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Effect of the duration of the vegetative phase on crop growth, development and yield in two contrasting pearl millet hybrids

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SUMMARY

The phenotype of medium duration pearl millet varieties grown in West Africa differs from that of the shorter duration millets grown in India. African varieties are usually much taller, have longer panicles, fewer productive tillers, and a lower ratio of grain to above-ground dry-matter (harvest index). The effect of crop duration on plant phenotype was investigated in two hybrids using extended daylengths to increase the duration of the vegetative phase (GS1: sowing to panicle initiation). The two hybrids, 841A × J104 and 81A × Souna B, were considered to represent the Indian and African phenotype, respectively. Tiller production and survival, leaf area, and dry-matter accumulation and partition, were monitored over the season. Grain yield and its components were determined at maturity.

The two hybrids responded similarly to the short and long daylength treatments. The duration of GS1 was increased from 20 to 30 days, resulting in increased number of leaves, leaf area, and stem and total dry-matter accumulation; there was no effect on tiller production and survival, or on panicle growth rate. Grain yield was, therefore, the same in both GS1 treatments, and harvest index (HI) was much reduced in the long GS1 treatment owing to the increased stem growth. One evident effect of a longer GS1 was on dry-matter partitioning between shoots; partitioning to the main stem (MS) was increased, whereas partitioning to the tillers was reduced.

There was no difference in crop development, growth or yield between the two hybrids in either GS1 treatment. The only significant differences were in the efficiency with which intercepted radiation was converted to dry matter, which was greater in 841A × J104 than in 81A × Souna B, and in the balance between MS and tillers; the grain yield of the MS was significantly greater in 81A × Souna B than in 841A × J104, but at the expense of number of productive tillers.

The results demonstrate that both African and Indian phenotypes are equally productive under good agronomic conditions. The lower HI in longer duration African millets is a consequence of a much extended stem growth phase and therefore increased competition between stem and panicle during grain filling. Possible ways to increase grain yield in the medium duration African millets are considered.

INTRODUCTION

Pearl millet (*Pennisetum americanum* (L.) Leeke) is a major crop of the semi-arid tropics and is mainly grown in two widely different geographical zones, north-west India (22–30° N) and the Sahelian zone of Africa (11–14° N). The major feature of varietal adaptation in these zones is the matching of the crop duration to the length of the growing season (e.g. Kassam & Andrews, 1975), which varies from 10 to 20 weeks (Virmani, Sivakumar & Reddy, 1982; Sivakumar, Virmani & Reddy, 1979). Response to daylength is an important component of this adaptation (Curtis, 1968; Lohani, 1985), with most millets showing a quantitative short day response (Begg & Burton, 1971; Belliard & Pernès, 1985). Most of the variation in crop duration can be attributed to variation in the duration of the vegetative phase (GS1: sowing to panicle initiation [PI]; there appears to be far less variation in the reproductive phase (GS2: PI to flowering [FL]) or the grain filling phase (GS3: FL to physiological maturity [M]) (Lambert, 1983*a*; Huda *et al.* 1984).

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African varieties generally have a longer crop duration than Indian varieties. Maturity ranges from 85–95 days in early, less photosensitive types (medium maturity varieties) such as Heini Kheire, Gero or Souna, to 120–160 days in late, highly photosensitive types such as Sanio or Maiwa (Lohani, 1985; Naino, Onendeba & Gonda, 1985; Bilquez, 1963; Bilquez & Clément, 1969). In comparison, standard Indian hybrids (early maturity varieties) such as BJ104 or MBH110 mature in 75–80 days in northern India (Alagarswamy & Bidinger, 1985). African varieties are also usually much taller, have larger panicles (over 1 m long in Zongo millets from Niger: Naino *et al.* 1985), fewer productive tillers and a lower harvest index (HI: ratio of grain to above ground dry-matter) than Indian varieties (International Crops Research Institute for the Semi-Arid Tropics, 1982; Jacquinot, 1972; Lambert, 1983*a*; Kassam & Kowal, 1975).

