

Potential and Realized Yield in Pearl Millet (*Pennisetum americanum*) as Influenced by Plant Population Density and Life-Cycle Duration

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ABSTRACT

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A single hybrid of pearl millet, 841A×J104, was grown at four plant populations covering the range 2-20 plants m⁻² under 13.5 or 15.5-h photoperiods during the vegetative phase (emergence to floral initiation) to effect a short (75-day) or long (90-day) crop duration, respectively. The effect of these treatments on tiller production, leaf-area production, dry-matter accumulation and grain-yield is described, and the relationship between radiation interception (Q_i) during the phase from floral initiation to flowering (GS2), and number of grains (yield potential) and grain-yield is examined.

The treatments caused significant variation in tiller and leaf-area production, radiation interception and numbers of grains per unit area at maturity. Number of grains, which ranged from 37 to 71×10³ m⁻², was correlated ($r^2=0.83$) with intercepted radiation during GS2. Thus at high plant population in the long crop-duration treatment, where leaf area was highest during GS2, number of grains was greatest. Grain-yield was less strongly correlated ($r^2=0.63$) with intercepted radiation during GS2 because, in crops with many grains, grain-size was reduced. Possible reasons for reduced grain-size in crops with high yield-potential are discussed.

INTRODUCTION

Pearl millet is an important crop in the semi-arid areas of northern India and the Sahelian zone of West Africa. Agronomic practices are different in these two areas. In the Sahel, millet is hand-sown at low plant populations (1-2 plants m⁻²) in hills or pockets 0.5-2 m apart (Spencer and Sivakumar, 1987). In India, the crop is sown mechanically (by animal traction), in rows, at higher

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plant populations (9–18 plants m^{-2} ; Harinarayana, 1987). There are also differences in the varieties grown (Anand Kumar and Appa Rao, 1987). West African millets mature 20–30 days later and generally have fewer productive tillers than Indian millets (Craufurd and Bidinger, 1988b).

Pearl millet exhibits considerable plasticity in its response to population density. With adequate fertilizer and moisture, grain-yield reaches a plateau over the range 15–40 plants m^{-2} (Carberry et al., 1985). Under less-favourable conditions (i.e. drought), dry-matter reaches a maximum in the range 1.7–5 plants m^{-2} (Azam-Ali et al., 1984a,b). In both studies, tillers and tiller leaves contributed significantly to the maintenance of crop leaf-areas and yield. The study of Carberry et al. (1985), however, was based on individual plant data, and no attempt was made to examine grain-yield in terms of population effects on yield formation and realization.

Total seasonal radiation interception (Q_i) and dry-matter accumulation are usually greater in longer-duration crops, but this additional dry-matter is not always partitioned to grain, so that harvest index (HI; the ratio of grain to total above-ground dry-matter) remains low (Jaquinot, 1972; Lambert, 1983; Craufurd and Bidinger, 1988b). Previous studies (Craufurd and Bidinger, 1988a,b) have shown that the lower HI of longer-duration crops could be attributed to increased rate and duration of stem growth as compared to panicle growth. It has also been observed that the number of grains per unit area does not differ significantly between short and long-duration crops, suggesting that the increased radiation interception of longer-duration crops does not result in increased yield-potential.

In cereals, yield-potential is strongly correlated with the rate of growth and, therefore, with Q_i during the phase from floral initiation to flowering, GS2 (e.g. Hawkins and Cooper, 1981; Fischer and Palmer, 1984; Ong and Squire, 1984; Fischer, 1985). If this holds for millet, variation in plant population density and crop duration should cause considerable variation in radiation interception and therefore in yield-potential. The aim of this study was to examine the interaction of crop growth and development in determining yield-potential and grain-yield in a range of plant populations (2–20 plants m^{-2}) with short (75-day) and long (90-day) crop durations. The study was part of a wider study comparing Indian and African varieties and management practices.

EXPERIMENTAL DETAILS

The experiment was carried out in the field at the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India, during the monsoon season (June–October) 1986. The weather during the growing period is summarised in Table 1. The crop was furrow-irrigated twice, on 1 July and 27 August.

