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EFFECTS OF HIGH SOIL SURFACE TEMPERATURE ON SEEDLING SURVIVAL IN PEARL MILLET

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SUMMARY

A field technique to screen pearl millet genotypes for their emergence and survival at high soil surface temperatures is described. Genetic variation in seedling emergence and survival is shown and it is argued that this variation is largely due to tolerance of high temperatures rather than tolerance of soil moisture deficit, although some interaction occurred. An index for 'thermotolerance' is defined and genotypes are ranked accordingly for this trait, which is shown to be highly heritable. The technique is repeatable and allows a large number of genotypes to be screened at the same time.

Temperatura y supervivencia de plántulas en el mijo perlado

RESUMEN

Se describe una técnica de campo para estudiar la emergencia y supervivencia de genotipos de mijo perlado en altas temperaturas de superficie del suelo. Se presentan las variaciones genéticas en la emergencia de las plántulas y su supervivenica, y se discute si dicha variación se debe en gran parte a la tolerancia a las temperaturas elevadas y no a la tolerancia de la falta de humedad en el suelo, si bien se produjo cierta interacción. Se define un índice de 'termotoleran-cia', y los genotipos se clasifican según este concepto, demostrando ser una característica altamente hereditaria. La técnica puede repetirse y permite estudiar una gran cantidad de genotipos a un mismo tiempo.

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is an important cereal grain crop in many parts of the semi-arid tropics, such as Sahelian and southern Africa and the Indian state of Rajasthan (O'Neill and Diaby, 1987; Soman *et al.*, 1987). Poor seedling establishment is one of the major factors limiting its production, and high soil surface temperatures (above 55°C) have been reported to reduce seed germination and the emergence and survival of pearl millet seedlings in these regions (Peacock, 1982; Soman and Peacock, 1985; Gupta, 1986). High soil temperatures have also been reported to have similar damaging effects on sorghum seeds and seedlings. (Wilson *et al.*, 1982; Ougham *et al.*, 1988). Recently, Peacock *et al.* (1990) demonstrated that high temperatures (above 45°C) around the shoot meristem of sorghum seedlings inhibited seedling growth even when

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moisture was not limiting and that at 54°C seedlings died as a result of 'heat girdling' of the mesocotyl, which apparently caused the blockage of phloem and so prevented the flow of carbohydrates to the roots.

A breeding programme was recently initiated to produce pearl millet genotypes for Rajasthan that combine the apparent environmental adaptation of local landrace cultivars and the yield potential of improved genotypes from the Indian National Research Programme and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). The breeding programme can be made more effective by the use of screening methods to evaluate genotypes for thermotolerance to supplement the conventional multilocational yield testing method.

This paper describes a technique that was used to examine the effect of high temperatures on the survival of pearl millet seedlings in the field in Rajasthan. It was designed to investigate the hypotheses that seedling mortality is largely due to high soil surface temperatures and that there is genetic variation among pearl millet genotypes in seedling survival and thermotolerance.

MATERIALS AND METHODS

Location and soil conditions

The experiments were conducted at Fatehpur, Rajasthan, India (latitude 27° 37'N), during the pre-monsoon summer months (April and May) of 1989 and 1990. The soil of the experimental site belongs to the Devas Series and is classified as a member of the mixed hyperthermic family of the type Gypsiorpthids. It is 88% sand, 4% silt and 8% clay and has a bulk density of 1.46 Mg m^{-3}. The field capacity of the top 200 mm of soil is 10% and wilting point is reached at a soil moisture content of 2%, as determined using a pressure plate extractor.

Seed material and experimental layout

Four experiments were conducted, two in 1989 (Experiments 1 and 2) and two in 1990 (Experiments 3 and 4). In 1989, 75 millet genotypes and one sorghum genotype (*Sorghum bicolor* SPV 386), selected to cover a range of landrace, hybrid and varietal variation, were tested. In 1990, the 26 genotypes showing the most susceptibility or tolerance to high soil temperatures were tested again. In 1989 the seeds were obtained from various sources at ICRISAT, whereas in 1990 all the seed was produced under uniform growing conditions in the post-rainy season at ICRISAT.

In all the experiments, each plot was a row, 2.50 m long, with 30 cm between rows. Plots were arranged in a randomized block design with three replications in 1989 and four replications in 1990.

