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Effect of the Duration of the Vegetative Phase on Shoot Growth, Development and Yield in Pearl Millet (*Pennisetum americanum* (L.) Leeke)

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ABSTRACT

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The duration of the vegetative phase (DVP) in millet, which is the major cause of variation in the crop duration, has marked effects on the number of productive tillers per plant and on mainshoot (MS) and tiller grain yield. Daylength extensions were used to vary the DVP and the effect on factors affecting panicle (tiller) number per plant and panicle yield examined in millet hybrid 841A × J104, grown in the field at Hyderabad, India. Tiller appearance, shoot leaf appearance and leaf area, and stem and panicle growth, in both MS and primary tillers (PTs), were monitored at frequent intervals over the season. At maturity grain yield per shoot was measured.

The concept of thermal time was used to describe shoot development. The rates of tiller appearance and shoot leaf appearance were linearly related to thermal time and were not affected by DVP treatments. The duration of the growth phase from panicle initiation to flowering (GS2) and from flowering to maturity (GS3) was 320 and 390 degree days (°Cd), respectively. There was no difference in rates of leaf or tiller appearance or development between MS and PTs. Tiller appearance, tiller leaf appearance and tiller apical development all ceased at the same time in the later initiated PTs, approximately 550 °Cd from sowing, shortly after rapid stem growth had begun. Tillers that did not survive were all vegetative or in the early stages of reproductive development at this time.

The rate of accumulation of dry matter per plant was similar in all DVP treatments, but in the longer DVP treatments a greater proportion of the dry matter was partitioned to the MS. Mainshoot stem and panicle growth rates were increased by a longer DVP, as was grain yield on the MS, and these were related to increased MS leaf area. Concurrently, growth rates and yields in later initiated tillers were reduced in relation to their leaf areas. Stem growth rate was proportionately increased more than panicle growth rate in the longer DVP treatments and this, combined with a longer duration of stem growth, resulted in greater stem dry matter at maturity and, therefore, in reduced harvest index.

Key words—Pearl millet, thermal time, growth, development, yield.

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INTRODUCTION

Pearl millet (*Pennisetum americanum* (L.) Leeke = *P. typhoides* Staph and Hubbard) is widely grown in two main areas, i.e. N.W. India and the Sahelian zone of W. Africa. In both these zones the major feature of varietal adaptation is the matching of crop duration to the available moisture; thus varieties considered early mature in 85–95 d in W. Africa compared

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with 70–75 d in India. Associated with this difference in crop duration are differences in plant phenotype; longer duration millets typically have higher biomass, higher grain yield per panicle but a lower number of productive tillers (panicles) per plant, and a lower harvest index (HI) (Lambert, 1983*a*; Alagarswamy and Bidinger, 1985; Carberry and Campbell, 1985). Increasing the number of productive tillers and the HI in longer duration millets is considered an important breeding aim (ICRISAT, 1982; Egharevba, Ibrahim, and Okolo, 1983). The work reported here examines the effect of the duration of the vegetative phase (DVP) (the major cause of variation in crop duration: Lambert, 1983*a*; Huda, 1987) on tiller growth and development, their relationship to tiller survival and yield and the implications for breeding for increased number of panicles per plant.

Comprehensive descriptions of tiller appearance and individual tiller yield under various agronomic treatments, including short and long duration environments, have been given by Ramond (1968), Lambert (1983*a*, *b*), Ong (1984), Ong and Monteith (1985), Carberry and Campbell (1985) and Alagarswamy and Bidinger (1985). Generally, tiller appearance is closely related to leaf appearance (Ramond, 1968; Ong, 1984; Coaldrake and Pearson, 1985*a*) and tiller production ceases when stem and canopy growth is rapid (Ong, 1984; Coaldrake, 1985). Less is known about the factors affecting tiller survival, since few studies (but cf. Ong, 1984) have attempted to examine individual tiller growth or development. Data presented by Ong (1984) do suggest, though, that the reproductive status of a tiller may be important in determining its chances of survival.

Both Ong (1984) and Coaldrake and Pearson (1985*b*) have found a significant relationship between number of leaves and grain yield per shoot, which may itself be linked to the size of the apical dome at the commencement of differentiation of the panicle (Coaldrake and Pearson, 1985*b*, 1986). This would suggest that individual shoot yield is related to the duration (longer growth phase) and/or rate (larger apex) of shoot growth, which may be determined by the leaf area of individual shoots. The negative correlation between number of panicles and panicle yield with a longer DVP may be a consequence of a change in partitioning between shoots due to increases in growth rates of the earliest developing shoots.

Dry matter accumulation is increased in longer duration crops, but this does not result in increased grain yield because the additional dry matter is partitioned to stem rather than to panicle growth (Craufurd and Bidinger, 1987; Alagarswamy and Bidinger, 1985; Carberry and Campbell, 1985). Competition from stem growth would appear to be a major limitation to increased yield, but it is not known whether this is a consequence of increased duration and/or rate of stem growth.

Studies by Ong and his colleagues at the University of Nottingham (see Ong and Monteith, 1985 and references therein) have shown that developmental processes in millet (e.g. leaf and tiller appearance) can be described in terms of a base temperature (Tb) and a thermal time (θ), and that growth and development can be combined on a radiation per unit thermal time basis to describe grain yield (Ong and Squire, 1984). Therefore, thermal time has been utilized in this study, having the additional advantages of removing effects of any differences in temperature over the season and in providing field data from a semi-arid environment to compare with the glasshouse studies at Nottingham.

MATERIALS AND METHODS

The experiment was conducted in the field at the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India, in the monsoon (June to October) season 1985. Mean daily temperature was 25 °C and the mean daily incident radiation 17 MJ m^{-2}. Rainfall was 477 mm, about 30% below the long-term average and the crop was irrigated on two occasions.

A single pearl millet hybrid, 841A × J104, which is of medium height (2 m), has 3–4 panicles per plant at maturity and flowers in 45–50 d, was machine sown on ridges 75 cm apart on 21 June. Nitrogen and phosphorus (P_2O_5), at 40 kg ha^{-1}, were broadcast and incorporated into the seedbed before planting, followed by a side dressing of 100 kg urea ha^{-1} 25 d after sowing (DAS). The crop was thinned to 15 cm between plants, giving 90 000 plants ha^{-1}. Plot size was 18 m × 8 rows.

The design was a latin square with three duration of vegetative phase (DVP) treatments and three replications. Pearl millet is a quantitative short-day plant (Ong and Everard, 1979) and the DVP treatments were achieved by imposing daylengths of 13·5 h (normal daylength at Hyderabad in June = DVP1), 14·5 h (+1 h = DVP2) and 15·5 h (+2 h = DVP3). Daylength extensions were achieved by suspending strings of 100 W bulbs over the plots (see Mahalakshmi and Bidinger, 1985; Carberry and Campbell, 1985 for full details), and treatments started 12 DAS (while plants were still in the juvenile phase: Ong and Everard, 1979) and ended 47 DAS, when all plots had started panicle development.

