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RESPONSE OF PEARL MILLET TO LIGHT AND TEMPERATURE

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ABSTRACT

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Temperature exerts a major effect on the rate at which crop plants develop and on processes of expansion and extension. Light determines the rate of growth (i.e., dry-matter production) at any stage of development. But there are important interactions: development can be slowed by low light and growth can be retarded when the temperature is too high or too low.

The simplest development response is that of germination when light is not a factor. Germination rate of pearl millet cv. BK 560 increased linearly with temperature from a base of 10—12°C to a sharply defined optimum at 33—34°C and declined to zero at about 45—47°C. Other developmental processes such as leaf and spikelet initiation and tillering responded similarly to temperature. The limited information available suggests that the base temperature at which development stops is different for contrasting varieties: the rate and the duration of specific developmental processes also differ.

Rate of leaf extension is also a linear function of temperature up to about 34°C so that the time needed to form a complete canopy decreases with increasing temperature below that limit. However, the amount of dry matter produced per unit of intercepted radiation appears to be conservative at about 2.4 g/MJ (+10%) for mean air temperatures ranging from 20 to 36°C. The highest yield, both biological and economic, was obtained at 22°C, mainly because the duration of cv. BK 560 was about 30 days longer at 22 than at 31°C, for example.

The effects of temperature on the distribution of photosynthate and nitrate and nitrogen uptake in other cultivars of pearl millet are also discussed. Priorities for research are summarised in the Conclusion.

GENERALISATIONS

Although many tropical crops are grown in regions where lack of rain is the main restraint on productivity, yields are by no means insensitive to geographical and seasonal differences in other climatic factors. In particular, temperature is the main factor determiming the time from sowing to maturity for an annual crop and the availability of light within the growing season

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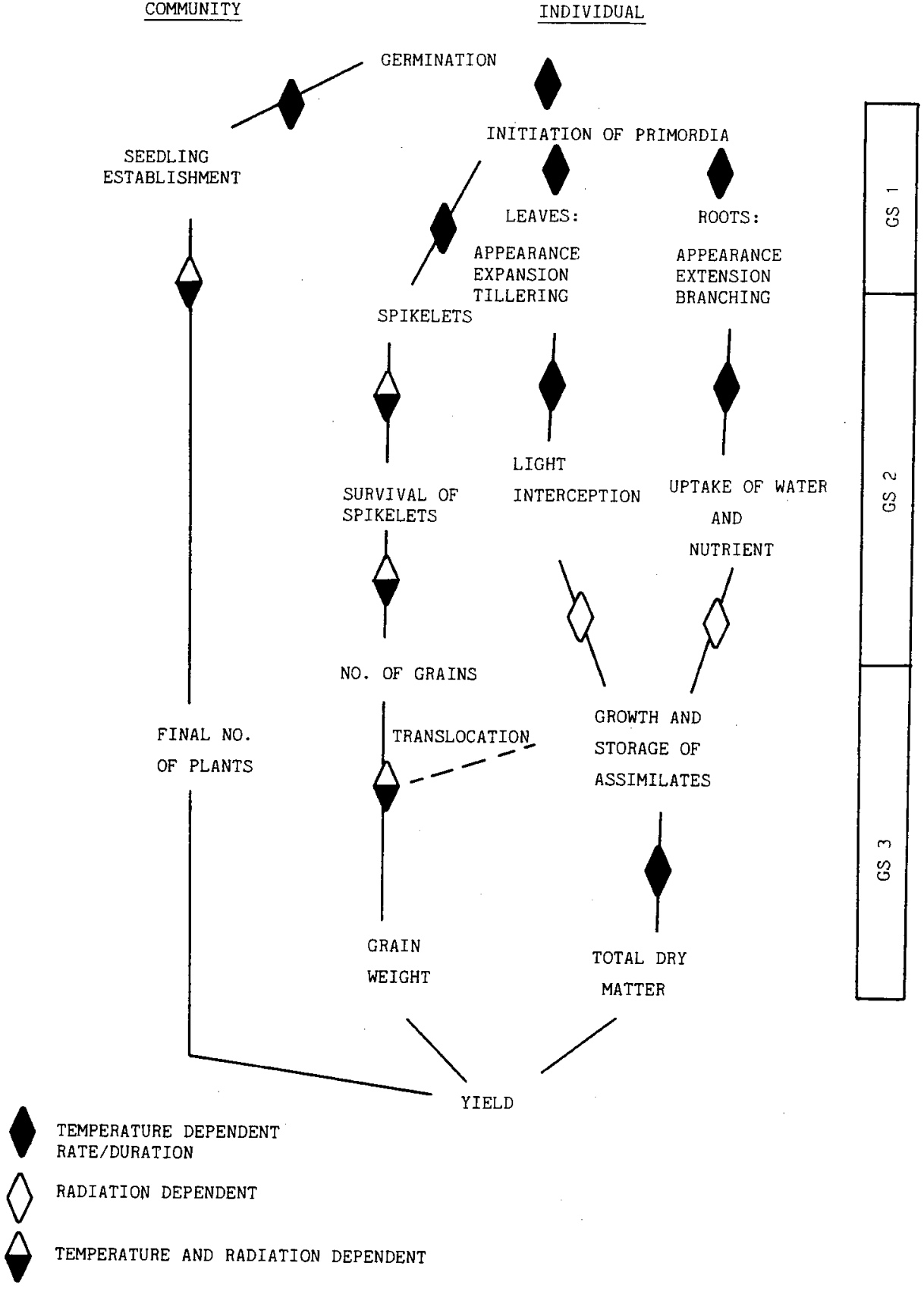

Fig. 1. Flow diagram of the stages of plant development which are influenced by light and temperature.

sets an upper limit to the amount of dry matter which the crop can accumulate when water is abundant. Figure 1 provides a framework for the review of experimental evidence which follows.

All green plants grow and reproduce within a range of temperatures, roughly from 0 to 35° C for species which thrive in temperate climates and from 10 to 45° C for tropical species. The metabolic processes responsible for organised growth cannot function outside these limits. Most processes achieve a maximum rate at a temperature towards the upper end of the range, i.e. at above 25—30° C (temperate) or 30—35° C (tropical). Within this range, temperature, sometimes in association with daylength, controls the developmental timetable of plants. Temperature also interacts with light and with water supply to control the assimilation of carbon by green leaves and the rate at which individual organs grow.

