 1972; Blum and Ebercon 1976; Sullivan and Ross 1979) has shown that genetic variability for both heat and desiccation tolerance exists in sorghum. The inability to survive high temperature may give rise to the phenomena known as "leaf firing" (Sullivan et al. 1977; Peacock 1979; Jordan and Monk 1980). Research in Botswana (Peacock 1979) showed that leaf firing occurred in the hybrid RS 610 at a leaf temperature of 43°C. This relatively low leaf temperature suggests that it would be advantageous to select lines having a high critical leaf temperature or so-called heat tolerance.

At Nebraska the leaf disc method (which essentially estimates the electrolytic leakage from a leaf disc by measuring the electrical conductivity) has been extensively used to measure heat tolerance (Sullivan 1972). In addition Sullivan and Ross (1979) showed that in two populations (M35-1 conversion hybrids and NP9BR lines) heat tolerance was positively correlated with higher yields (Fig. 5).

At ICRISAT germplasm and breeders source material have been screened for heat and desiccation tolerance. Lines were sown at Sangareddy (25 km from ICRISAT Center) in April 1980 and established with irrigation. No further water was applied until the monsoon broke in early June. During the period air temperatures reached 43°C

Plate 1. The effect of high soil surface temperature on plumule emergence in sorghum. Plumules of the cultivar to the right of the steel blade are bent over and will not emerge; those of the cultivar to the left are unaffected.

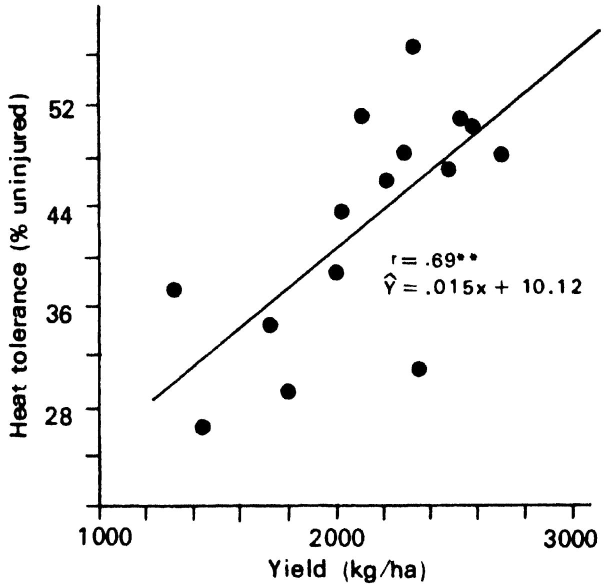

Figure 5. The relationship between heat tolerance and yield of fifteen M35-1 conversion hybrids determined during a period of maximum stress in Nebraska (from Sullivan and Ross 1979).

and leaf temperature exceeded 55°C. Leaf desiccation (firing) occurred but the extent and variation did not become so apparent until 10 days or more after the rains had started. It was then obvious that some lines had been completely "fired", others partially fired, whilst some were unaffected. Despite having made the measurements of leaf temperature (which are many times easier to measure than either stomatal conductance or solute and water potentials) material was selected by visual scoring. Over a 1000 lines could be evaluated in a day. Good correspondence was also obtained when the same material was grown at Anantapur (India) and Gadambalia (Sudan) (Plate 2) under naturally occurring drought during the normal growing (rainy) season. It should be emphasized however that these were pilot experiments. Eventually the physiological basis of the visual scores should be known and this will be carried out on a limited number of susceptible and tolerant lines at a later stage.

Experiments conducted in 1981 using the line source irrigation technique (Hanks et al. 1976;

and Kramer 1981) and all three books should be referred to for details of the biochemical and physiological processes involved

In sorghum a number of the relationships between temperature and growth have already been discussed in this paper so it is proposed to deal only with the specific effects of low temperature on sorghum and to cover those areas which will enable a crop improvement team to generate improved cold-tolerant lines from the sources of resistance identified *Sorghum bicolor* is known to be particularly chilling sensitive (Bagnall 1979) However some grain sorghums are known to possess varying degrees of cold tolerance (Singh 1977) and a substantial amount of these have been grown in the highlands of Ethiopia, Uganda, Yemen Arab Republic and to a limited extent in the highlands of Kenya, Zaire, Cameroun and New Mexico In some areas, for example Botswana, cold night temperatures are at present one of the major factors limiting sorghum production (Peacock and Ntshole 1976)