Samples of two 0·8 m lengths of row (approximately 1·2 m^2) per plot were taken every 3–4 d from 14 DAS to 14 d after flowering. For each sample the number of plants was recorded and the sample divided into shoot categories: mainshoot (MS), primary tillers (PT_n, where n is the subtending leaf-sheath) and secondary tillers (ST). For each shoot category dry matter was separated into green leaf blade, stem (including sheaths), panicle and dry leaf components. Leaf area was measured on a leaf area meter. Individual shoot dry weights were obtained by dividing the shoot weights of the 1·2 m^2 sample by the number of shoots. A final harvest of 1·6 m^2, taken one week after maturity (M) on the MS, was treated in a similar manner.

A subsample of one median plant, based on the number of tillers, was taken from each replicate and the number of PTs, STs and the number of leaves on each tiller recorded. A tiller was counted when its leaf tip was visible above the ligule of its subtending leaf sheath. Similarly, a leaf was counted when its tip was visible above the whorl of preceding leaves. Tillers were no longer counted when the most recently expanded leaves had turned brown.

After recording the number of leaves each individual shoot was dissected and the stage of apical development (panicle morphogenesis) noted. Apical development from panicle initiation (PI) to flowering (FL) was described according to a series of distinct morphological stages of, successively, the panicle, spikelet and pistil, based on Maiti and Bisen (1978), Powers, Kanemasu, Piara Singh, and Kreitner (1980) and Waddington, Cartwright, and Wall (1983) (Table 1). The stage of apical development was assessed on the most advanced part of the panicle, which progresses acropetally (Maiti and Bisen, 1978). Since the duration of the phase from PI to FL is constant in thermal time (Ong and Monteith, 1985; Coaldrake and Pearson, 1985*a*), at least in a single hybrid, the scale can be quantified according to the number of degree days required to reach each stage. The scale given was

TABLE 1. *Scale of apical development for use in pearl millet*

Numbers in brackets refer to figures given in Powers *et al.* (1980). Thermal time (°Cd) calculated assuming $Tb = 10$ °C. Data based on hybrid 841A × J104 grown in the glasshouse.

Developmental stage		°Cd (from PI)
Number	Description	
0	Vegetative apex (1)	0
1	Panicle initiation-apical dome elongated (2)	17
2	Branch primordia present at base of apex	50
4	Branch primordia cover 75% apex, starting to expand (4)	85
6	Spikelet and branch primordia present (6, 7)	120
8	Empty glume visible (8)	155
10	Two floret primordia present (10)	190
12	Carpel/ovule primordium present (13)	225
14	Style primordia present	260
16	Style elongation (16)	300
18	Stigmatic branches differentiating, hairs on anthers (17)	335
20	Stigmas fully emerged, pollination (22)	

TABLE 2. *The effect of the DVP treatments on the thermal time (°Cd) to panicle initiation (PI), flowering (FL), maturity (M) and the duration of GS2 and GS3 in the mainshoot*

DVP treatment (daylength)	PI/duration of GS1 (°Cd)	Duration of GS2 (°Cd)	FL (°Cd from sowing)	Duration of GS3 (°Cd)	M (°Cd from sowing)
1 (13·5 h)	360±9·0	325	685±10·5	405	1090±11·8
2 (14·5 h)	470±7·8	360	830± 7·8	370	1200±23·4
3 (15·5 h)	505±6·9	325	830± 6·6	385	1215± 9·9

quantified using two hybrids, 841A × J104 and 81A × Souna B, grown in the glasshouse (Craufurd, unpublished data).

Thermal time (accumulated degree-days, °Cd) was determined from soil and air temperatures recorded at the experimental site on a data logger (Grant Instruments, Cambridge). Soil temperature was used to estimate development while the apex was at or below ground level (stem length < 5·0 cm) and air temperature once the apex was above ground level (Ong, 1983*a*). *Tb* was taken as 10 °C (Ong and Monteith, 1985).

The percentage light interception (f) was calculated from the leaf area (L) using the equation

$$f = 1 - \exp(-KL)$$

where K is the extinction coefficient. The value of K was 0·30 (Squire, Marshall, Terry, and Monteith, 1984; Alagarswamy and Bidinger, unpublished data).

Rates of development and growth on thermal time were all described by linear regression techniques. Plots of stem dry weight on thermal time showed that the linear phase of growth started when stem dry weight was approximately 1·0 g and ended approximately 6 d after FL and regressions were, therefore, fitted between these two points. Panicle growth rate was determined from the early boot stage, about 10 d before FL, through to M. Rates were compared using the method given by Snedecor and Cochran (1980), p. 386.

The lengths of the major growth phases of the individual shoots were determined as the thermal time elapsed between the beginning and end points of those phases, viz., GS1: start of shoot development to PI; GS2: PI to FL (first stigma emergence); GS3: FL to M. The start of shoot development (in thermal time) was estimated using the regression equations of leaf number (Y) on thermal time, where the start was taken as $Y = 0$. PI and FL were estimated from observations made in the field and confirmed by regression equations of apical development on thermal time (not presented). Maturity (black layer formation: Fussell and Pearson, 1978) on the MS was recorded from field observations.

RESULTS

Phenology

The phenology of the MS under the three DVP treatments is given in Table 2. PI was delayed by 110 and 140 °Cd in DVP2 and DVP3, respectively, giving a range in the length of the vegetative phase of 360–500 °Cd. Although the daylength extension treatments continued to 640 °Cd from sowing and, therefore, into the reproductive phase (GS2), they had no effect on the duration of the phase from PI to M which, for this hybrid, was 723±6·7 °Cd.

MS leaf and tiller appearance

MS leaf appearance rates were the same in all DVP treatments (Fig. 1). The thermal time (θ) for MS leaf appearance was 34·3±1·2 °Cd leaf^{-1}. The duration of leaf appearance was extended in DVP2 and DVP3 treatments, since PI was delayed, and the number of MS leaves increased significantly ($P < 0{\cdot}01$) from 19·2 in DVP1 to 22·5 in DVP3.