Increasing number of productive tillers and HI, and therefore grain yield, in medium maturity varieties is a long-term breeding aim (International Crops Research Institute for the Semi-Arid Tropics, 1982; Gupta, 1985; Lohani, 1985; Egharevba, Ibrahim & Okolo, 1983). Studies at the International Crops Research Institute for the Semi-Arid Tropics (Alagarswamy & Bidinger, 1985; Carberry & Campbell, 1985) have shown that small increases in the duration of GS1 result in significant increases in leaf area and total dry weight at FL. However, this increase in dry matter neither supported more productive tillers nor resulted in an increase in yield. Indeed, it appears that there is a negative relationship between the duration of GS1 and number of productive tillers (Alagarswamy & Bidinger, 1985; Lambert, 1983*a*), which may limit progress in increasing number of productive tillers in medium-duration varieties.

The objective of the work reported here was to understand the relationship between duration of GS1 and phenotype in pearl millet, and the consequences of this relationship for yield improvement in medium duration millets. In this paper, the effect of varying the duration of GS1, to simulate an 'Indian' and an 'African' crop duration, on factors affecting dry-matter accumulation and partition are examined in two hybrids, 841A × J104 and 81A × Souna B, considered to be representative of the Indian and an African medium-maturity phenotype, respectively.

MATERIALS AND METHODS

The study was conducted on an alfisol at the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India (17° 30′ N, 78° 16′ E) in the monsoon (June to October) season 1985. The weather for the growing period is summarized in Fig. 1. Soil and air temperatures were measured at the experimental site; rainfall and incident solar radiation were measured at a meteorological site 1 km away. Rainfall for June to October was 477 mm, about 30% below the long-term average, and the crop had to be irrigated twice, at 26 and 59 days after emergence (DAE).

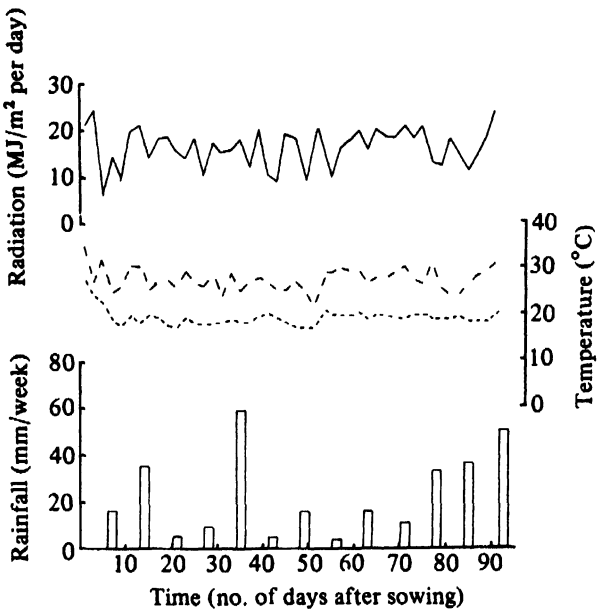

Fig. 1. Weekly total rainfall (□), daily minimum (- - -) and maximum (– –) temperature, and the incident solar radiation (——) during the experimental period.

Two pearl millet hybrids, 841A (a reselected, downy mildew resistant version of 5141A) × J104 and 81A × Souna B, were selected for detailed study as part of a larger experiment (P. Q. Craufurd and F. R. Bidinger, unpublished data). The hybrids were machine sown on ridges 75 cm apart on 21 June, following 21·6 mm of rain. Emergence was 3 days later and was designated as DAE = 1. Nitrogen and phosphorus (P_2O_5), at 40 kg/ha, were broadcast and incorporated into the seed bed before planting, followed by a side dressing of 100 kg urea/ha 22 DAE. The crop was thinned to 15 cm between plants, giving 90000 plants/ha. Plot size was 18 m × 8 rows.

The design was a latin square with a split-plot arrangement of subplots. The main plots were three duration-of-GS1 treatments and three replications. The hybrids were subplots. Pearl millet is generally a quantitative short-day plant and the duration-of-GS1 treatments were achieved by imposing three daylength treatments of 13·5 h (normal daylength at Hyderabad in June), 14·5 and 15·5 h (plus 1 and 2 h extensions, respectively). The daylength extension treatments started 9 DAE, while the plants were still in the juvenile phase (Ong & Everard, 1979), and were continued until 44 DAE, when all plots had completed GS1. A full description of the lighting

system used can be found in Mahalakshmi & Bidinger (1985) and Carberry & Campbell (1985).