When a crop is sown, the time which elapses before the germination and emergence of seedlings is strongly dependent on temperature as well as on moisture in the seed bed. When the mean temperature is close to either end of the physiological range, slow germination is usually associated with poor establishment because seeds have been attacked by pests or pathogens or simply because the surrounding soil has become too dry. No amount of favourable weather during the growing season can compensate for the small populations of plants so common in the semi-arid tropics, where germination often occurs in rapidly drying soil close to the upper limit of temperature.

In seedlings, the initiation of primordia is the first stage in the development of leaves and roots, sometimes known as "growth stage" 1 (or GS 1) although "development stage" would be more appropriate. The rate at which these organs appear, extend and sub-divide depends strongly on the temperature of the appropriate meristem tissue (and on daylength in varieties of some species).

Early in the life of a cereal crop, the switch of primordial initiation from leaves to spikelets appears to be controlled mainly by daylength or vernalisation. The second stage of growth which follows (GS 2) is marked by the appearance and expansion of successive leaves and by corresponding growth of the root system. In a dense population of plants where roots have access to abundant water and fertiliser, the leaf area index (LAI) usually increases until the foliage forms a canopy intercepting about 95% of the incident light. Thereafter, lower leaves in cereals tend to die as new upper leaves emerge. The amount of foliage needed to achieve this limit ranges from a LAI of about 3 in stands with very horizontal leaves to 10 or more when the leaf disposition is very vertical. For many cereals, including millet, the range appears to be about 4 to 6. On the other hand, when the population is small, or when the expansion of leaves is restricted by lack of water or nutrients, the interception of light at the end of GS 2 may be only a small fraction of the maximum possible figure.

During GS 2 the rate of tillering depends on the number of leaves on the

main culm, which is governed by temperature and daylength. The duration of tillering is mainly influenced by the supply of assimilates which is determined, for example, by plant population or timing of reproductive growth.

During GS 2, the rate at which spikelets are initiated and the number which survive to become florets depends in a complex way both on light (determining the supply of assimilates) and on temperature (determining the rate of development). For some cereals, including millet, and over a restricted range of temperature, the number of spikelets and grains seems to depend on the supply of assimilate per unit of time as perceived by the reproductive system. The most appropriate way of expressing this quantity appears to be in grams of dry matter per degree day or in megajoules per degree day in cases where the rate of dry matter production is strongly correlated with intercepted radiation.

In the third stage of growth (GS 3), growth proceeds at a rate which depends both on light through the current supply of assimilates and on temperature through its control of cellular division and expansion. In many cereals, and particularly in millet, it appears that adverse weather during this stage can be compensated by the translocation to grain of material previously stored in stem tissue. In ideal conditions, grains continue to grow until they reach a maximum size which is genetically determined; but growth can be curtailed by the premature death of all green tissue and the exhaustion of stored material. In the semi-arid tropics, the length of GS 3 is often determined by the amount of water available to the root system at a time when roots, like leaves, are rapidly dying.

Finally, the yield of a crop per unit of field area depends on the product of three factors whose dependence on temperature and light has already been indicated:

(1) the number of plants per unit of field area depending mainly on soil temperature and water after sowing and during GS 1;

(2) the weight per plant, depending mainly on the interception of light per plant during GS 2 and 3 and on the length of these stages as determined by temperature and water;

(3) grain weight as a fraction of total dry weight. This fraction depends mainly on grain number per plant and therefore on light and temperature in GS 2. There is usually much less fractional variation in weight per grain except when weather is very unfavourable in GS 3.

We now consider the influence of temperature and light on the growth and yield of pearl millet, drawing heavily from experimental work by our own group in glasshouse and laboratory work at the University of Nottingham (Monteith et al., 1983).

GERMINATION AND EMERGENCE

Both for germination and for initiation, a rate of development can be specified as the reciprocal of a time t, e.g. the time from sowing seed to the

emergence of a radicle of specified length or the time between the successive appearance of primordial cells. For any range of temperature over which the rate of development is a linear function of temperature T, it is convenient to write

$$1/t = (T - T_b)/\theta$$

where T_b is a base temperature (obtained by extrapolation) at which development stops and θ is the "thermal time" for the process, often expressed as an "accumulated temperature" with units of degree days. The equation is valid for development at temperatures between T_b and a well-defined optimum T_o beyond which the development rate decreased with increasing temperature.

In millet (BK 560) germination rate increased linearly with temperatures from a base of 10—12° C to a sharply defined optimum at 33—34° C and declined to zero at about 45—47° C (Fig. 2; Garcia-Huidobro et al., 1982). Other developmental processes such as leaf and spikelet initiation and the duration of GS 2 respond similarly to temperature (Ong, 1983a). Figure 3 shows the relation obtained for the rate of leaf appearance and temperature.

Table 1 summarises measurements of several processes in BK 560. T_b is conservative, but associated with each process is a specific value of θ which