Tiller appearance followed MS leaf appearance very closely. The first tiller which, in this hybrid, arose in the axil of the third leaf (i.e. PT3), appeared 212 °Cd from sowing (Fig. 2)

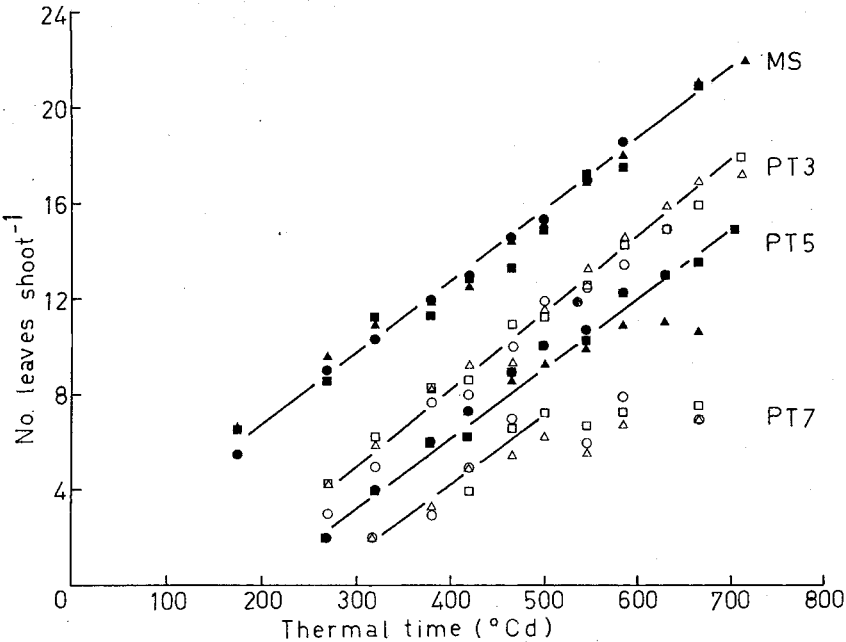

FIG. 1. Leaf appearance against thermal time in the mainshoot (MS) and primary tillers (PT3, PT5 and PT7) in DVP1 (o), DVP2 (□) and DVP3 (▲) treatments. Fitted lines are: MS, $y = 1{\cdot}07 + 0{\cdot}029x$, $r^2 = 0{\cdot}99$; PT3, $y = -4{\cdot}14 + 0{\cdot}032x$, $r^2 = 0{\cdot}99$; PT5, $y = -5{\cdot}40 + 0{\cdot}030x$, $r^2 = 0{\cdot}97$; PT7, $y = -6{\cdot}82 + 0{\cdot}028$, $r^2 = 0{\cdot}92$. Slopes not significantly different.

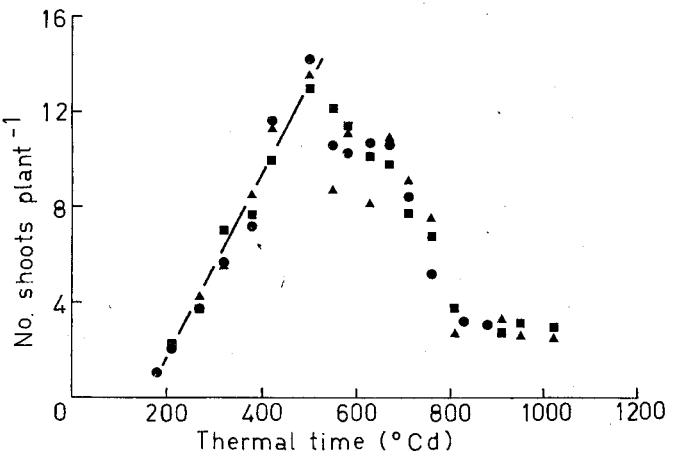

FIG. 2. The number of shoots per plant appearing against thermal time in DVP1 (o), DVP2 (□) and DVP3 (▲) treatments. Fitted line: $y = -6{\cdot}28 + 0{\cdot}039x$, $r^2 = 0{\cdot}97$, $P < 0{\cdot}001$.

when the 5th MS leaf was expanding. θ for tiller appearance was $25{\cdot}6 \pm 1{\cdot}4$ °Cd tiller^{-1} and 12–13 tillers appeared on the MS. Separating tiller appearance into PTs and STs gave values of θ of $43{\cdot}5 \pm 1{\cdot}09$ and $29{\cdot}4 \pm 3{\cdot}70$ °Cd tiller^{-1}, respectively, with STs appearing in the same sequence at PTs, i.e. the first ST appeared when PT3 had 5 leaves, approximately 330 °Cd from sowing.

Tiller appearance ceased and the number of tillers started to decline 500–530 °Cd from sowing. The number of tillers at FL + 14 d (875–1 018 °Cd) was similar in all DVP treatments (Fig. 2).

Leaf appearance in the PTs

Leaf appearance rates in the PTs were the same as on the MS, giving an overall value for θ of $33{\cdot}2 \pm 1{\cdot}7$ °Cd leaf^{-1} (Fig. 1). In the later-initiated PTs (PT5, PT6 and PT7 in DVP3 and PT6 and PT7 in DVP1 and DVP2) leaf appearance ceased before the tiller flag leaf appeared (Fig. 1). The cessation of leaf appearance in these tillers, estimated from the regression equations of leaf appearance on thermal time, was $515 \pm 8{\cdot}4$ °Cd from sowing. Thus tiller appearance and leaf appearance on non-productive tillers ceased at approximately the same thermal time. These later initiated tillers, though they expanded no more leaves, did not die until much later, between 700–800 °Cd from sowing.

Phenology and apical development of MS and PTs

The length of the vegetative phase (start of shoot development to PI), which was shorter in the PTs than the MS because of their later start of development, was affected in all shoots by the DVP treatments (illustrated by DVP1 and DVP3: Table 3). PTs in the same leaf axil

TABLE 3. *The effect of the DVP treatment on the start of tiller development, panicle initiation (PI), flowering (FL) and the duration of GS1 and GS2 in the mainshoot (MS) and primary tillers (PT3–PT7)*

Shoot	Start of tiller development (°Cd from sowing)	Duration of GS1 (°Cd)	PI (°Cd from sowing)	Duration of GS2 (°Cd)	FL (°Cd from sowing)
			DVP1		
MS	—	360	360 ± 9·0	325	685 ± 10·5
PT3	145 ± 9·6	245	390 ± 6·3	290	680 ± 6·3
PT4	160 ± 13·3	245	405 ± 11·2	300	705 ± 12·2
PT5	195 ± 7·6	220	415 ± 7·9	315	730 ± 7·9
PT6	230 ± 14·0	210	440	50[a]	—
PT7	271 ± 20·7	195	465	35[a]	—
			DVP3		
MS	—	505	505 ± 6·9	325	830 ± 6·6
PT3	135 ± 13·0	420	535 ± 7·6	305	840 ± 7·2
PT4	145 ± 8·6	400	545 ± 13·3	315	860 ± 14·2
PT5	175 ± 15·7	370	545	45[a]	—
PT6	220 ± 17·4	345	565	15[a]	—
PT7	280 ± 42·6	Veg[b]	—	—	—

[a] Apical development ceased during GS2.
[b] Apex still vegetative.

started to develop at the same time in all treatments, but their vegetative phase was extended due to the delay in PI in DVP2 and DVP3 treatments. Within each DVP treatment, the occurrence of PI among shoots was fairly synchronous; for example, in DVP1 the MS and PT7 reached PI within 105 °Cd, a difference of about 7 d at a mean temperature of 25 °C.