Growth analysis samples of 1·2 m^2 quadrats were taken every 3–4 days from 11 DAE to 14 days after FL. For each sample the number of plants was counted and the sample divided into shoot categories: main stem (MS), primary (true-leaf), secondary and nodal (aerial) tillers. For each shoot category dry matter was partitioned into stem (stem + sheath), leaf blade, dead leaf and panicle components. Green leaf area was measured on a leaf area meter. Phenological observations on the MS included the date of PI, FL and M (black layer formation: Fussell & Pearson, 1978). The number of expanded leaves (ligule visible) on the MS was recorded twice weekly on ten plants per plot. A final harvest of 6 m^2 was taken 7 days after M on the MS and the components of yield determined.

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

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

where K is the extinction coefficient. The value used for K was 0·30 ± 0·019, determined from light interception and leaf area measurements in 40 crops of 5141A × J104 at ICRISAT Centre (G. A. Alagarswamy and F. R. Bidinger, unpublished data), and therefore in good agreement with other published values for millet (Squire *et al.* 1984; Gregory & Squire, 1978).

All variables measured at maturity were analysed by ANOVA using the complete data set for the experiment (9 hybrids × 3 duration-of-GS1 treatments: P. Q. Craufurd and F. R. Bidinger, unpublished data), giving a S.E. for comparing means with 8,48 D.F. t tests were used to compare the significance of duration and genotype effects in the treatments presented here.

All growth analysis data presented are the mean of three replications. Data were plotted against DAE and linear regressions fitted to describe leaf and tiller appearance, and stem and panicle growth. Regressions of tiller and leaf appearance on time were fitted from 9 DAE, through to maximum number of tillers, approximately 30 DAE, and flag leaf appearance, 51–58 DAE, respectively. The start of the linear phase of stem growth was taken as 50 g/m^2 stem dry matter and regressions fitted from 29–32 to 54–64 DAE. Regressions were fitted to panicle dry weight first from approximately 10 days before FL to FL and secondly from FL to M. The regression equations were used to estimate the rates of growth or appearance, maximum numbers or weights, and the start of growth phases. The slopes of the regressions were compared using the method given by Snedecor & Cochran (1980). Unless otherwise stated, comparisons of GS1 treatments used the genotype means, and comparisons of genotypes the GS1 treatment means.

RESULTS

The daylength extension treatments had the desired effect of producing variation in the duration of GS1 in both genotypes, from 20–22 days under 13·5 h days (herein termed as the short GS1 treatment) to 32 days under 15·5 h days (herein termed as the long GS1 treatment) (Table 1). Extending the duration of GS1 had no effect on the duration of GS2 (28 ± 0·2 days) or GS3 (28 ± 0·2 days), which were similar in both genotypes. The phenology of both genotypes was, therefore, similar in the short and long GS1 treatments. This has permitted us to examine both the effect of genotype and the effect of duration of GS1, without the confounding effects of phenological differences in other growth periods.

Table 1. *The effect of the daylength extension treatments on the phenology of* 841*A* × *J*104 *and* 81*A* × *Souna B*

Daylength (h)	Duration of GS1* (days)	Duration of GS2† (days)	No. of days to flower	Duration of GS3‡ (days)	No. of days to maturity
		841A × J104			
13·5	20	28	48	29	77
14·5	28	28	58	28	86
15·5	32	27	59	28	87
		81A × Souna B			
13·5	22	28	50	28	78
14·5	30	28	58	28	86
15·5	32	27	59	28	87

* GS1: sowing to panicle initiation.
† GS2: panicle initiation to flowering.
‡ GS3: flowering to maturity.

Table 2. *The effect of the duration of GS1 on main stem (MS) leaf and tiller production and the number of tillers and panicles at maturity in 841A × J104 and 81A × Souna B*

	Duration of GS1 treatment				
	Short		Long		
	841A × J104	81A × Souna B	841A × J104	81A × Souna B	S.E.*
No. of leaves	19·2	19·4	22·5	21·3	0·61
Rate of leaf appearance (per day ± S.E.)†	0·41 ± 0·011	0·37 ± 0·012	0·37 ± 0·014	0·34 ± 0·011	
Rate of tiller appearance (per m^2 per day ± S.E.)†	3·1 ± 0·47	2·8 ± 0·29	3·1 ± 0·28	3·1 ± 0·36	
Maximum no. of tillers (per m^2 ± S.E.)†	78 ± 3·6	90 ± 8·8	74 ± 4·2	76 ± 7·9	
No. tillers at maturity (per m^2)	41	41	38	39	5·2
No. panicles at maturity (per m^2)	32	18	31	16	3·0

* S.E. for comparing genotype × treatment means.
† Estimated from the regression.