Low Temperature Effects on Processes and Growth Stages

Germination and Establishment

Large-scale screening of the germplasm at low temperature has not been carried out, but according to Quinby et al (1958) the minimum temperature for germination is between 7 2°C and 10°C which is remarkably close to the range of 8° -10°C quoted by Pinthus and Rosenblum (1961) Both groups indicate that a higher temperature (15 6°C), was required for subsequent emergence More recently Thomas and Miller (1979) have established that the minimum germination temperature may vary within species from 4 6°C to 16 5°C and the implication of these data are discussed further by Miller (1981) Singh and Dhaliwal (1972) obtained 55% emergence at 15°C reaching an optimum between 25° and 30°C They obtained no emergence at all at 5° and 10°C McWilliam et al (1979) found that initial germination, seedling-respiration and mesocotyl extension in three sorghum species all declined as the temperature was reduced from 24° down to 8°C The rate of decline, however, varied between species (*S leiocladum, S verticilliflourm, S bicolor*), especially in the lower part of the temperature range below about 12°C.Arrhenius plots of germination rate for two of the species, a commercial U S hybrid (*S bicolor*) and a wild tropical species (*S verticilliflorum*) are shown in Figure 6a A characteristic of the responses is the sudden increase the Q_{10} values below a certain temperature range In this case it was higher (14°-16°C) for the more sensitive tropical species than for the commercial U S hybrid (11°-12°C) A similar response has been observed for the elongation of the mesocotyl of sorghum seedlings (Fig 6b) McWilliam (1981) suggests that these high Q_{10} s below about 12°C indicate extremely high activation energies and may help explain the poor response at these temperatures Genetic differences were also observed by Pinthus and Rosenblum (1961), and Stickler et al (1962) found that Kaoliangs (sorghum originating in the mountainous regions of central and western China) germinated and emerged faster than standard grain sorghum varieties, particularly at low temperatures

Sorghum seedlings are normally killed when temperatures drop below 0°C although some seedlings have been reported to withstand a slight frost (Martin 1941) Seed however will survive temperatures down to -12°C provided the seed moisture content is below 15% (Gritton and Atkins 1963, Rosenow et al 1962, Bass and Stanwood 1978) However at higher moisture levels (30-35%) subsequent germination was markedly affected (Carlson and Atkins 1960, Rosenow et al 1962, Kantor and Webster 1967)

Leaf Area Development, Stem Growth, and Tillering

There is a dearth of information on the effects of low temperature on leaf area development, stem growth, and tillering Recent work by Major et al (1981) in a controlled environment chamber showed that reductions in leaf number and plant height caused by chilling temperatures (13°C/8°C day/night) were only temporary but tiller number was increased from three to as many as eight per plant Major's (1981) work however showed that exposure to chilling temperatures (13°C/8°C day/night) did not affect grain growth, grain number per panicle or yield per panicle The period of low temperature was in the dark and there is evidence that the growth of sorghum is much less sensitive to a period of low temperature given during the night period than under conditions of high irradiance during the day (Bagnall 1979) McWilliam