Sowing operations

Experiment 1 was sown on 23 April and Experiment 2 on 16 May 1989. On the night before sowing, 15 mm of water was applied uniformly to all plots from two

parallel sprinkler lines spaced 12 m apart. This brought the top 300 mm of the soils to field capacity and ensured that the soil profile down to a depth of 150 mm did not dry out during the first 15 days of seedling growth. The rows were opened on the day of sowing to a depth of 50 mm with the sharp edge of a metal rake, 50 seeds were immediately sown by hand and the soil replaced and compacted lightly with the flat edge of the rake to ensure good seed to soil contact.

Experiment 3 was sown on 26 April and Experiment 4 on 25 May 1990 into a dry seedbed. Each plot was sown with 80 seeds at a depth of 50 mm using a manually operated machine planter. After sowing, 15 mm water was applied, using the same sprinkler system as in 1989.

Environmental measurements

Soil temperature at a depth of 5 and 50 mm and air temperature 200 mm above the ground were measured using copper–constantan thermocouples. These measurements were replicated three times and recorded at hourly intervals on an automatic data logger from one day after sowing (DAS) until the end of the experiments.

Soil samples were taken at depths of 25, 50, 75 and 100 mm immediately after sowing in 1989 and after the 15 mm irrigation in 1990, and then daily at 0600 local time until 10 DAS, using a multiple ring soil sampler. Subsequently, samples were taken approximately every three days. When the seedling roots had reached 200 mm, samples were taken at 100 mm intervals to a depth of 300 mm using a conventional soil sampler. Soil moisture at each level was estimated gravimetrically from three replicate samples.

Plant measurements

Recording of seedling emergence commenced immediately the first seedlings were seen and continued daily at 1700 local time until there was no further emergence.

The numbers of live seedlings were counted daily and dead seedlings were marked with wooden match-sticks. This method provided a check against loss of seedlings by any other means, for example removal by birds or rodents.

A 'thermotolerance index' (TI) was calculated as the ratio of seedlings surviving to the total number of seedlings which emerged.

RESULTS

The environment

Maximum soil surface temperatures (at 5 mm) ranged from 29.8°C (following rain) to 64.0°C. Both these extremes occurred in Experiment 4 (Table 1). The range of maximum temperatures from sowing to the final date of seedling death were similar in all the experiments except Experiment 3. Soil surface temperatures measured throughout the experiments were similar to those previously reported by Gupta (1983, 1986) for similar soils in Rajasthan.

Table 1. *Maximum daily soil temperatures (°C) at 5 mm depth from the first day after sowing (DAS) until the final seedling death count*

	1989		1990	
DAS	Expt 1	Expt 2	Expt 3	Expt 4
1	50.1	51.8	—	—
2	52.6	49.7	52.3	—
3	54.4	57.1	56.4	56.0
4	54.1	48.8	55.4	57.8
5	56.6	42.8	53.7	61.3
6	57.6	55.3	46.0	57.2
7	57.9	50.6	46.5	45.6
8	48.9	52.8	56.2	52.8
9	46.5	54.0	29.8	53.8
10	53.9	55.6	57.7	53.1
11	59.4	57.2	51.6	58.2
12	58.6	45.3	62.3	57.8
13	58.2	50.0	57.8	58.1
14	57.8	51.8	55.4	58.2
15	61.5	51.8	49.1	59.2
16	—	56.3	49.5	58.3
17	—	54.8	64.1	58.6
18	—	51.8	59.6	—
19	—	55.9	59.9	—
20	—	—	59.5	—
21	—	—	58.5	—

The soil moisture content in the 0–50 mm horizon was initially between 5 and 6% in Experiments 1, 2 and 4, and 10% in Experiment 3 (Fig. 1). In all experiments there was a steady drop in moisture content in the three days following sowing. In Experiment 1, 2 mm rainfall three days after sowing partly replenished the soil moisture and in Experiment 2 irrigation (5 mm) was used to restore the soil to field capacity (10% moisture). In 1990, 11 mm rain at 6 DAS in Experiment 3, and 7 mm at 6 DAS in Experiment 4, brought the soil back to field capacity. In Experiments 1, 2 and 4 the loss in soil moisture was about 1.25% a day in the 0–50 mm horizon but in Experiment 3 the daily loss was about 2.3%. However, because the initial moisture content was greater in Experiment 3, the moisture content at 3 DAS when the first seedlings emerged was similar in all experiments. Following the replenishment of soil moisture by rain or irrigation, there was a steady loss of moisture in all experiments to a minimum of about 1% at 14 DAS. In a study conducted in similar soils in western Rajasthan in May, daily losses in soil moisture were about 1.8% in the top 25 mm (Gupta, 1986).