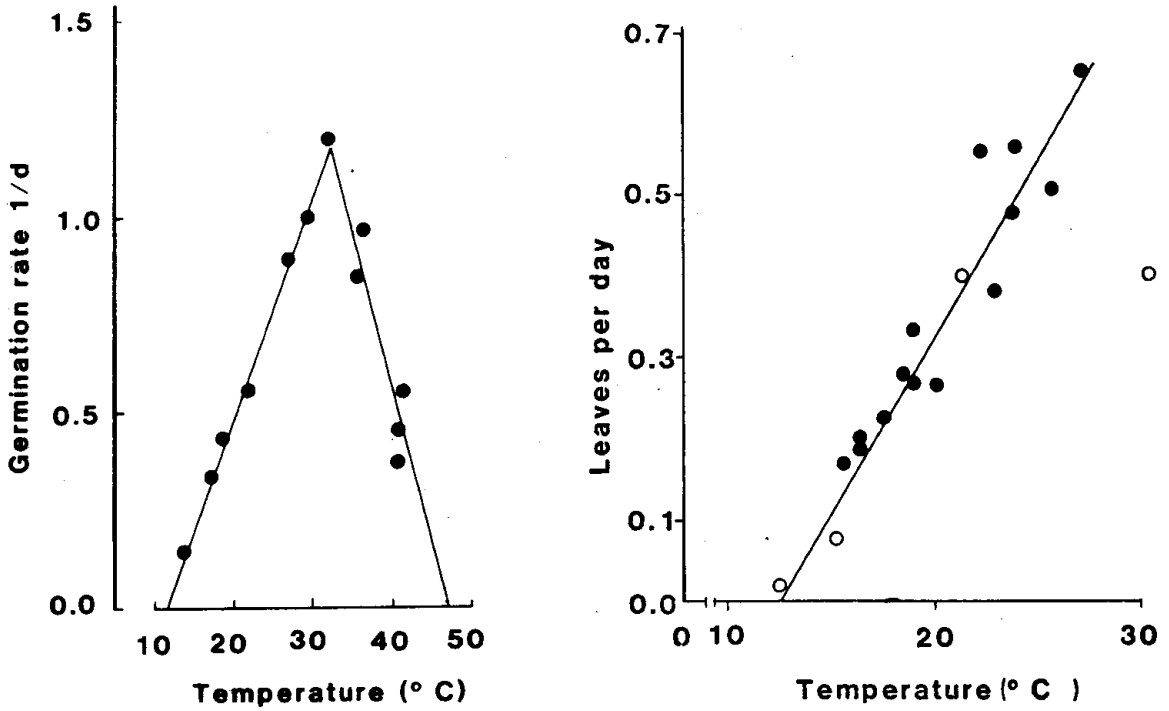

Fig. 2. Germination rate of pearl millet (cv. BK 560) as a function of temperature. Rate is expressed as the reciprocal of time in days for 50% of the seeds in a batch to germinate (Garcia-Huidobro et al., 1982).

Fig. 3. Rate of leaf appearance of millet (cv. BK 560) (•), MX001 (○) and temperature. Data for MX001 are from Pearson (1975).

TABLE 1

Summary of the thermal time θ and base temperature T_b for each specific process or phase of development

Process	θ (°C day)	T_b (°C)
1. Seedling emergence from sowing		
Start	28.0 ± 2.6	11.4 ± 1.1
50%	42.4 ± 1.8	
90%	60.0 ± 6.1	
	Per leaf	
2. Leaf initiation	25.6 ± 3.4	11.3 ± 1.8
3. Leaf appearance	25.0 ± 3.5	12.4 ± 2.0
	24.8 ± 1.7	13.2 ± 3.1
	28.6 ± 1.7	12.0 ± 1.5
4. Tillering from sowing	Start 140—150	
	39.5—45.5 per tiller	
5. Vegetative phase (GS 1) 17 days	Independent of meristem temperature	
6. Early reproductive phase (GS 2)	464	10.0
7. Grain-filling phase (GS 3)	300	10.0

appears to be insensitive to natural variations in irradiance, daylength or saturation deficit, for example. For some aspects of development, closely related varieties also appear to have similar values of θ. For example, there is little variation in θ for leaf appearance in BK 560, MBH 104 (dwarf), GHB 1399 (dwarf), ICH 190, MBH 110 and ICH 105. For these varieties, it is duration of specific development phases which differs.

In contrast, recent studies at Sutton Bonington by H. Mohamed on millet varieties adapted to different environments confirm that there is genetic variation, not only in the rate of germination but also in cardinal temperatures. For instance, a heat tolerant variety, Oasis (P-938) has a low T_b (8.0°C) as well as a high optimum temperature (35.5°C). At a mean soil temperature of 40°C, Oasis would germinate after 1 day compared to 3.3 days for Sanio, a variety from Senegal. This observation confirmed a similar finding at ICRISAT with sorghum that there is a large genetic variation in the ability of seedlings to emerge at high soil temperature (Wilson et al., 1982). Comparable variation in the rate of emergence exists within seed populations and in BK 560 it has been shown that such variation is largely due to differences in the value of θ. The reason for such variation is unknown. Possible causes under investigation include seed size, degree of

seed maturity and storage condition. Rapid emergence and establishment are essential to minimise the risk of heat and moisture stress in areas where soil surface temperatures often exceed 40°C.

When seeds were exposed to pairs of alternating temperatures, the rate of germination and the germination percentage were close to values predicted from measurements at constant temperature, provided the maximum temperature did not exceed 42° C during imbibition. Exposure to high temperature during imbibition slowed germination and reduced the number of seeds which germinated. No seeds germinated where the maximum temperature of the cycle exceeded 47° C. The adverse effects of heat stress were much less severe when seeds were allowed to imbibe water for 8 h before exposure to high temperature. These laboratory observations by Garcia-Huidobro (1982) are directly relevant to problems of poor germination in the tropics where the temperature a few centimetres below the surface of bare soil is frequently in the range 40 to 50° C during the day (Monteith, 1979).

DEVELOPMENT OF LEAF AREA AND INTERCEPTION OF RADIATION

After seedling emergence, both temperature and light influence yield since dry matter production is almost proportional to intercepted radiation during the vegetative growth of cereals (Gallagher and Biscoe, 1978).

In millet, the maximum number of leaves produced is determined during GS 1, a duration which is largely controlled by daylength (Ong and Everard, 1979). During this period, the temperature of the soil surface determines the rate of leaf initiation (Watts, 1974) so that more leaves are produced at high