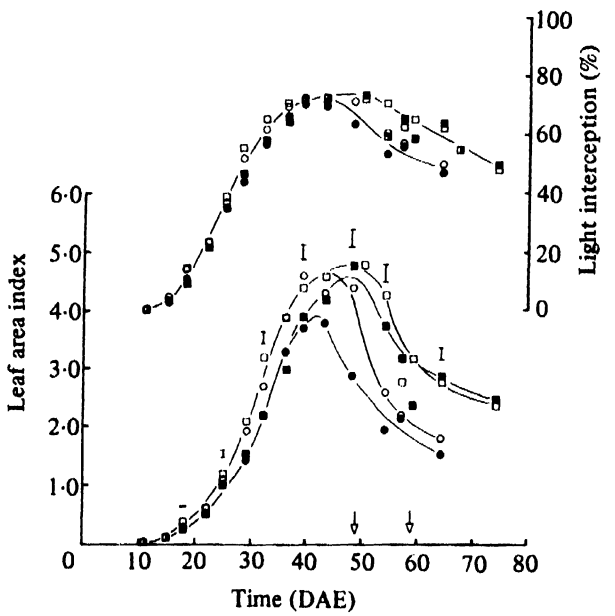

Fig. 2. The effect of the short-(○) and long-(□) duration GS1 treatments on the time course of leaf area index and the calculated percentage light interception in 81A × Souna B (open symbols) and 841A × J104 (closed symbols). Curves fitted by eye. ↓, FL; I, S.E. of the means, 12 D.F.

Leaf and tiller production

A direct consequence of increasing the duration of GS1 was to increase significantly ($P < 0·01$) the number of leaves initiated on the MS (Table 2). The rate of leaf appearance was reduced in the long GS1 treatment, though not significantly. There were significant differences ($P < 0·01$) between genotypes in leaf appearance rate, but not in final number of leaves.

There was no effect of the duration of GS1, nor of genotype, on the rate of primary tiller appearance, on the maximum number of tillers produced, or on the number of tillers at maturity (Table 2). However, while the number of tillers that survived to maturity was similar in both GS1 treatments and genotypes (approximately 50% of the total number produced), the number of productive (panicle-bearing) tillers was significantly higher ($P < 0·001$) in 841A × J104 than in 81A × Souna B, with no effect of the duration of GS1.

Leaf area and light interception

The time curves for leaf area and the calculated percentage light interception are presented in Fig. 2. Maximum leaf area was increased and the duration of the leaf area extended by the long GS1 treatment, the effect being somewhat greater in 841A × J104. The duration of GS1, however, had no effect on the rate of leaf area accumulation, which was consistently, though not significantly ($P < 0·1$), greater in 81A × Souna B (2400 ± 160 cm^2/m^2 per day) than in 841A × J104 (2000 ± 80 cm^2/m^2 per day) over the period of maximum rate (29–39 DAE).

The percentage light interception followed leaf area very closely, increasing from effectively zero at 10 DAE to a maximum of 70% at a leaf area index of 3·5 (Fig. 2). Maximum light interception was reached 36 DAE in 81A × Souna B, approximately 3 days earlier than in 841A × J104. The duration of GS1 had no effect on the time to maximum percentage light interception. In the long GS1 treatment, though, maximum interception was main-

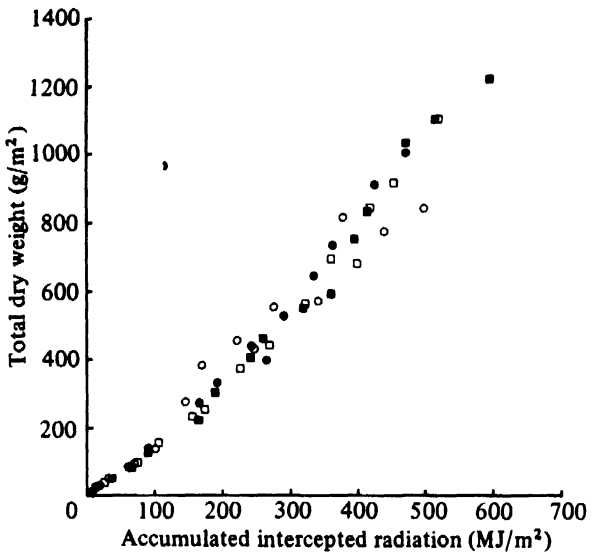

Fig. 3. The relation between dry matter and intercepted radiation in 81A × Souna B (open symbols) and 841A × J104 (closed symbols). ○, Short-duration GS1; □, long-duration GS1.