In the 50–100 mm horizon (Fig. 2), soil moisture did not fall below 5% (which is well above the wilting point for these soils) during the time (up to 10 DAS) that the root tips were in this horizon. The root tips of the longest roots of most genotypes had reached a depth of 100 mm by 6 DAS and those of genotype BSEC C4, which had the poorest rate of seedling survival, had reached a depth of 120 mm, confirming that subsequent seedling death was not due to lack of water.

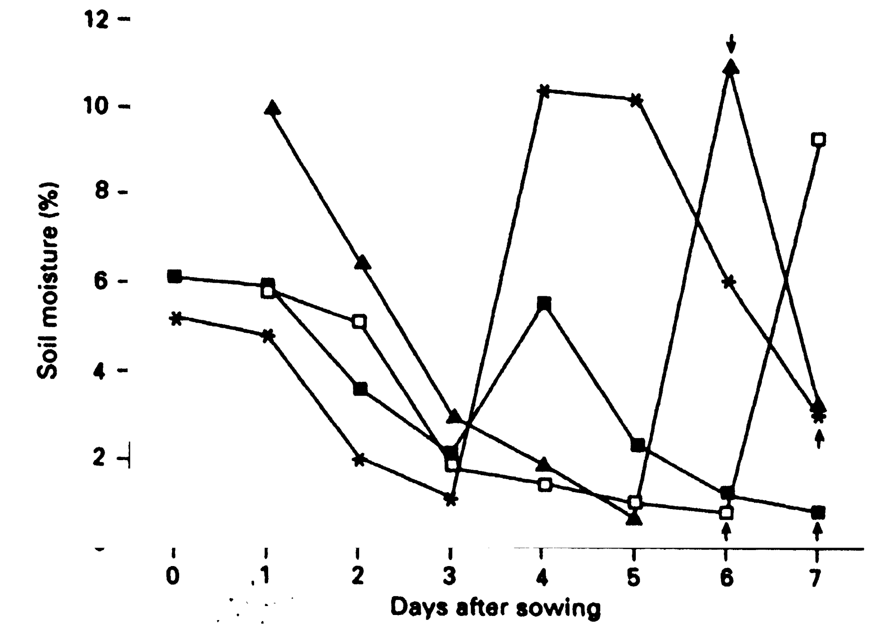

Fig. 1. Soil moisture (at 0–50 mm depth) on successive days after sowing in Experiment 1 (■), 2 (*), 3 (▲), and 4 (□); (arrows denote final seedling emergence in each experiment).

Plant measurements

There was considerable variation between years in seedling emergence (Table 2). This was largely a reflection of the different method of planting and the different seed lots used in the two years. In 1989 when the seeds came from various sources some genotypes, notably BSEC C4 and RCB 2, were subsequently shown

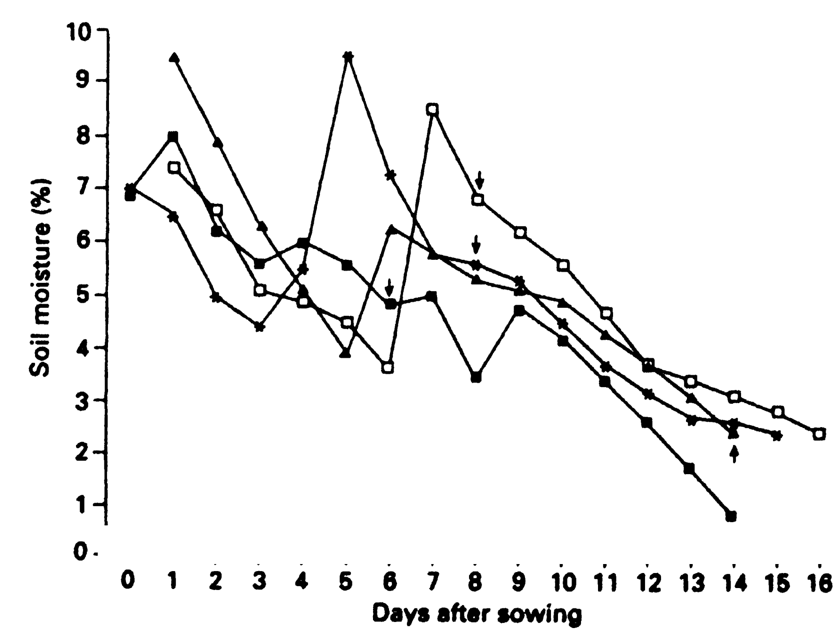

Fig. 2. Soil moisture (at 50–100 mm depth) on successive days after sowing (symbols as in Fig. 1; arrows denote the days when the first seedlings died in each experiment).