Extending the DVP had no effect on the duration of the reproductive phase (GS2) (Table 3); θ for this phase was $320 \pm 5{\cdot}1$ °Cd. Thus in all shoots that flowered the rate of apical development from PI to FL was similar, with a mean rate of $0{\cdot}06 \pm 0{\cdot}003$ developmental units $°Cd^{-1}$ (cf. Table 1). In the later-initiated PTs (PT6 and PT7 in DVP1 and DVP2, and PT5 and PT6 in DVP3) apical development ceased during branch initiation (stage 4: Table 1), between 500 and 600 °Cd from sowing depending on DVP (Table 3). Tiller apical development, therefore, ceased at approximately the same time as tiller appearance and tiller leaf appearance. However, the cessation of tiller apical development was not related to the stage of development on the MS, which was at stage 9 (glume to floret primordium) in DVP1 and stage 5 (branch to spikelet primordium) in DVP3. Apex death (meristem discoloured, loss of turgor), however, was not observed until 750–800 °Cd from sowing.

The similar rates of apical development and the near synchrony of PI resulted in all productive shoots flowering within 55 °Cd (about 3 d). Extending the DVP also had no effect on the duration of the grain filling phase (GS3) on the MS; θ for this phase was $387 \pm 9{\cdot}5$ °Cd (Table 2).

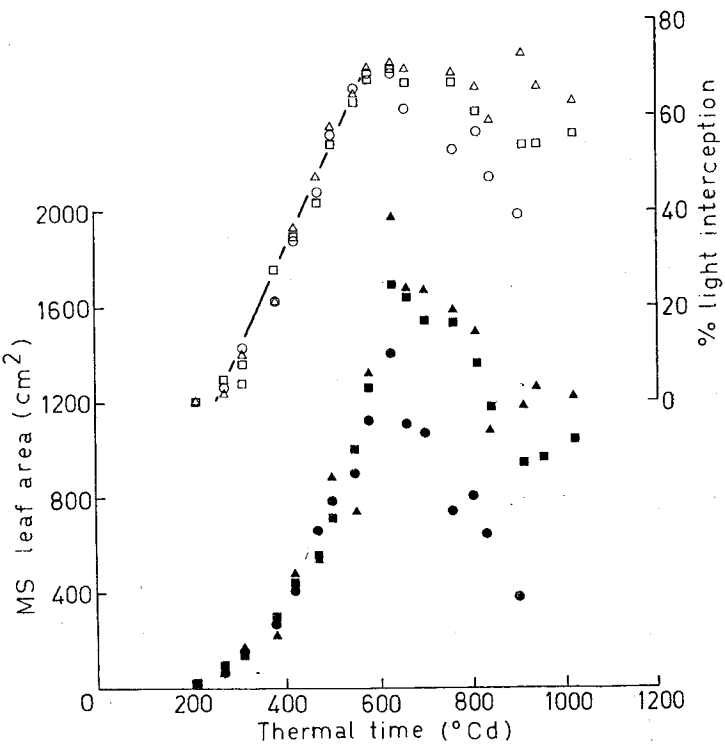

FIG. 3. Mainshoot (MS) leaf area and the calculated percentage light interception by the canopy against thermal time in DVP1 (○), DVP2 (□) and DVP3 (△) treatments. Fitted line for light interception: $y = -58{\cdot}3 + 0{\cdot}22x$, $r^2 = 0{\cdot}98$, $P < 0{\cdot}001$.

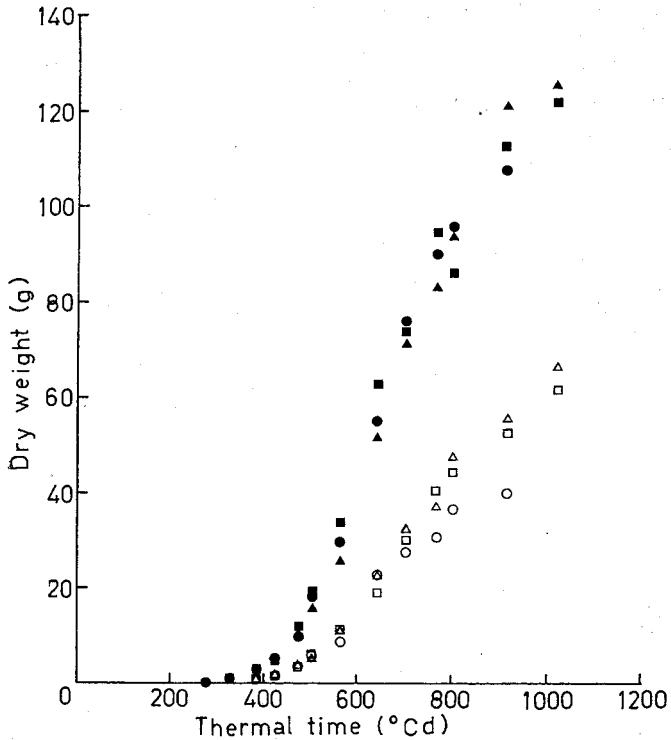

FIG. 4. Total plant above ground dry weight (closed symbols) and mainshoot (MS) dry weight (open symbols) against thermal time in DVP1 (○), DVP2 (□) and DVP3 (△) treatments.

Leaf area, light interception and dry matter accumulation

The DVP treatments affected MS (Fig. 3) and, to a lesser extent PT3, leaf area accumulation, but had no effect on leaf area accumulation in other shoots. Leaf area started to accumulate rapidly from about 300 °Cd in the MS (Fig. 3) (and successively later in the tillers) in all DVP treatments and maximum leaf areas were reached 600–650 °Cd from sowing. The DVP treatments had no effect on the rate of leaf area accumulation, but did extend the duration slightly, resulting in increased maximum leaf area on the MS in DVP2 and DVP3.

Although leaf area per shoot was increased on the MS and PT3 in the DVP3 treatment, there was no increase in the maximum percentage of light intercepted by the canopy. For the canopy as a whole, interception increased from effectively zero at 260 °Cd from sowing to 70% at 570 °Cd from sowing (Fig. 3), when LAI was 3·5 (Craufurd and Bidinger, 1987). In all DVP treatments interception declined after FL.