tained for a longer period, such that in both treatments interception started to decline at the same stage of development, about 5 days before FL, 45 and 55 DAE in the short and long GS1 treatments, respectively.

Intercepted radiation and total dry-matter accumulation

The relationship between accumulated intercepted radiation, calculated from the incident radiation and percentage light interception, and the total dry matter accumulated from 9 DAE to 14 days after FL, is shown in Fig. 3. In both genotypes dry-matter accumulation was proportional to the intercepted radiation. The long GS1 treatment increased interception and dry-matter accumulation by approximately 40% (Table 3), reflecting the delay in FL and the longer duration of the leaf area in this treatment. There was no significant effect of duration of GS1 on the efficiency (e: g dry matter per MJ radiation) over the period of maximum crop growth in either genotype (Table 3). However, there were significant differences ($P < 0.01$) in e between the genotypes; 841A × J104 was approximately 20% more efficient than 81A × Souna B.

Stem and panicle growth

Growth rates, derived from linear regressions of dry weight on time, are presented in Table 4. The duration of GS1 did not have a significant effect on the start of the linear phase of stem growth (Table 4). However, a longer GS1 did result in increased rate ($P < 0.05$) and in increased duration of stem growth, resulting in much greater (approximately double) stem dry weight at M. There were no differences between the genotypes in stem growth.

The start of panicle growth was significantly ($P < 0.001$) delayed in the long GS1 treatment (Table 4), in line with the observed delay in the start of reproductive development (PI, Table 1). The long GS1 treatment also increased panicle dry weight at FL and M, and panicle growth rate during grain filling (Table 4), though none of these effects was significant for differences between GS1 treatments or genotypes.

Dry-matter partitioning between shoots

There were marked effects of both GS1 treatment and genotype on the dry-matter partitioning between shoots (Fig. 4). In the long GS1 treatment the size of the MS was increased at the expense of the tillers; for example, in 81A × Souna B at FL, the weight of main stems was 58·0 ± 3·91 and 76·3 ± 1·67 g/m² in the short and long GS1 treatments, respectively, a proportional increase of 31%. This effect of GS1 treatment was more pronounced and consistent in 841A × J104. Similarly, partitioning to the MS was much greater in 81A × Souna B than in 841A × J104; for example, at FL in the short GS1

Table 3. *The effect of the duration of GS1 on the total of intercepted radiation and dry matter accumulated 14 days after flowering and the conversion efficiency (e) in 841A × J104 and 81A × Souna B*

	Duration of GS1 treatment			
	Short		Long	
	841A × J104	81A × Souna B	841A × J104	81A × Souna B
Total intercepted radiation (MJ/m²)	425	441	594	596
Total dry matter accumulated (g/m²)	915	781	1236	1107
e (g/MJ per m² ± S.E.)*	2·42 ± 0·171	1·89 ± 0·227	2·42 ± 0·098	2·12 ± 0·115

* Calculated from the start of stem growth to flowering + 14 days.

Table 4. *The effect of the duration of GS1 on stem and panicle growth in 841A × J104 and 81A × Souna B*

	Duration of GS1 treatment				
	Short		Long		
	841A × J104	81A × Souna B	841A × J104	81A × Souna B	S.E.*
		Stem			
Start of growth (DAE)†	30	30	33	34	
Rate of growth (g/m^2 per day ± S.E.)	15·8 ± 1·05	15·4 ± 1·11	20·0 ± 0·81	19·0 ± 0·87	
Duration of growth (days)	28	29	53	48	
Dry weight at maturity (g/m^2)	496	501	1112	972	±78·4
		Panicle			
Start of growth (DAE)	42	39	50	49	
Dry weight at flowering (g/m^2)	58·3	56·7	66·7	59·6	±6·09
Rate of growth (g/m^2 per day ± S.E.)	16·6 ± 0·95	15·6 ± 0·93	18·3 ± 0·87	17·4 ± 1·07	
Dry weight at maturity (g/m^2)	516	504	582	541	±41·4

* S.E. for comparing genotype × treatment means.
† See text for details.