Table 2. *Percentage emergence of pearl millet and sorghum genotypes*

	1989		1990	
	Expt 1	Expt 2	Expt 3	Expt 4
Pearl millet				
HHB 67	81	73	80	73
IP 3201	77	76	84	62
IP 3173	63	73	84	74
HiTiP 88	37	38	33	52
NCD2	69	76	85	80
RCB 2	8	13	84	82
ICMH 451	79	63	82	73
IP 3188	74	76	79	56
Sadore Local	59	75	85	72
CZMP 84	75	69	77	69
LaGraP 88	39	52	88	71
WRajPop	53	49	85	74
IP 3273	58	65	83	83
IP 3258	55	62	73	73
IP 3228	90	66	86	73
LaGraP 87	47	45	82	68
IP 3342	79	64	48	53
IP 11145	73	70	88	69
ICMH 423	77	73	89	69
ICTP 8203	49	55	86	71
EC87	50	33	79	81
IP 3218	87	67	88	67
CIVT	31	30	87	75
ICMV 84400	29	29	81	37
BSEC C4	9	7	82	75
Sorghum (SPV 386)	45	49	85	56

to have a poor germination percentage. Although there was considerable variation in germination percentage among genotypes, as found also by Mohamed (1984), the variation was consistent in the two experiments.

In 1990, all the seeds were obtained from panicles harvested in the same field in the same season and all genotypes had a good germination percentage. The percentage emergence was higher in Experiment 3 than in Experiment 4 because the soil moisture content at sowing was greater in Experiment 3. However, differences among genotypes in their percentage emergence were similar in Experiments 3 and 4, except in the case of ICMV 84400 which had very poor emergence in Experiment 4. The poorer emergence in Experiment 4 may be attributed to the higher maximum temperatures between sowing and emergence (Table 1). These could have reduced seed germination, which is particularly thermosensitive (Garcia-Huidobro *et al.*, 1985; Abernethy *et al.*, 1989; Howarth, 1989; Khalifa and Ong, 1990).

In all the experiments the final emergence of HHB 67 was above 70%. This may be because it has a faster germination rate, which Khalifa and Ong (1990) argue may allow it to escape the damaging effects of supra-optimal temperatures.

Table 3. *Thermotolerance index (TI) for pearl millet and sorghum genotypes (rank order in parentheses)*

	1989		1990		
	Expt 1	Expt 2	Expt 3	Expt 4	Mean
Pearl millet					
HHB 67	0.91 (6)	0.76 (6)	0.83 (1)	0.94 (1)	0.86
IP 3201	0.97 (1)	0.82 (2)	0.78 (3)	0.84 (8)	0.85
IP 3173	0.80 (11)	0.81 (3)	0.71 (4)	0.83 (10)	0.79
HiTiP 88	0.72 (18)	0.80 (4)	0.78 (2)	0.80 (13)	0.70
NCD2	0.95 (2)	0.76 (9)	0.46 (16)	0.89 (4)	0.77
ICMH 451	0.92 (3)	0.70 (13)	0.58 (7)	0.79 (16)	0.75
RCB 2	0.76 (16)	0.79 (5)	0.61 (5)	0.82 (12)	0.75
IP 3188	0.91 (5)	0.76 (9)	0.46 (15)	0.83 (11)	0.74
CZMP 84	0.77 (14)	0.63 (15)	0.61 (6)	0.90 (3)	0.73
Sadore Local	0.75 (17)	0.76 (9)	0.55 (8)	0.85 (7)	0.73
LaGraP 88	0.78 (13)	0.76 (9)	0.52 (10)	0.79 (16)	0.71
WRajPop	0.85 (8)	0.61 (16)	0.48 (14)	0.87 (5)	0.70
IP 3273	0.84 (9)	0.75 (11)	0.27 (24)	0.90 (2)	0.69
IP 3258	0.90 (7)	0.82 (1)	0.36 (20)	0.64 (21)	0.68
LaGraP 87	0.84 (10)	0.74 (12)	0.53 (9)	0.55 (23)	0.67
IP 3228	0.79 (12)	0.66 (14)	0.51 (11)	0.69 (18)	0.66
IP 3342	0.92 (4)	0.55 (18)	0.29 (23)	0.80 (14)	0.64
IP 11145	0.69 (19)	0.50 (21)	0.43 (18)	0.84 (9)	0.62
ICMH 423	0.67 (20)	0.53 (20)	0.50 (12)	0.75 (17)	0.61
ICTP 8203	0.66 (21)	0.48 (22)	0.48 (14)	0.66 (19)	0.57
EC 87	0.62 (22)	0.46 (23)	0.33 (21)	0.85 (6)	0.57
IP 3218	0.77 (15)	0.31 (25)	0.45 (17)	0.60 (22)	0.53
CIVT	0.53 (23)	0.37 (24)	0.36 (19)	0.65 (20)	0.48
ICMV 84400	0.48 (24)	0.54 (19)	0.31 (22)	0.53 (24)	0.47
BSEC C4	0.42 (25)	0.55 (17)	0.13 (25)	0.38 (26)	0.37
Sorghum (SPV 386)	0.42 (26)	0.26 (26)	0.12 (26)	0.40 (25)	0.30