The rate of accumulation of dry weight per plant in thermal time was similar in all DVP treatments (Fig. 4), reflecting the lack of effect of the DVP treatments on % light interception per unit area (Fig. 3). The total dry weight produced was greater in the DVP2 and DVP3 treatments, however, since the crop duration was longer.

Although at any time total dry weight per plant was the same in all the DVP treatments, there was a progressive difference in the partitioning of dry matter between MS and tillers

TABLE 4. *The effect of DVP treatment on the timing and stage of apical development at which stem growth started, on the rate of stem growth, the duration of stem growth, and the maximum stem dry weight in the mainshoot (MS) and primary tillers (PT3–PT5)*

	Shoot			
	MS	PT3	PT4	PT5
			DVP1	
Start of stem growth (°Cd from sowing)[a]	461	478	472	507
Start of stem growth (stage of development)[b]	7	7	6	7
Rate of growth (g shoot^{-1} °Cd^{-1} ± s.e.)	0·071 ±0·0045	0·039 ±0·0011	0·029 ±0·0035	0·025 ±0·0030
Duration of stem growth (°Cd)[c]	310	356	396	396
Maximum stem weight (g)[d]	22·2	11·9	9·3	7·3
			DVP3	
Start of stem growth (°Cd from sowing)[a]	497	515	521	544
Start of stem growth (stage of development)[b]	0	0	0	0
Rate of growth (g shoot^{-1} °Cd^{-1} ± s.e.)	0·104 ±0·0066	0·050 ±0·0032	0·034 ±0·0046	0·014 ±0·0022
Duration of stem growth (°Cd)[c]	389	472	397	493
Maximum stem weight (g)[d]	40·5	23·6	13·5	6·9

[a] Defined as stem dry weight = 1·0 g.
[b] Stage of shoot apical development (Table 1).
[c] Duration = maximum weight/rate of growth.
[d] Estimation from the regression of stem dry weight on thermal time.

(Fig. 4); the proportion of dry weight in the MS was 37, 51 and 53% of the total dry weight at M in DVP1, DVP2 and DVP3, respectively. Therefore, a reduced proportion of dry matter was allocated to the tillers.

Stem growth on the MS and PTs

Stem growth parameters for DVP1 and DVP3 are presented in Table 4. Extending the DVP slightly delayed the start of the linear phase of stem growth on the MS, but only by 40 °Cd, compared to a delay in the start of PI of 130 °Cd (Table 2). At least in this hybrid, therefore, there was no fixed relationship between the start of the rapid stem growth phase and MS apical development; stem growth started during spikelet initiation in DVP1 (stage 7) and before PI in DVP3 (stage 0) (Table 4). Stem growth started on the PTs after the MS and roughly in the order of tiller appearance. The start of stem growth was, nonetheless, fairly synchronous between the MS and PTs, both in thermal time and apical development stage, with no effect of the DVP treatments (Table 4). Across DVP treatments and shoots, the linear phase of stem growth can be reasonably considered to start 500 ± 6·7 °Cd from sowing in the hybrid used.

The DVP treatments had marked effects on stem growth rates (Table 4); growth rate was increased in the MS and PT3, but reduced in PT5. The increase in stem growth rate on the

MS was linearly related ($r^2 = 0{\cdot}99$) to the DVP (the growth rate increased 22 mg °Cd^{-1} for each °Cd of vegetative phase), but across all shoots there was no simple relationship between growth rate and DVP. As indicated above, the DVP treatments had marked effects on shoot leaf areas which might account for the differences in growth rates between shoots. Indeed, Fig. 5 shows a linear relationship between maximum leaf area and shoot growth rate.

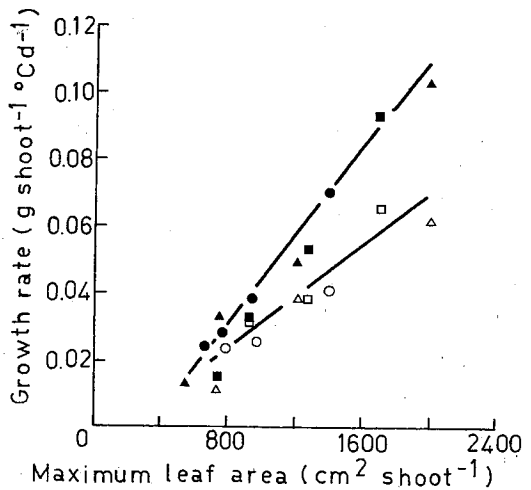

FIG. 5. The relation between stem (closed symbols) and panicle (open symbols) growth rates and maximum shoot leaf areas in DVP1 (○), DVP2 (□) and DVP3 (△) treatments. Fitted lines are: stem, $y = 0{\cdot}022 + 0{\cdot}000065x$, $r^2 = 0{\cdot}97$; panicle, $y = 0{\cdot}009 + 0{\cdot}000039x$, $r^2 = 0{\cdot}90$. Lines significantly different at $P < 0{\cdot}001$.

The DVP treatments also had marked effects on the duration of the stem growth phase, since growth started at about the same thermal time and continued to approximately the same stage of development (FL + 6d); the mean durations of stem growth were $365 \pm 9{\cdot}8$ and $440 \pm 26{\cdot}0$ °Cd in DVP1 and DVP3, respectively.

These effects of DVP on both rate and duration of stem growth resulted in much larger maximum MS and PT3 dry weights (Table 4). Dry weight of stems in PT4 and PT5 were much less affected by the DVP treatments, however, since increased duration was compensated for by reduced growth rate in these shoots.

Panicle growth on the MS and PTs

Panicle growth was also described by fitting linear regressions to weight on thermal time; the growth rates and derived parameters are presented in Table 5.

In contrast to stem growth, there was a significant ($P < 0{\cdot}05$) delay in the start of MS panicle growth due to DVP treatment; panicle growth started $613 \pm 8{\cdot}7$ and $711 \pm 6{\cdot}7$ °Cd from sowing in DVP1 and DVP3, respectively (Table 5). This reflects the much closer relationship between apical development and panicle growth than between apical development and stem growth; while there was some variation among shoots, panicle growth can be considered to start at stage $13 \pm 0{\cdot}5$, i.e. about the time of ovule appearance.

Panicle growth rates responded to changes in the DVP in a similar manner to stem growth rates (Table 5). Like MS stem growth rate, MS panicle growth rate was also linearly related ($r^2 = 0{\cdot}99$) to the DVP (the growth rate increased 15 mg °Cd^{-1} for each °Cd of vegetative

phase), though the increase in rate $°Cd^{-1}$ was less than for stem growth. Similarly, panicle growth rate in all shoots was related to their maximum leaf area (Fig. 5), though again the increase in rate of panicle growth cm^{-2} leaf area was significantly ($P < 0.001$) less than for stem growth.