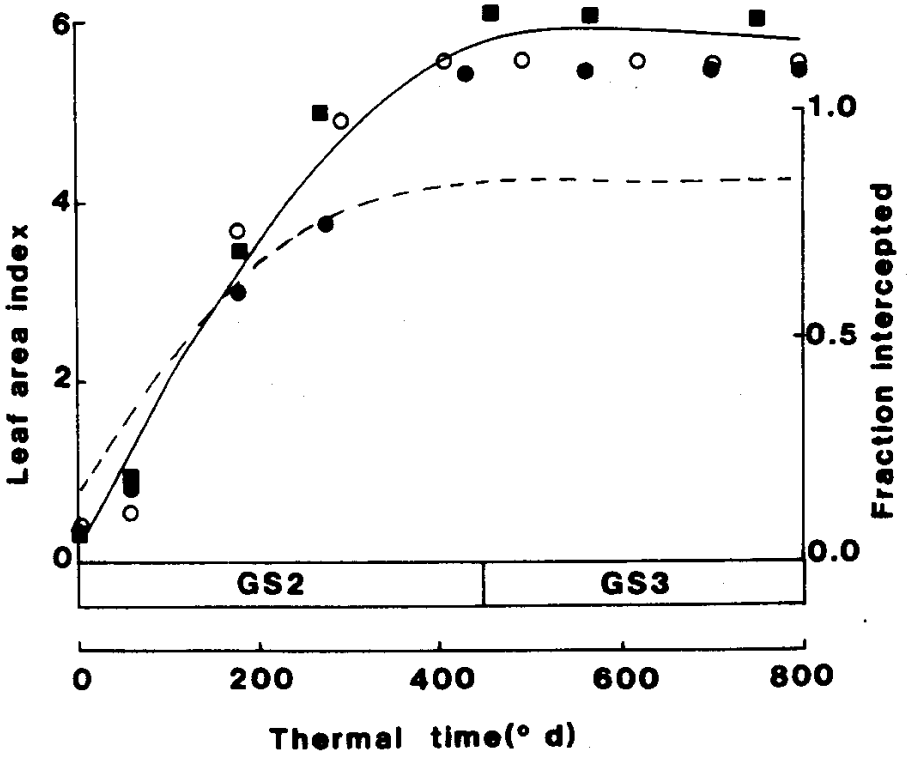

Fig. 4. Formation of leaf area index and interception of light (-------) of millet (cv. BK 560) at 31 (•), 25 (▪) and 19 (○) °C.

temperatures (Helmers and Burton, 1972; Coligado and Brown, 1975, for maize; Ong, 1983a).

During the rapid increase in LAI characteristic of GS 2, the rate of leaf expansion in cereals increases almost linearly with temperature. Figure 4 demonstrates this response for three stands of millet cv. BK 560 grown at mean air temperatures of 31, 25 and 19°C with a diurnal cycle of ± 5°C. For each temperature regime, maximum LAI was reached at the end of GS 2 when θ was approximately 450°C day corresponding to a range of durations from 52 days at 19°C to 25 days at 31°C. These canopies intercepted 70% of the incident radiation when LAI approached 3 to 3.5.

Reduction in the length of GS 2 at higher temperatures more than offsets the apparent benefit of warmth in shortening the time taken to achieve maximum light interception. It is clear from the measurements summarised in Table 2 that high temperature can severely reduce yield by shortening the period over which light is intercepted. The implications of this interaction between temperature, intercepted radiation and the duration of GS 2 on grain yield will be explored later.

TABLE 2

Duration of GS 2 and the accumulated intercepted radiation at five mean temperatures

Mean air temperature (°C)	Duration of GS 2 (days)	Total intercepted radiation during GS 2 (MJ m^{-2})
31	25.1	93
28	30.5	133
25	33.1	178
22	41.4	205
19	51.6	238

Little is known about the effects of high temperature (> 32°C) on leaf area development. Evidence from maize (Watts, 1974) and sorghum (Peacock and Heinrich, 1984) suggests that the rate of leaf extension declines rapidly between 35 and 40°C. Our own measurements suggest an optimum temperature of 32—34°C for millet (Fig. 5). High temperature is usually associated with rapid transpiration, so that the maximum rate of extension is seldom maintained except for brief periods in the morning. The measurements summarised in Fig. 4 suggest that the increase of LAI is slightly slower at 31°C than at 28°C, probably because of a greater demand for evaporation. In contrast to sorghum (Peacock, 1982), the base temperature is nearer 10°C than 15.5°C (Fig. 5). A T_b of 10°C is consistent with the extrapolated values obtained for several developmental processes (Table 1).

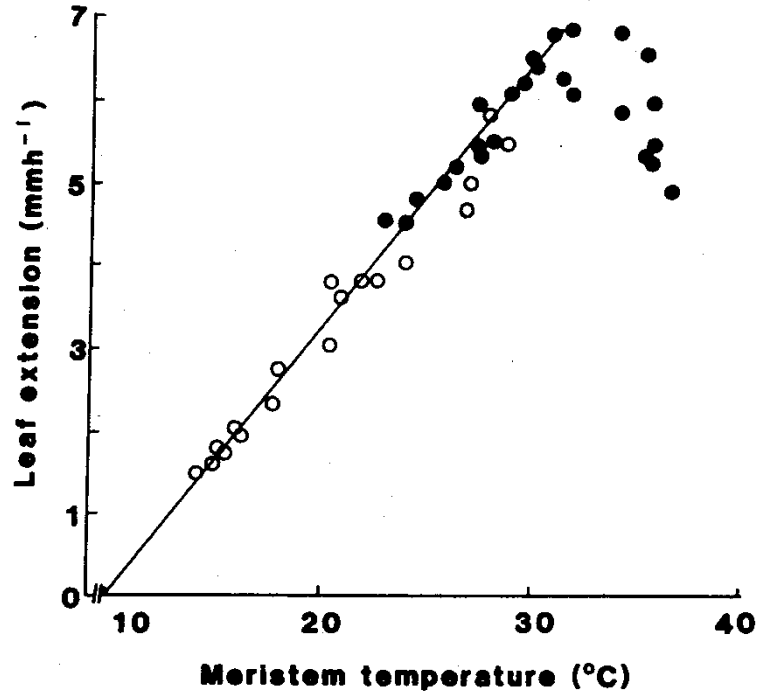

Fig. 5. Rate of leaf extension of millet (cv. BK 560) as a function of temperature (Ong, 1983c). Hourly extension rate of leaf 7 of plants at 19°C (○) and 31°C (●).