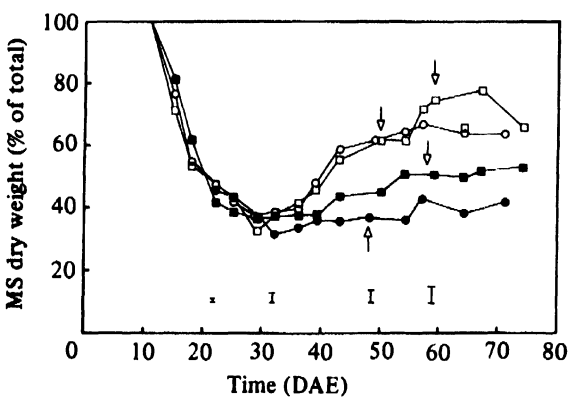

Fig. 4. The effect of the short-(○) and long-(□) duration GS1 treatments on main stem (MS) dry matter, expressed as a proportion of the total dry-matter at each harvest, in 81A × Souna B (open symbols) and 841A × J104 (closed symbols). ↓, FL; I, S.E. of the means, 12 D.F.

treatment the weight of main stems was 58·0 ± 3·91 and 33·5 ± 1·48 g/m^2 in 81A × Souna B and 841A × J104, respectively, a proportional increase of 24%.

Yield and yield components

Despite effects of the GS1 treatments on crop duration and dry-matter production, and of genotypic effects on partitioning between shoots, there were no significant differences in grain yield between genotype or duration treatments (Table 5). All the extra dry matter accumulated in long GS1 treatment was partitioned to the stem (Table 4), resulting in a significant ($P < 0·001$) reduction in HI (Table 5). Nonetheless, there were significant differences between genotypes in the components of yield (Table 5). Generally, 841A × J104 had more, smaller panicles per plant than 81A × Souna B, resulting in a significant ($P < 0·01$) increase in the number of grains/m^2. However, larger grain in 81A × Souna B meant that there was no difference in yield between the genotypes.

Both genotypes showed some response to GS1 treatment in terms of panicle size and number (Table 5). Increasing the duration of GS1 resulted in an increase in number of grains and yield per panicle, but this was associated with a reduction in number of panicles, though within a genotype neither effect was significant.

DISCUSSION

In this experiment daylength extension treatments were used to vary the duration of the vegetative phase. These treatments had no effect on rates of vegetative development (leaf and tiller appearance), reproductive development (duration of GS2 and GS3), or on rate of leaf area accumulation or light interception. In pearl millet rates of vegetative and reproductive development are temperature-dependent processes (Ong & Monteith, 1985) and are apparently independent of daylength (Ong & Everard, 1979; Carberry & Campbell, 1985). This is in contrast to temperate cereals such as wheat and barley where daylength has marked effects on rates of development (Kirby, 1969).

The major effect the daylength treatments had

Table 5. *The effect of the duration of GS1 on grain yield and selected yield components in 841A × J104 and 81A × Souna B*

	Duration of GS1 treatment				
	Short		Long		
	841A × J104	81A × Souna B	841A × J104	81A × Souna B	S.E.*
Grain dry weight (g/m^2)	430	411	448	422	33·9
No. of grains ($\times 10^2/m^2$)	668	533	721	540	51·3
1000-grain weight (g)	6·4	7·7	6·2	7·8	0·58
Total dry weight (g/m^2)	1012	1005	1693	1513	101·1
Harvest index (%)	42	41	27	28	2·3
No. of panicles per plant	3·9	1·9	3·2	1·8	0·47
No. of grains per panicle ($\times 10^2$)	21·3	31·0	23·1	35·7	2·93
Grain dry weight per panicle (g)	13·7	23·6	14·3	27·8	1·90

* S.E. for comparing genotype × treatment means.

was on the duration of several processes. Since most pearl millets are quantitative short-day plants (Ong & Everard, 1979), longer daylengths delayed panicle initiation, increased the number of leaves, and most importantly, increased the duration of the leaf area and therefore the duration of light interception. Increased leaf area in the longer daylength treatments, which is due to increased leaf size (Ong & Everard, 1979; Mahalakshmi & Bidinger, 1985), did not have a significant effect on light interception, since in millet maximum interception is reached at a leaf area index of about 3·5 (Squire *et al.* 1984; Fig. 2).