Our results suggest that the poor stand establishment of some pearl millet genotypes may be due to poor emergence rather than to subsequent seedling survival, and environmental conditions prior to emergence may be critical. The data suggest that variation in emergence between genotypes could be reduced if all seeds were produced under similar conditions. One genotype, HiTiP 88, showed poor emergence in all four experiments.

Seedling death in Experiments 1, 2 and 4 commenced between 6 and 8 DAS. In Experiment 3 seedlings started to die at a much later stage (16 DAS) because rainfall at 6 DAS reduced temperatures. Indeed, the first seedling deaths did not occur until eight days after the final emergence count in Experiment 3 whereas in the other experiments deaths started to occur at final emergence. In Experiment 3 the seedlings were at a different developmental stage from those in the other three experiments when subjected to heat stress. This resulted in some differences between the experiments in values of the TI (Table 3), most notably in the case of NCD2, IP 3273 and IP 3342, indicating that the capacity of seedlings to withstand heat stress changes with age. The soil temperature and moisture data show that the edaphic conditions, particularly the soil surface temperatures (Table 1), were very similar in Experiments 1 and 4 so that the mean TIs for the two experiments were also similar. Although there were some exceptions, the TI rankings were generally similar between experiments, particularly for the top and bottom performing millet genotypes.

DISCUSSION

There was considerable genotypic variation in the thermotolerance index, which was consistently low in genotypes BSEC C4 and ICMV 84400 but higher in a number of genotypes including the hybrid HHB 67 and the local landrace material IP 3201 (Table 3). These genotypes have now been selected for further study. The superior performance of the ten most thermotolerant genotypes can be explained to some extent by examining their background. Three are local landraces (IP 3201, IP 3173 and IP 3188). IP 3201 is of the 'Barmer' type and grown in sandy soils in western Rajasthan where the rainfall is less than 300 mm (Appa Rao *et al.*, 1986). IP 3173 is a 'desert' type landrace and IP 3188 a 'chadi' type. These landraces are normally grown on sand dunes with limited moisture (Appa Rao *et al.*, 1986). CZMP 84 and RCB 2 are selected open-pollinated varieties from the dry region of Rajasthan. NCD2 is a Nigerian composite that has performed well in extreme environments in Namibia, and Sadore Local originates from the Sahel. HHB 67 is a hybrid that has a pollinator bred from a landrace from western Rajasthan, and HiTiP 88 is an ICRISAT population that is being developed for this region. The good performance of the ICRISAT hybrid ICMH 451 is very encouraging and was unexpected. The pedigree of this hybrid is now being closely examined.

Caution is needed in evaluating the TI data for those genotypes with poor emergence (Table 2). For example HiTiP 88, which has a high TI value, showed poor emergence, which limits its suitability for this region. Likewise, results from 1989, when some genotypes showed poor germination, must be evaluated with care. It may be necessary to combine the data obtained for final emergence with that for TI to produce a 'survival index' as a guide to environmental adaptation.