ROOTS

The rate of root elongation of millet is also a linear function of temperature with a T_b of about 12°C (Fig. 6). Similar rate/temperature relationships have been established for the roots of maize (Blacklow, 1972) and cotton

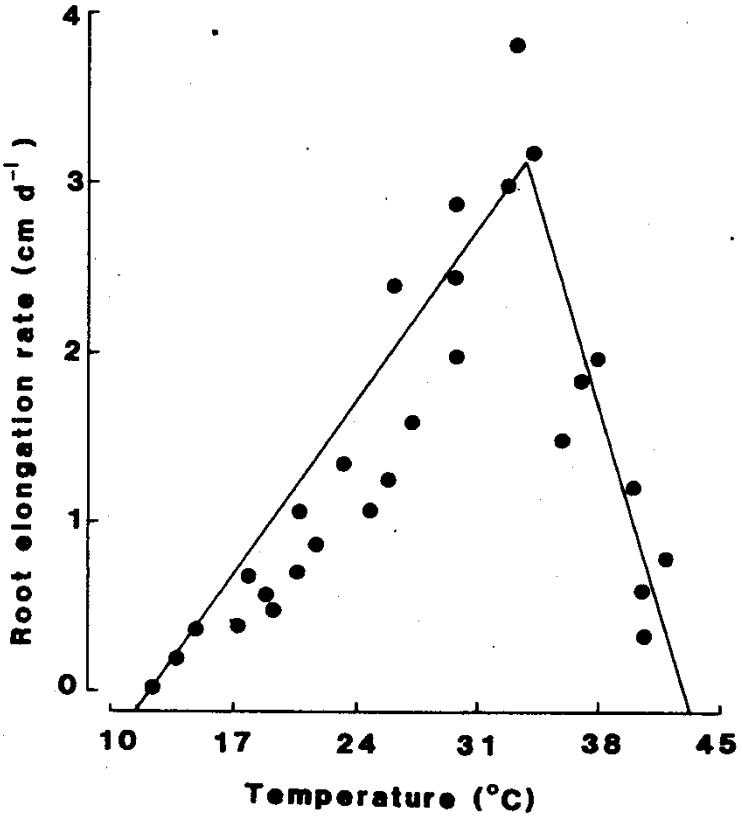

Fig. 6. Rate of root elongation of millet (cv. BK 560) as a function of temperature. Lines are fitted by eye. (reproduced from Garcia-Huidobro, 1982).

(Arndt, 1945). The elongation of roots is usually measured on young seedlings since it becomes increasingly difficult to extract all the roots from the soil. The production of root axes in cv. BK 560 is closely correlated with the number of leaves produced on the main culm and with the soil temperature at 5 cm depth (Gregory, 1983). For this process too, the value of T_b obtained by extrapolation is about 10°C which is consistent with values established for many developmental processes (Table 1). Root elongation, as recorded experimentally, is a consequence of both cell division and cell expansion.

TILLERING

Leaves from tillers can account for 60 to 70% of the total leaf area in a healthy millet crop (Gregory and Squire, 1979). Although the photosynthetic efficiency of leaves on tillers may be less than on the main culm (since they are usually shaded) they sometimes make a major contribution to final yield (Egharevba, 1977). There is much evidence that tillering in cereals is sensitive to both temperature and light. In general, basal tillers start to emerge after the production of a specific number of leaves which can be quantified in terms of thermal time (Ong, 1984). Subsequent tillers are produced at a rate which is further associated with the number of leaves on the main culm. Varietal differences in tillering have been reported. Begg (1965) found that the variety Katherine Pearl tillered after four to five leaves were present compared to eight to nine leaves for cv. Ingrid Pearl (Pearson, 1975).

Many workers concluded that T_b and T_o for rate of tillering are both lower than for the production and expansion of leaves (Pearson, 1975; Ivory and Whiteman, 1978). Our own studies on vegetative and reproductive plants suggest that although differences are small they may exist when the dominance of the main stem is modified by photoperiod or when the light regime within the canopy is modified by temperature or plant spacing. In long days, for instance, the longer duration of GS 1 increased the number of tillers produced mainly because tillering continues for a longer period (Ong, 1983a). When light competition is reduced or delayed by decreasing plant population or low temperature, tillering increases dramatically. For millet (BK 560) grown in Niger, a stand with 2.9 plant m^{-2} had 2.8 times more tillers than a stand with 11.5 m^{-2} (Azam-Ali et al., 1984). Fussell et al. (1980) reported even more prolific tillering for the same species: 7.8 times more at 21°C than at 30°C.

Temperature has a major influence on the final number of tillers produced, the productivity of basal tillers and tiller survival (Table 3). Comparison of tiller fertility and survival at five temperatures showed that the optimum temperature was 25°C but the optimum for the grain yield of basal tillers was slightly lower — about 22°C.

The agronomic significance of tillering is most evident in a millet—legume intercrop when most of the increase in yield is usually derived from the additional tillers produced (Reddy and Willey, 1980).

In pure stands, high tillering ability may be disadvantageous in those areas where it is grown for grain. Although tillers may make up over 60% of the total dry matter of the crop they represent only about 15% to the grain yield since many failed to produce grains. Egharevba (1977) concluded that, in Nigeria, reducing tillers from ten to three or five consistently increased grain yield of millet (cv. Ex-Bornu) by 15 to 30%. On the other hand uniculm plants yielded about 20% less than the high tillering control.

TABLE 3

Final number of tillers per plant, tiller fertility, tiller survival and grain yield (Ong, 1984)

	Treatment (°C)				
	19	22	25	28	31
Number of tillers per plant	6.6 ± 2.4	5.1 ± 2.3	4.6 ± 1.6	4.4 ± 1.0	3.7 ± 1.4
Tiller fertility (%)	40	45	50	43	42
Tiller survival (%)	83	70	80	77	75
Grain yield g per tiller					
MC	9.6 ± 6.5	15.5 ± 4.0	15.9 ± 7.0	11.7 ± 0.5	10.3 ± 3.0
T3	9.1 ± 2.7	13.6 ± 4.1	11.9 ± 6.0	8.4 ± 2.0	9.4 ± 2.3
T4	7.0 ± 3.6	4.0 ± 2.8	2.8 ± 1.8	2.0 ± 1.5	1.5 ± 0.8

PHOTOSYNTHESIS, DRY MATTER PRODUCTION AND LIGHT

The photosynthesis of millet leaves has been measured in the laboratory but not in the field as far as we are aware. McPherson and Slatyer (1973) established light-response curves for the leaves of cv. Katherine Pearl exposed to artificial light with a specific quantum flux density up to 4000 μE m^{-2} s^{-1}. When the irradiance was less than about 400 μE m^{-2} s^{-1} (equivalent to about 170 W m^{-2} or one fifth of full sunlight) the photosynthesis rate increased almost linearly with irradiance at about 6.0 g CO_2 per MJ of total radiation. At an irradiance equivalent to half of full sunlight, the efficiency was about 4.5 g/MJ and in full sunlight it was about 2.7 g/MJ. Assuming arbitrary factors of 60% for the loss of CO_2 by respiration and 30/44 for the relative weight of dry matter and CO_2, corresponding figures for the efficiency of dry matter production are 2.5, 2.0 and 1.1 g per MJ of *total* radiation for 20, 50 and 100% of full sunlight.