The consequence of the daylength effects on the processes given above was that the total of radiation intercepted over the season was increased in the long GS1 treatment, and since dry-matter accumulation is proportional to intercepted radiation (at least in the vegetative phase in ideal conditions) (Gallagher & Biscoe, 1978; Squire *et al.* 1984; Marshall & Willey, 1983) the total dry matter accumulated was also greater. Conversion efficiency, computed over the linear phase of crop growth, was similar to other reported values for millet in the rainy season (Marshall & Willey, 1983; Alagarswamy & Bidinger, 1985). Because conditions were ideal, the duration of GS1 had no effect on the conversion efficiency.

It is not known what contributed to the increased efficiency in 841A × J104, since comparative studies of photosynthesis in pearl millet do not appear to have been done. It is known that the upper leaves of the canopy contribute most to total dry-matter gain by the crop (Pearson, 1984) and that tillers contribute about 70% of the leaf area at maximum interception (Gregory & Squire, 1978). Therefore it is possible that in 81A × Souna B, which has one dominant shoot and many vegetative tillers, that interception was over-estimated by using a simple relationship between leaf area and light interception.

The 50% increase in dry-matter accumulation in the long GS1 treatment did not support more tillers or panicles, or result in increased grain yield. Reduced number of panicles would seem to be an inevitable result of increased competition for resources from the main stem to the detriment of the tillers. One interpretation of this change in partitioning is that duration × genotype treatments cause a difference in the shoot growth rate of the main stem, which may be related to increased number of nodes and increased meristem size (Coaldrake & Pearson, 1985). There is no evidence from this study that tiller production or tiller survival in the long GS1 treatment, or in 81A × Souna B, is limiting increased grain yield. It is of interest to note, though, that a longer vegetative phase did not result in a longer tillering phase because in millet tillering ceases when the canopy closes and stem growth starts (Ong, 1984; Lambert, 1983*b*), and in contrast to temperate cereals (e.g. Kirby & Appleyard, 1984), the timing of these events is not linked to reproductive development and is therefore unaffected by the duration of GS1.

The major limitation to yield improvement in crops with a longer duration of GS1 is the failure to translate the extra dry matter accumulated into increased panicle and grain growth. This is primarily a problem of increased duration of stem growth; in the long GS1 treatment stem growth continued throughout GS3 in direct competition with panicle growth, compared with growth for only 10 days after flowering in the short GS1 treatment. Both stem, and to a lesser extent panicle, growth rates were also higher, suggesting that daylength had some effect on shoot growth rate, and since dry-matter accumulation rates were similar, on shoot:root ratio. However, it is not clear how much the longer duration of stem growth was due to the continued growth of later initiated tillers (Carberry, Campbell & Bidinger, 1985), since it was noted that in panicle-bearing tillers stem growth ceased about

6–10 days after flowering (see also Carberry & Campbell, 1985).

This study has two major implications for crop improvement. First, under good growing conditions there is no evidence that the phenotype of the African hybrid is inferior to the phenotype of the Indian hybrid for grain yield. Differences in phenotype probably reflect both the effects of crop duration (fewer, larger panicles and a lower harvest index) and a large element of farmer selection and/or management practice (planting in hills *v.* rows, harvesting of panicles *v.* harvesting of the whole plant). Secondly, improved yield and harvest index will have to come from reduced stem growth, or by corollary, from increased panicle growth. This might be achieved by selecting dwarf hybrids (Alagarswamy & Bidinger, 1985), by searching for variation in the duration of the stem growth phase, by reducing the amount of stem growth in non-panicle bearing tillers, perhaps by reducing tiller production (Egharevba, 1977), or by searching for increased duration of GS2 (cf. Ong & Squire, 1984).

In conclusion, this study suggests that differences in yield potential between African and Indian crops are largely environmental, and that improvements in the yielding ability of pearl millet for Africa lie in improvements in environment and management, rather than in changes in phenotype.

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