TABLE 5. *The effect of DVP treatment on the timing and stage of apical development at which panicle growth started, on the rate of panicle growth, the duration of panicle growth, and the panicle dry weight at maturity in the mainshoot (MS) and primary tillers (PT3 and PT4)*

	Shoot		
	MS	PT3	PT4
		DVP1	
Start of panicle growth (°Cd from sowing)[a]	598	628	611
Start of panicle growth (stage of development)[b]	14	15	13
Rate of growth (g shoot^{-1} °Cd^{-1} ± s.e.)	0·042 ±0·0056	0·026 ±0·0049	0·025 ±0·0052
Duration of panicle growth (°Cd)[c]	467	469	428
Dry weight at maturity (g)	19·6	12·2	10·7
		DVP3	
Start of panicle growth (°Cd from sowing)[a]	700	723	710
Start of panicle growth (stage of development)[b]	12	12	10
Rate of growth (g shoot^{-1} °Cd^{-1} ± s.e.)	0·062 ±0·0068	0·039 ±0·0037	0·012 ±0·0004
Duration of panicle growth (°Cd)[c]	425	428	483
Dry weight at maturity (g)	26·4	16·7	5·8

[a] Defined as panicle dry weight = 0 g.
[b] Stage of shoot apical development (Table 1).
[c] Duration = maximum weight at maturity/rate of growth.

Because of the close relationship between apical development and the start of panicle growth, there was no effect of DVP treatment on the duration of panicle growth, giving a mean of 447 ± 7·4 °Cd for this phase.

Panicle dry weights at M, therefore, reflected panicle growth rates, with increased MS and PT3 weights and reduced PT4 weight in the DVP3 treatment (Table 5).

Yield components on the MS and PTs

There was no effect of DVP treatment on grain yield per plant (Table 6). Thus, although the yield of the MS was increased in the longer DVP treatments, this was associated with reduced yield from the tillers due to reduced number of grain bearing panicles per plant (Table 6). Grain yield on each shoot was directly proportional to shoot growth rate (Fig. 6). Differences in stem dry weight show a similar pattern to differences in grain yield, though proportionately stem dry weights were increased much more than grain dry weights on the MS and PT3 in the DVP3 treatment, reflecting the differences in effects of DVP on rates and

TABLE 6. *The effect of DVP treatment on measured grain yield, the number of grain bearing panicles, stem dry weight, and harvest index in the mainshoot (MS) and primary tillers (PT3–PT6), and the totals per plant*

	DVP treatment	Shoot					Total plant^{-1}
		MS	PT3	PT4	PT5	PT6	
Grain dry weight (g)	1	14·7	9·6	7·7	5·4	1·3	38·7
	3	20·2	11·2	4·2	2·9	1·3	39·8
s.e.[a]		±3·88	±3·60	±2·05	±1·79	±2·05	—
No. grain bearing panicles	1	1·00	0·93	0·95	0·72	0·22	3·4
	3	1·00	0·91	0·47	0·28	0·07	2·5
s.e.		0	±0·151	±0·149	±0·144	±0·201	±0·43
Stem dry weight (g)	1	18·6	10·5	9·0	5·7	2·2	46·0
	3	39·6	23·3	6·9	5·9	4·1	79·8
s.e.		±3·80	±3·30	±2·58	±1·72	±2·33	—
Harvest index (%)	1	35·1	38·1	34·2	35·8	15·2	
	3	26·7	25·4	28·2	17·7	7·4	
s.e.		±3·76	±6·40	±6·30	±7·40	±9·20	

[a] s.e. for comparing treatment means.

durations of stem and panicle growth (Tables 4 and 5). HI was, therefore, significantly reduced in the DVP3 treatment. However, within each DVP treatment HI was similar on the MS and those tillers that contributed most to yield.

DISCUSSION

The results presented here for tiller and leaf appearance, and for leaf area accumulation and light interception, support the argument of Ong and Monteith (1985) that the concept of thermal time can be usefully applied to describe developmental processes in millet.

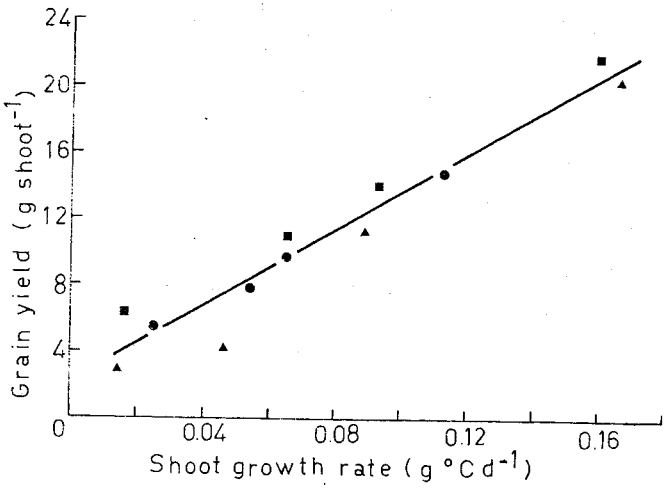

FIG. 6. The relation between grain yield per shoot and shoot growth rate in DVP1 (○), DVP2 (□) and DVP3 (△) treatments. Fitted line: $y = 2{\cdot}09 + 114x$, $r^2 = 0{\cdot}93$, $P < 0{\cdot}001$.

Comparison with data for BK 560 from the glasshouse studies at Nottingham University (Ong, 1983*a*, *b*, 1984; Squire *et al.*, 1984) gives very similar values of θ for developmental processes. For example, θ for leaf appearance was 29 and 32 °Cd leaf^{-1} and θ for primary tiller appearance 46 and 43 °Cd tiller^{-1} in BK 560 and 841A × J104, respectively. Furthermore, the data also provide further circumstantial evidence that daylength has no effect on developmental rates in millet (Ong and Everard, 1979; Carberry and Campbell, 1985); the only effects of the extended daylength treatments were to delay panicle initiation and increase leaf size (Ong and Everard, 1979; Mahalakshmi and Bidinger, 1985).