In a crop canopy, the average irradiance of a leaf is usually less than the irradiance as measured on a horizontal surface above the canopy. When the sun is shining, the average irradiance is approximately KI where the extinction coefficient K, depending on the architecture of the canopy and the

geometry of the sun, has a value of about 0.5 for millet (Marshall and Willey, 1983) during the central hours of the day. The efficiency of dry matter production by a canopy would therefore be expected to be in the range 2.0 to 2.5 g/MJ. For comparison with field measurements by our colleagues, by ICRISAT staff and by Begg (1965), we have calculated the weight of dry matter produced by stands of millet per unit of radiation intercepted by the foliage before anthesis (Table 4). Values for three well-watered crops ranged from 2.15 to 2.37 g/MJ, consistent with prediction. For an unirrigated stand growing mainly on stored water after the monsoon the figure was 2.0 g/MJ, and for a crop growing entirely on stored water on a sandy soil in Niamey it was 1.5 g/MJ. Corresponding figures for the period from sowing to harvest were smaller by about 30% on average, consistent with the decline in canopy photosynthesis after anthesis in the absence of new leaves.

When we repeated this type of analysis for crops growing in our glasshouse at mean temperatures between 19 and 31°C, we obtained mean figures of 3.1 g/MJ (to anthesis) and 2.4 g/MJ (whole season). These values were expected to be larger than those for field crops growing in the tropics because the irradiance was only 10 MJ m^{-2} day^{-2} but the pre-anthesis figure was not

TABLE 4

Dry matter production, insolation, temperature and conversion rate at three sites

	Hyderabad (India)			Niamey[3] (post monsoon)	Katherine, Australia[4]
	1977 (post monsoon)[1]		1978 (monsoon)[2]		
	Irrigated	Unirrigated			
Total dry matter at maturity (g m^{-2})	622	312	810	300	2174
Maturity (days after sowing)	68	68	75	70	112
Mean air temperature (°C)	21.5	21.5	25.8	27.4	28.1
Mean daily insolation (MJ m^{-2})					
Whole season	15.2	15.2	17.9	17.0	21.3
Pre-anthesis	14.1	14.1	18.0	19.0	21.0
Total intercepted radiation (MJ m^{-2})					
Whole season	448	290	530	256	1576
Pre-anthesis	207	192	170	153	887
Conversion rate (g MJ^{-1})					
Whole season	1.49	1.14	1.38	1.17	1.26
Pre-anthesis	2.35	2.0	2.15	1.50	2.37

Reference: [1] Squire et al. (1984); [2] Marshall and Willey (1984); [3] Azam-Ali et al. (1984); [4] Begg (1965).

expected to exceed the dim light figure of 2.5 g/MJ which McPherson and Slatyer obtained for single leaves. Either their leaves were stressed — which is unlikely — or our plants were intercepting more light than we calculated, possibly because of lateral illumination in a stand which was 2.0 m high but only 32 m^2 in area. We did not harvest plants growing within 0.3 m of the walls but this precaution may not have been adequate.

Although the absolute values of efficiency for our glasshouse plants may be somewhat too large because of edge effects, we have no reason to doubt the validity of *relative* values measured at different temperatures as shown in Fig. 7. Above 21° C, the fractional change of efficiency with temperature is small but there is a broad maximum at about 25° C. The single leaves monitored by McPherson and Slatyer reached a maximum photosynthesis rate at about 35° C (and, very surprisingly, maintained about 60% of the maximum rate even at 50° C). Their measurements and ours can be partly reconciled if our lower maximum reflects the effects of temperature on senescence as well as on the maximum photosynthesis of a young leaf. We were measuring the response of a population of leaves which aged the faster, the higher the temperature was.

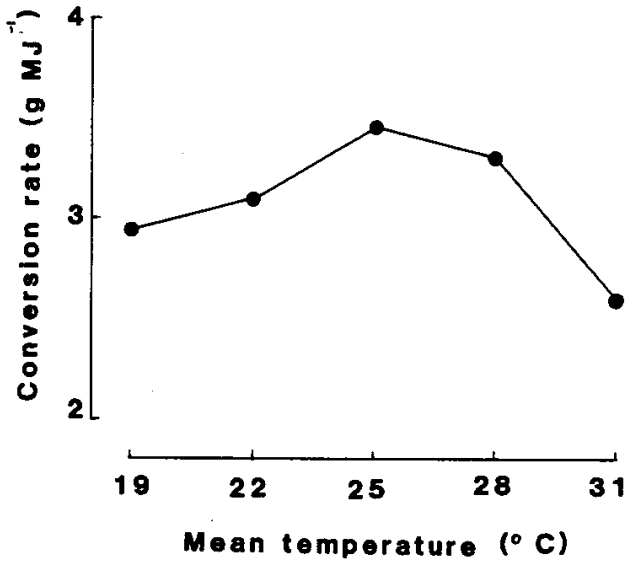

Fig. 7. Rate of dry matter conversion (g/MJ) of millet stands (cv. BK 560) at five mean temperatures. From Squire et al., 1984.

TRANSLOCATION OF ASSIMILATES

Pearson and his co-workers (Pearson et al., 1977; Pearson and Derrick, 1977) compared the photosynthesis and translocation rate of three millet genotypes at four mean temperatures between 15.5 and 30.5° C. Photosynthetic rate was relatively high above 24° C (90 ng CO_2 cm^{-2} s^{-1}) but fell to 20 ng CO_2 cm^{-2} s^{-1} at 15.5° C when all genotypes retained more photosynthate and had a higher concentration of sucrose. The two cold-tolerant hybrid millets retained more photosynthate than the cold-sensitive genotype, Ingrid Pearl, which was unable to accumulate chlorophyll in the mesophyll

of some leaves. Sensitivity of photosynthesis to low temperature was apparently not related to the physical properties of membranes because there was no change within 5 days at 15.5° C.