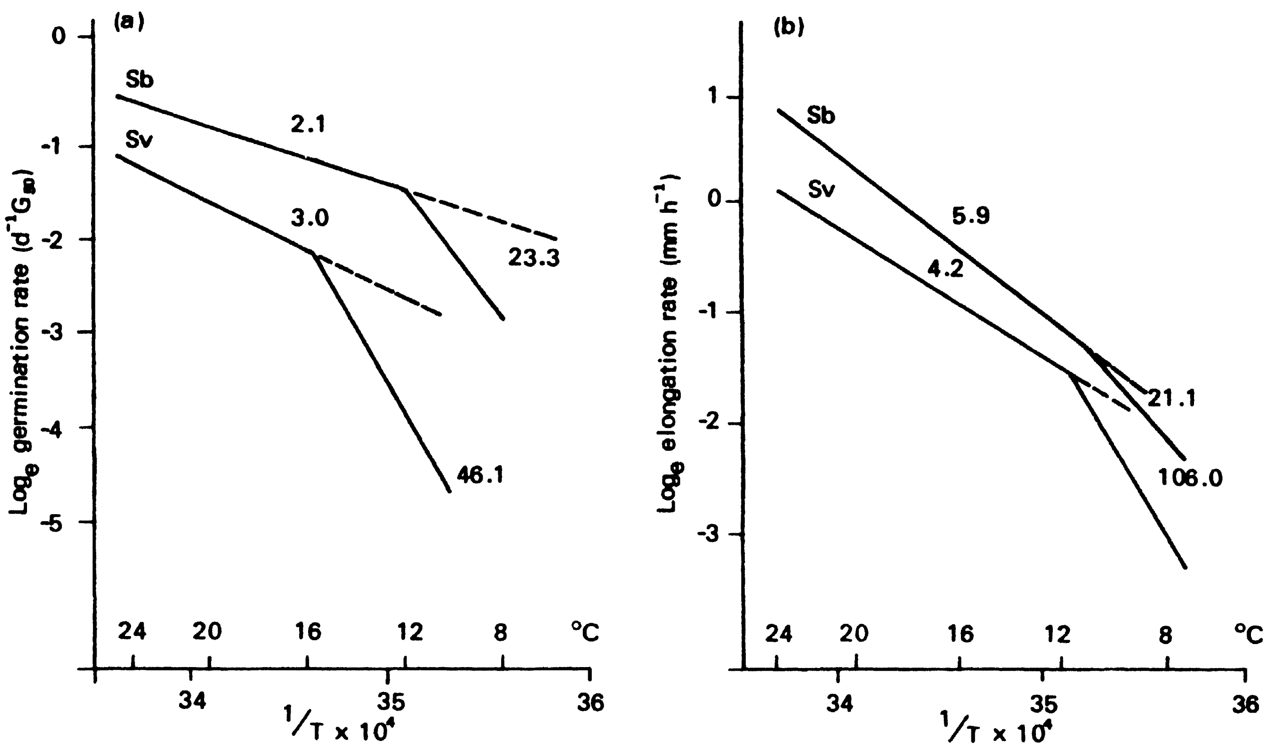

Figure 6. Arrhenius plots for (a) germination rate (reciprocal of days to 50% germination) and (b) mesocotyl elongation rate for two sorghum species (Sb., S. bicolor, *commercial hybrid;* Sv, S. verticilliflorum, *tropical wild sorghum).* Q_{10} *values derived from regressions are indicated for each slope. (Adapted from McWilliam 1981.)*

(1981) claims that light accelerates and intensifies low temperature injury in chilling-sensitive tissue.

Another common symptom of chilling injury during early growth is chlorosis on the first formed leaves. Chlorophyll synthesis is severely depressed at low temperatures in many chilling sensitive species and Slack et al. (1974) observed irreversible chlorotic bands on sorghum leaves exposed to temperatures close to 0°C. Recent evidence (McWilliam et al. 1979) from electron micrographs of sorghum leaf tissue suggest that the failure to develop chlorophyll under these conditions is associated with the arrested development of the thylakoid membrane system of the developing plastids. Apart from this work, there is nothing to my knowledge and like the earlier work reported on leaf area development at high temperature it needs examining. Possible sites in countries of Eastern Africa, Mexico could be identified for detailed studies in the 1980s.

Root Growth and Nutrient Uptake

As with high temperature, there is apparently no information.

Panicle Initiation and Development—The Components of Yield

Unlike high temperature effects, there is apparently very little information on the effects of low temperature on panicle initiation and development, although Downes and Marshall (1971) demonstrated in glasshouse experiments that night temperatures of 13°C or less during meiosis can induce male sterility. Taylor (1973) speculated that poor grain sorghum yield in New Zealand may have been due to pollen sterility induced by low temperature. This was examined further by Brooking (1976) who was able to induce male sterility by exposure to low night temperatures. However, as yet, there is no unequivocal evidence for the occurrence of low temperature-induced pollen sterility in sorghum crops in New Zealand and further detailed field work is required to elucidate the potential importance of this type of sterility induction. Peacock (1977a) argued that the low yields of late planted sorghum in Botswana were almost certainly due to the low night temperature (4°–12°C) occurring during GS3. In-

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