The poor thermotolerance of BSEC C4 may be explained by the fact that it is based on Togo/Ghana materials that have performed poorly in the Sahel (ICRISAT, 1989). The poor thermotolerance of the ICRISAT variety ICMV 84400 cannot at present be explained from its origin or pedigree. IP 11145 is a landrace genotype from Punjab in India, and the results obtained here indicate that this line is not well adapted to the more extreme environment of Rajasthan. However, IP 3218 (a Rajasthan landrace) performed surprisingly badly for material that has evolved in an area similar to that in which the field trials were held. This landrace is of the 'chadi' type and has a characteristic nodal tillering habit (Appa Rao *et al.*, 1986), which may compensate for its poor stand establishment. Its performance between the replicates in the four experiments was highly variable. The consistently poor emergence and seedling survival of

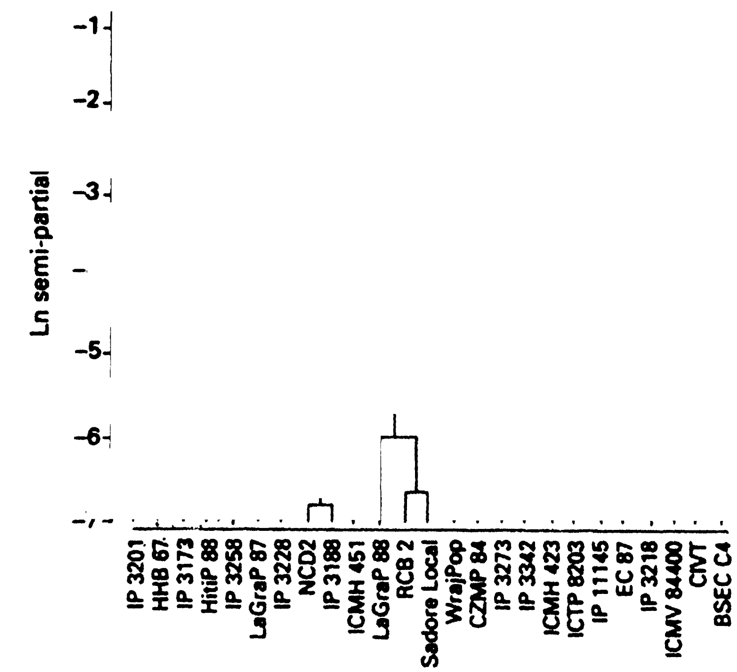

Fig. 3. Dendogram showing the grouping of the 25 millet genotypes on the basis of their thermotolerance index (TI).

sorghum in the experiments supports the hypothesis that pearl millet is more thermotolerant than sorghum (Sullivan *et al.*, 1977).

A dendogram of the log of the semi-partial R^2 values for the 25 genotypes, calculated using War's Minimum Variance Cluster Analysis (Fig. 3), in general reflects the rankings of TIs shown in Table 3. There are three major sub-groups of 4, 13 and 8 genotypes which clearly separate genotypes with high and low TIs. The two genotypes with the highest TIs, HHB 67 and IP 3201, are directly paired and come in the first sub-group. BSEC C4, with the lowest TI, is closely paired with ICMV 88440 and comes in the third group. WRajPop, CZMP 84 and RCB 2, which are open-pollinated varieties selected for this region, are closely paired and fall into the middle sub-group. RCB2, one of the most popular open-pollinated varieties with the farmers of this region, is directly paired with Sadore Local, which is the farmers' local line in many parts of the Sahel, where sowing conditions are almost identical. With the exception of IP 3218, all the landraces collected in the dry regions are clustered together in sub-groups 1 and 2.

The variation in seedling survival among genotypes of pearl millet is now being exploited to determine the mechanism of thermotolerance and to develop a laboratory-based screening technique which will evaluate the thermosensitivity of a given genotype. In sorghum, embryo protein synthesis has been shown to vary with temperature and genotype (Ougham *et al.*, 1988; Howarth, 1989). There is considerable evidence that specific heat shock proteins are involved in the development of thermotolerance (Howarth, 1990); their potential use in the development of quantitative screening procedures is currently being examined. The physiological processes involved in seedling death by 'heat-girdling', caused by extreme soil surface temperatures, are also being investigated. Shoot and leaf growth in graminaceous seedlings occurs from meristems situated near the soil surface and it is the temperature of this region that determines growth rate (Peacock, 1975). Heat injury in this region would affect subsequent shoot growth and survival. There may also be indirect effects, such as the restriction of the movement of carbohydrates to the roots, that ultimately lead to seedling death (Peacock *et al.*, 1990).

The lack of a significant interaction between genotype and experiment showed that the field screening method was repeatable. The broad sense heritability ($h^2 = 0.82$) of the TI trait was high. The nature of the genetic control of seedling thermotolerance is currently being investigated.

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