The rate of translocation is strongly influenced by the thermal history of the plant: Fussell and Pearson (1978a) found that the rate remained slow when plants previously grown in a 21/16° C day day/night regime were transferred to 33° C. They suggested that the slow translocation was due to an inefficient leaf structure, although panicle growth was retarded.

UPTAKE AND DISTRIBUTION OF NITRATE

The rate of nitrate uptake was closely correlated with dry weight increment so that 41 mg N was accumulated per gram of whole plant dry weight, irrespective of temperature (15.5 to 27.5° C) for two contrasting millet genotypes (Theodorides and Pearson, 1981). The relative rate of N uptake was more than twice as fast at 27.5° C than at 15.5° C. In contrast to the constancy of N uptake per unit dry weight, the distribution of N was affected by low temperature, which resulted in high levels of total root N and nitrate in root and stem apices. The accumulation of N at low temperature was due to slow nitrate reduction in the roots (Theodorides and Pearson, 1982). Temperature has no effect on the proportional distribution of N between organs of the shoots.

THE EFFECT OF TEMPERATURE AND LIGHT ON GRAIN YIELD

The damaging effect of extremes of temperature on spikelet survival and the number of grains per panicle is well documented (Fussell et al., 1980; Ong, 1983b). Figure 8 shows the relation between the number of grains produced by two millet varieties as a function of mean air temperature. Both sets of data indicate an optimum temperature of 22 to 25° C above and below which grain number declines sharply. At low temperatures, grain number is probably reduced by the direct effects of spikelet death, spikelet sterility and male sterility (cf. Downes and Marshall, 1971, for sorghum).

Environmental factors which affect either growth rate per plant or development rate, through temperature, have a clear influence on grain number at final harvest (Fig. 9). For example, the difference between the 22 and 28/29° C treatments in two consecutive years was caused by the amount of radiation intercepted. On the other hand, differences between temperature treatments in 1979 were strictly due to the rate of development. The Hyderabad data confirmed the finding that post-anthesis growth rate had neglible influence on grain number since the unirrigated stand stopped growing after anthesis (44 DAS) while the irrigated stand grew for another 26 days. Final plant weight reached 10.9 and 22 g respectively.

Even more conclusive evidence for the importance of the duration of GS 2 is reported by Fussell et al. (1980). They showed that when plants were

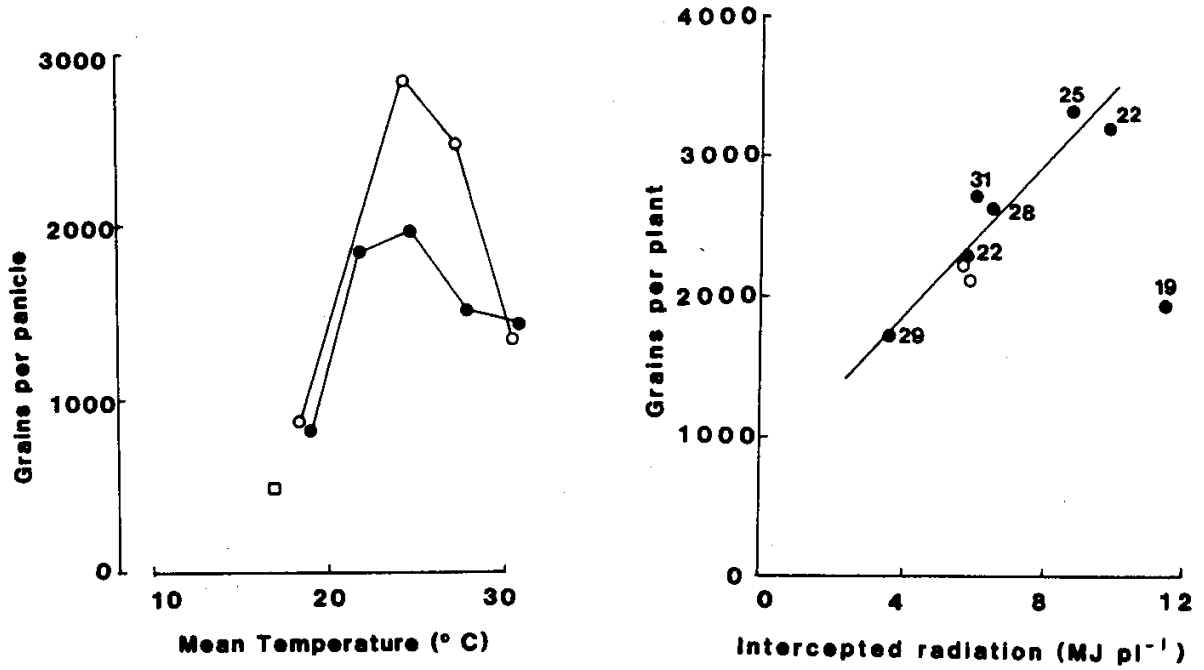

Fig. 8. Final number of grains per panicle as a function of mean temperature. Data for BK 560 (•) and Trift (○) cultivar (Fussell et al., 1980) were obtained from glasshouse experiments and field data (□) from Fussell and Pearson (1978b).

Fig. 9. Final grain number per panicle as a function of radiation intercepted during GS 2 (cv. BK 560). Mean temperatures are indicated on glasshouse data (•). Data from ICRISAT experiment (Gregory and Squire, 1979) are represented by open symbols.

transferred from one temperature regime to another, at various stages of development, the greatest response of grain number to temperature was during GS 2. Transfer to different temperature regimes after anthesis had little effect on the number of grains produced. Temperature after anthesis appeared to determine the *duration* of grain growth when water was not limiting but had a relatively little influence on the *rate* of grain-filling. Thus the production of larger grains at low temperatures is explained by the longer duration of grain growth. An increase in grain weight was also observed when grain number is reduced during GS 2. However, such compensatory growth was seldom large enough to increase the harvest index, even when growing conditions improve after anthesis.