The experiment was arranged in three randomised complete blocks of six

TABLE 1

Climatic variables for consecutive 7-day periods during the cropping season

	Rainfall (mm)	Temperature (°C)		Radiation (MJ m ⁻² day ⁻¹)
		Max.	Min.	
June				
18	33.3	30.8	23.2	14.5
25	8.9	30.3	23.0	10.9
July				
2	7.0	34.2	24.2	20.5
9	20.1	31.9	23.9	14.8
16	93.6	27.9	21.9	10.9
23	2.3	29.6	21.7	15.9
30	58.0	29.9	21.9	18.1
August				
6	107.8	27.5	21.9	13.2
13	69.2	27.0	21.3	14.2
20	4.1	29.1	21.4	19.2
27	0.0	31.4	22.3	22.8
September				
3	49.2	31.4	22.3	19.2
10	4.4	30.3	22.3	17.7
17	2.3	33.0	22.2	21.7
24	1.4	33.2	21.8	19.9

plots. Main plots were two duration-of-GS1 (the phase from sowing to floral initiation) treatments achieved by varying the photoperiod, and each main plot was divided into four subplot plant-population densities. Plot size was eight ridges each 25 m long. A high-tillering, short-duration hybrid, 841A × J104 (Craufurd and Bidinger, 1988b), was sown on ridges 0.75 m apart on 19 June and emerged 3 days later. Seeds were sown to give a density of 20 plants m⁻² and plots were thinned 11 days after emergence (DAE) to give the four target populations, viz. 20, 12, 4.5 and 2 plants m⁻². Nitrogen and phosphorus fertilizers were broadcast at 40 kg ha⁻¹ each of N and P and incorporated into the seedbed before planting. A top dressing of nitrogen fertilizer giving 100 kg N ha⁻¹ was applied at 31 DAE.

Pearl millet is (generally) a quantitative short-day plant (Belliard and Pernes, 1985), in which long photoperiod delays floral initiation. In the present experiments, the time of floral initiation was varied by artificially extending the natural photoperiod of 13.5 h at Hyderabad in June to 15.5 h using lights suspended over the designated main plots (Mahalakshmi and Bidinger, 1985). Photoperiod treatments started 8 DAE and continued until panicle (floral) initiation had occurred in all treatments.

Samples were taken at weekly intervals throughout the season from the sub-

plots thinned to 12 and 4.5 plants m^{-2} . A single sample was taken at 10 days before flowering from the subplots thinned to 20 and 2 plants m^{-2} . Plants were taken from 1.2 m^2 of rows 2 and 3 or rows 5 and 6. The samples were processed as described in Craufurd and Bidinger (1988b).

The date of panicle (floral) initiation, PI, was determined from dissection of mainshoot apices. Flowering (FL, when 50% of the stigmas on the mainshoot had emerged) and maturity (M, when the black layer had formed on 50% of the grain on the mainshoot; Fussell and Pearson, (1978)) were scored by direct observation in the field. The periods from sowing to panicle initiation, panicle initiation to flowering, and flowering to maturity are referred to as GS1, GS2 and GS3, respectively. The durations of these phases (Table 2) were measured in days and in thermal time, $^{\circ}Cd$, calculated as

$$\sum (\text{mean daily temperature in phase } (^{\circ}C) - T_b)$$

where T_b is the base temperature, taken for millet as $10^{\circ}C$ (Ong and Monteith, 1985).

The intercepted radiation during GS2 (all treatments) and for the whole season (12 and 4.5 plants m^{-2}) was calculated from estimates of the percentage light interception ($\%Q_i$) and the incident solar radiation (measured at the ICRISAT meteorological site). In the 2- and 20-plants m^{-2} treatments, $\%Q_i$ was measured at mid-day every 3–4 days during GS2 using tube solarimeters and integrators (Delta-T Devices, Burwell, Cambridge, Great Britain). Solarimeters were placed between two central rows in subplot and photosynthetically active radiation (Q_{pa} , 300–700 nm) was measured over a 3-min period. Intercepted radiation was calculated by expressing this Q_{pa} as a percentage of