It appears from this study, and from the studies of Ong (1983*b*) and Huda (1987), that the durations of GS2 and GS3 in millet are conservative in terms of a thermal time requirement. The durations of GS2 and GS3 were, respectively, 320 and 390 °Cd (Table 2), 380 (panicle initiation to 50% anthesis) and 380 °Cd (Ong, 1983*b*) and 330 and 400 °Cd (Huda, 1987), assuming a base temperature (*Tb*) of 10 °C. Data presented by Alagarswamy and Bidinger (1985) and Lambert (1983*a*) support this conclusion, though data presented by Huda, Sivakamar, Alagarswamy, Virmani, and Vanderlip (1984) and Coaldrake and Pearson (1985*a*, 1986) do show some variation in GS2 (e.g. 286–650 °Cd in an Australian cv. MX001: Coaldrake and Pearson, 1985*a*, 1986). Indeed, Coaldrake and Pearson (1986) have proposed that the duration of GS2 depends on the number of leaves initiated, i.e. GS2 is a function of a constant thermal time per leaf. The data presented here, both for DVP treatment effects on MS leaf number and differences between tillers in leaf number, do not support this hypothesis. The variation between genotypes in, and for environmental effects on the duration of GS2 and GS3 need to be determined, but indications are that most of the variation in crop duration is due to variation in the length of the vegetative phase (Huda *et al.*, 1984; Huda, 1987), which is determined by daylength (Ong and Everard, 1979).

Extending the duration of the vegetative phase did not affect tiller production. The first tiller to appear in millet arises in the axil of the third leaf (Lambert, 1983*a*; Coaldrake and Pearson, 1985*a*), even though tiller buds are present in the axils of the first and second leaves (Craufurd, unpublished data). One possible reason for this pattern of tillering could be that in millet initial leaf area expansion is extremely slow relative to development (because of small leaves: ICRISAT, 1978) and there is no significant light interception until > 260 °Cd (Fig. 3); thus tillering in the early stages may be limited by assimilate availability.

Tiller production and tiller leaf appearance in the later-initiated tillers ceased at approximately the same thermal time, 530–580 °Cd after sowing in all DVP treatments, suggesting that both ceased in response to a common physiological control mechanism. The event most closely associated with the cessation of tiller development was the start of rapid stem growth in the most advanced shoots (Table 4) which, in this hybrid, started at 500 ± 6·7 °Cd from sowing and was, therefore, in contrast to temperate cereals (Kirby and Appleyard, 1984), independent of stage of apical development of the MS. Ong (1984) and Coaldrake (1985) also observed a similar relationship between tillering and stem growth which could be attributable both to shading of the later-initiated tillers as the canopy extends and to the changing pattern of assimilate distribution within the plant once stem growth starts (Quinlan and Sagar, 1962; Khan and Kassam, 1984).

The real limitation to increasing the number of panicles at maturity in longer duration millets is the failure of more tillers to continue development and produce a panicle. In this study and in Ong (1984), tillers that did not survive were either vegetative or in the early stages of reproductive development when stem growth in the more advanced shoots started. ^{14}C-studies in wheat (Quinlan and Sagar, 1962; Lupton and Pinthus, 1969) have indicated that the developmental status of a tiller may be an important factor influencing survival; later-initiated tillers that had not reached the stage of floral differentiation (stage 10) by the

time the second node appeared (i.e. rapid extension growth had started) in the MS did not survive. Whether reduced development is a consequence of lower growth rates in the later tillers or the failure to attain a critical growth rate for further development (Charles-Edwards, 1984; Carberry, 1986) is not known. ^{14}C-studies, where labelling is done in relation to specific shoot development and shoot growth events would provide useful additional information on this subject.

It was previously considered that the failure of more tillers to survive and produce grain was limiting an increase in the yield potential of longer duration millets (Alagarswamy and Bidinger, 1985). Data presented here shows clearly, however, that changes in the number of panicles and MS panicle yield are inversely related (i.e. an increase in MS growth rate and yield results in a reduction in tiller growth rate and yield) and that these changes reflect effects of duration on shoot growth rates and partitioning of dry weight between shoots. This can be interpreted both as an increase in available resources (larger leaf area) and an increase in potential growth rate (more nodes: Alagarswamy and Bidinger, 1987 and increased meristem size: Dale and Wilson, 1979; Coaldrake and Pearson, 1985*b*, 1986). Potential growth rates in the tillers may also be increased in the longer DVP treatments, but the actual growth rate is determined by tiller leaf area, which is reduced relative to the MS leaf area, presumably as a result of increased competition from the MS.

The major limitation to increased yield potential in longer duration millets is the reduction in HI and results from the relatively greater effect of DVP on stem growth, both rate and duration, compared to panicle growth (Fig. 5). It is not known why the increase in stem growth rate in longer DVPs per °Cd or cm^2 leaf area should be significantly higher than that in panicle growth rate, though the increase in stem growth could be interpreted as being an alternative sink for dry weight since stem growth starts much earlier relative to panicle growth in the longer DVP treatments.

In pearl millet, in common with other cereals (Fischer, 1985), potential yield (number of grains) per plant is determined by the amount of radiation intercepted during GS2 (Ong and Squire, 1984). In this experiment the duration of GS2 did not vary among treatments (Table 2) and light interception during GS2 was only increased by about 15% in the longer DVP treatments (Fig. 3, Craufurd and Bidinger, 1987), with little resultant effect on number of grains m^{-2}. The failure of the DVP treatments to increase grain yield may reflect the lack of effect of the treatments on factors affecting potential yield, since increases in maximum leaf area and leaf area duration did not significantly increase radiation interception during GS2.

This study has several implications for crop improvement. Selecting for increased number of panicles is unlikely to result in a significant increase in potential yield because of the inverse relationship with panicle size. Furthermore, there is no evidence that the phenotype of longer duration millets, i.e. fewer, larger panicles, is inferior for yield (Craufurd and Bidinger, 1987). This study suggests that increased yield will have to come from increases in factors affecting potential grain numbers, i.e. in increased radiation interception in GS2. Increasing the duration of GS2 would be one way to increase radiation interception, but at present there appear to have been no experiments demonstrating that such variation exists or if it is of any value to increased yield potential. The alternative strategy would be to try and reduce competition from stem growth (Brooking and Kirby, 1981), though a preliminary study using dwarf hybrids did not improve yield or number of grains in longer duration crops (Alagarswamy and Bidinger, 1985). Changes in management, particularly plant population, would also be one way to alter light interception and growth rates, though for many water limited millet growing environments, low plant populations are optimal for water-use efficiency (Azam-Ali, Gregory, and Monteith, 1984).

LITERATURE CITED

ALAGARSWAMY, G., and BIDINGER, F. R., 1985. The influence of extended vegetative development and d_2 dwarfing gene in increasing grain number per panicle and grain yield in pearl millet. *Field Crops Research*, **11**, 265–79.

AZAM-ALI, S. N., GREGORY, P. J., and MONTEITH, J. L., 1984. Effects of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) grown on stored water. II. Water use, light interception and dry matter production. *Experimental Agriculture*, **20**, 215–24.