HARVEST INDEX

A comparison of harvest index and plant size for cv. BK 560 grown at different irrigation, spacing and temperature regimes supports the hypothesis that the final number of grains produced is determined early in the life of the crop and the large differences in plant size after anthesis have a relatively small effect on the final harvest index, unless tiller mortality is substantial (Fig. 10). From a spacing experiment in Niamey and an intercrop experiment in Hyderabad, harvest index was conservative in the range 0.34 to 0.45, despite a four to five-fold difference in plant size. During GS 2 there is unlikely to be a large difference between plants sown at the same

date and location either in terms of water extraction and/or radiation interception. Furthermore, the number of grains on fertile tillers is also determined early. The highest harvest index of this set was recorded in a post-monsoon crop (1977) with few vegetative tillers. We cannot explain the low harvest index in the monsoon crop (1978). Low temperature (19°C) in GS 2 also reduces the harvest index because of fewer grains and proportionally more vegetative tillers.

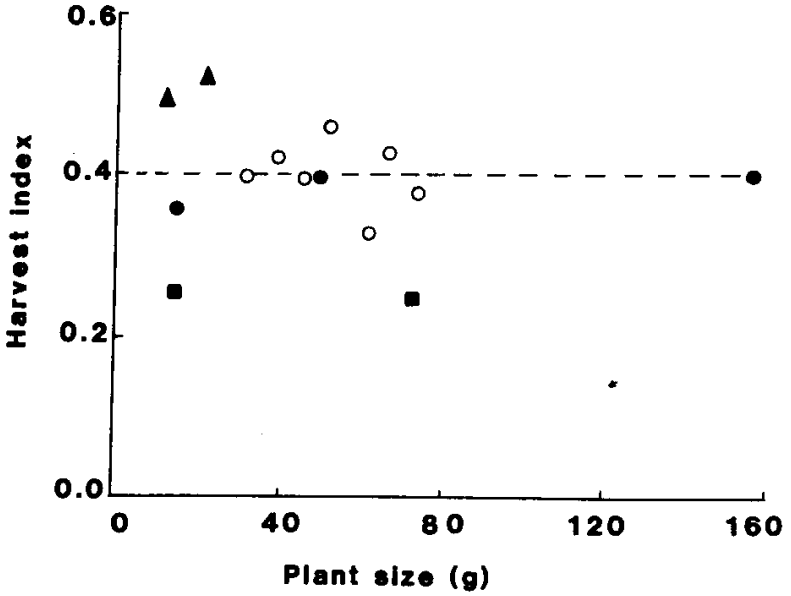

Fig. 10. Harvest index of pearl millet (cv. BK 560) and plant weight (g). Glasshouse crops (○); Niamey crop (●) (Azam-Ali et al., 1984); ICRISAT crops: post-monsoon 1977 (▲), monsoon 1978 (■) (Reddy and Willey, 1980).

CONCLUSIONS

In millet, and presumably in most cereals, developmental processes sensitive to temperature can be divided into two categories. The first category includes the initiation and appearance of leaves and the durations of GS 2 and 3 — processes which are independent of light and therefore of growth rate, at least when plants are exposed to normal sunlight in the field. The second category includes reproductive processes which determine yield potential as expressed by the number of spikelets or grains produced by an ear. Both in the field and in controlled environments, the final number of reproductive units depends on the growth rate of the whole plant (and therefore usually on irradiance) as well as on temperature. The relation between irradiance and thermal time suggested by Nix (1976) was a first step towards the combination of light and temperature in a physiologically appropriate form.

Examples of the first category are relatively well-documented for many cereals. We have been able to reconcile measurements on BK 560 grown in our glasshouses and at two contrasting sites, Niamey and Hyderabad. Both final leaf number and time to anthesis were close to the prediction derived from the thermal time of the duration of GS 1 and GS 2 phases.

In contrast, the second category is less well defined, although its agronom-

ic significance is obvious. The concept of a "thermal growth rate" which incorporates growth rate per unit rate of development is central to our understanding of how yield components are determined, not only in millet, but in all crop plants. A successful attempt has been made to use this concept to explain spikelet survival and grain number in millet (Ong and Squire, 1984) in maize by Hawkins and Cooper (1981), and in wheat by Rawson and Bagga (1979).

In this review, we were able to draw a number of general conclusions from our experience with a single cultivar, BK 560, but we are aware of many gaps in our understanding of how the growth and development of millet respond to environmental factors. The following list summarises priorities for research.

(1) *Germination.* The rate/temperature relationship which was established on a thermal gradient plate needs to be tested in farmers' fields. ICRISAT has already taken a lead in this respect. The value of T_b for contrasting varieties needs to be confirmed for other processes and phases of development as in cv. BK 560 (Table 1).

(2) *Daylength.* The influence of daylength on the duration of GS 1, GS 2 and GS 3 is still obscure. Most existing information fails to distinguish GS 1 and GS 2 and therefore has limited application. Regular apical dissection is necessary in experiments involving daylength treatments. In addition there is virtually no information on how daylength influences the rate of leaf appearance, tillering and growth. Ong and Everard (1979) indicated how morphology and partitioning in millet are particularly sensitive to daylength regimes.

(3) *Grain number.* This is the major component of grain yield, yet our understanding of the mechanisms controlling this process is so poor that no clear concept has been applied to explain variation from year to year and from site to site. The concept of a thermally adjusted growth rate is a promising first step in the analysis of field experiments.

(4) *Survival of spikelets and tillers.* The relation between survival and environment has not been studied systematically although it is widely recognised that the adaptability of millets is associated with tiller production and survival. Development is usually monitored so infrequently that it is difficult to understand the influence of ontogeny and phenology, let alone the physiological basis for tiller survival.

(5) *Genotypic differences.* Large differences in T_b and T_o have been established for the germination of contrasting varieties but the biochemical and genetic basis for this is still unknown.

Until research in these areas makes substantial progress, it will be unsafe to generalise to other seasons and other sites measurements made over a restricted number of seasons and sites. However, we do not believe that a better understanding of physiological processes will necessarily make models of crop growth even more complex. On the contrary, we have found that a search for conservative quantities in biological as in physical systems, can

greatly simplify their analysis and mathematical description. The possibility that base temperature is nearly constant for a wide range of developmental processes in BK 560 is a good demonstration of this principle.

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