BROOKING, I. R., and KIRBY, E. J. M., 1981. Interrelationships between stem and ear development in winter wheat: the effects of Norin 10 dwarfing gene, Gai/Rht2. *Journal of Agricultural Science, Cambridge*, **97**, 373–81.

CARBERRY, P. S., 1986. Growth and development simulation model in pearl millet. Ph.D. Thesis, University of Sydney, Australia: University of Sydney.

——and CAMPBELL, L. C., 1985. The growth and development of pearl millet as affected by photoperiod. *Field Crops Research*, **11**, 207–17.

CHARLES-EDWARDS, D. A., 1984. On the ordered development of plants. 1. An hypothesis. *Annals of Botany*, **53**, 699–707.

COALDRAKE, P. D., 1985. Leaf area accumulation of pearl millet as affected by nitrogen supply. *Field Crops Research*, **11**, 185–92.

——and PEARSON, C. J., 1985*a*. Development and dry weight accumulation of pearl millet as affected by nitrogen supply. Ibid. **11**, 171–84.

————1985*b*. Panicle differentiation and spikelet number related to size of panicle in *Pennisetum americanum*. *Journal of Experimental Botany*, **36**, 833–40.

————1986. Environmental influences on panicle differentiation and spikelet number of *Pennisetum americanum*. Ibid. **37**, 865–75.

CRAUFURD, P. Q., and BIDINGER, F. R., 1987. Effect of the duration of the vegetative phase on crop growth, development and yield in two contrasting pearl millet hybrids. *Journal of Agricultural Science, Cambridge*, **109**.

DALE, J. E., and WILSON, R. G., 1979. The effects of photoperiod and mineral nutrient supply on growth and primordia production at the stem apex of barley seedlings. *Annals of Botany*, **44**, 537–46.

EGHAREVBA, P. N., IBRAHIM, A. A., and OKOLO, A. A., 1983. Some morphological and physiological determinants of grain yield in pearl millet. *Maydica*, **28**, 15–24.

FISCHER, R. A., 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science, Cambridge*, **105**, 447–61.

FUSSELL, L. K., and PEARSON, C. J., 1978. Course of grain development and its relationship to black region appearance in *Pennisetum americanum*. *Field Crops Research*, **1**, 21–31.

HUDA, A. K. S., 1987. Simulating yield of sorghum and pearl millet in the semi-arid tropics. Ibid. **15**, 309–25.

——SIVAKUMAR, M. V. K., ALAGARSWAMY, G., VIRMANI, S. M., and VANDERLIP, R. L., 1984. Problems and prospects in modelling pearl millet growth and development; a suggested framework for a millet model. In *Agrometeorology of Sorghum and Millet in the Semi-Arid Tropics*. Proceedings of the International Symposium, 15–20 November 1982, ICRISAT Centre, India. Pp. 297–306. A.P., India: ICRISAT.

INTERNATIONAL CROPS RESEARCH INSTITUTE FOR THE SEMI-ARID TROPICS, 1978. Annual Report, 1977, Patancheru, A.P., India: ICRISAT. Pp. 77–80.

——1982. Annual Report, 1981. Patancheru, A.P., India: ICRISAT. Pp. 80–2.

KHAN, A. A., and KASSAM, A. K., 1984. Translocation of ^{14}C-photosynthates in millet during vegetative development. *Zeitschrift für Acker-und Pflanzenbau*, **153**, 62–71.

KIRBY, E. J. M., and APPLEYARD, M., 1984. *Cereal development guide* (2nd edn.). National Agricultural Centre, Stoneleigh, England: Cereal Unit. Pp. 96.

LAMBERT, C., 1983*a*. Influence de la precocité sur le developpement du mil (*Pennisetum typhoides* Stapf et Hubbard) en conditions naturelles. I. Elaboration de la touffe. *Agronomie Tropicale*, **38**, 7–15.

——1983*b*. Influence de la precocité sur le developpement du mil (*Pennisetum typhoides* Staph et Hubbard) en conditions naturelles. 2. Elaboration du rendement. Ibid. **38**, 16–26.

LUPTON, F. G. H., and PINTHUS, M. J., 1969. Carbohydrate translocation from small tillers to spike-producing shoots in wheat. *Nature*, **221**, 483–4.

MAHALAKSHMI, V., and BIDINGER, F. R., 1985. Water stress and time of floral initiation in pearl millet. *Journal of Agricultural Science, Cambridge*, **105**, 437–45.

MAITI, R. K., and BISEN, S., 1978. Studies on growth and development of panicles and grains in two contrasting genotypes of pearl millet. In *Physiology of sexual reproduction in flowering plants*. Ed. D. Powers. New Delhi, India: Kalyani Publishers. Pp. 115–25.

ONG, C. K., 1983*a*. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). I. Vegetative development. *Journal of Experimental Botany*, **34,** 322–36.

——1983*b*. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. &. H.). II. Reproductive development. Ibid. **34,** 337–48.

——1984. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). V. Development and fate of tillers. Ibid. **35,** 83–90.

——and EVERARD, A., 1979. Short day induction of flowering in pearl millet (*Pennisetum typhoides*) and its effect on plant morphology. *Experimental Agriculture*, **15,** 401–11.

——and MONTEITH, J. L., 1985. Response of pearl millet to light and temperature. *Field Crops Research*, **11,** 141–60.

——and SQUIRE, G. R., 1984. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). VII. Final number of spikelets and grains. *Journal of Experimental Botany*, **35,** 1233–40.

POWERS, D., KANEMASU, E. T., PIARA SINGH, and KREITNER, G., 1980. Floral development of pearl millet (*Pennisetum americanum* [L.] K. Schum). *Field Crops Research*, **3,** 245–65.

QUINLAN, J. D., and SAGAR, G. A., 1962. An autoradiographic study of the movement of ^{14}C-labelled assimilates in the developing wheat plant. *Weed Research*, **2,** 264–73.

RAMOND, C., 1968. Pour une meilleure connaissance de la croissance du developpement des Mils *Pennisetum*. *Agronomie Tropicale*, **23,** 844–63.

SNEDECOR, G. W., and COCHRAN, W. G. C., 1980. *Statistical methods*. (7th edn.). Ames, Iowa, USA: Iowa State University Press. Pp. 507.

SQUIRE, G. R., MARSHALL, B., TERRY, A. C., and MONTEITH, J. L., 1984. Response to temperature in a stand of pearl millet. VI. Light interception and dry matter production. *Journal of Experimental Botany*, **35,** 599–610.

WADDINGTON, S. R., CARTWRIGHT, P. M., and WALL, P. C., 1983. A quantitative scale of spike initial and pistil development in barley and wheat. *Annals of Botany*, **51,** 119–30.