TABLE 2

Durations of three growth-phases (in days) and in thermal time ($^{\circ}Cd$, above base temp of $10^{\circ}C$) of millet hybrid 841A \times J104 following short (13.5-h) and long (15.5-h) photoperiod treatments during GS1

Photoperiod during GS1	GS1 ¹		GS2 ²		GS3 ³		Maturity	
	(days)	($^{\circ}Cd$)	(days)	($^{\circ}Cd$)	(days)	($^{\circ}Cd$)	(DAE) ⁴	($^{\circ}Cd$)
	13.5 h	19	386	30	457	26	397	74
15.5 h	34	625	33	506	22	372	89	1503
SE*	0.5	9.3	0.6	7.7	0.7	10.8	0.7	9.5

¹GS1, Emergence to panicle initiation.

²GS2, Panicle initiation to flowering.

³GS3, Flowering to maturity.

⁴Days after emergence.

*SE for comparing means.

that measured by a solarimeter placed outside the crop. In the 12 and 4.5 plants m^{-2} treatments, $\%Q_i$ was estimated from a combination of measurements with solarimeters and from leaf area (A_1) using the equation

$$\%Q_i = 1 - \exp(-kA_1) \tag{1}$$

where k is the extinction coefficient. The value used for k was 0.30, determined from light interception and leaf-area measurements in 40 crops of 5141A \times J104 at ICRISAT center (G.A. Alagarswamy and F.R. Bidinger, unpublished data, 1978–80), and in good agreement with other published values of k for millet (Squire et al., 1984). The estimates of $\%Q_i$ obtained from solarimeters and from leaf areas were in good agreement.

At maturity, an area of 4.5 m^2 in each subplot was cut at ground level and total dry-matter, grain-yield and yield components determined.

RESULTS

Plant population

Target populations were achieved in all population treatments except the 20 plants m^{-2} treatment in the 13.5-h photoperiod: actual population in this treatment was 10.2 plants m^{-2} (Table 3).

TABLE 3

Intercepted radiation (Q_i) during GS1, GS2, GS3 and the seasonal total, the total above-ground dry-matter accumulated from sowing (S) to flowering (FL), FL to maturity (M), and at M, in the millet hybrid 841A \times J104 for a range of plant populations following short (13.5-h) and long (15.5-h) photoperiod treatments during GS1

Photoperiod during GS1	Population (plants m^{-2})	Q_i (MJ m^{-2})				Dry-matter (g m^{-2})		
		GS1	GS2	GS3	Total	S-FL	FL-M	@M
13.5 h	12	5	204	207	416	463	457	915
	10.2	—	184	—	—	—	—	945
	4.5	4	147	188	329	359	510	860
	1.8	—	156	—	—	—	—	782
15.5 h	20.5	—	449	—	—	—	—	1208
	12	48	399	297	744	974	520	1172
	4.5	33	372	282	687	940	542	1116
	1.8	—	307	—	—	—	—	1169
SE*		14.1	29.5	23.8	70.0	80.9	123.9	99.7

*SE For comparing means.

—, not measured.

Phasic development

There was no effect of plant population, or interaction of photoperiod and plant population, on phasic development. Panicle (floral) initiation occurred 19 days after sowing in the 13.5-h photoperiod (herein referred to as short-GS1 treatment) and 34 days after sowing in 15.5-h photoperiod (herein referred to as long-GS1 treatment). Following long photoperiod during GS1 the duration of GS2 was increased, but this was partially compensated by a reduction in the length of the phase from flowering to maturity (GS3).

The durations of GS2 and GS3 are temperature-dependent (Ong and Monteith, 1985). To ascertain if changes in the duration of GS2 and GS3 were due to change in mean temperature associated with later panicle initiation and flowering, thermal times were calculated (Table 2). These data confirm that, measured in thermal time, GS2 was significantly longer and GS3 significantly shorter following long photoperiod during GS1.

Tiller production

The maximum number of shoots per plant increased as the plant population decreased (Fig. 1a). In the short-GS1 treatment, increased tiller production

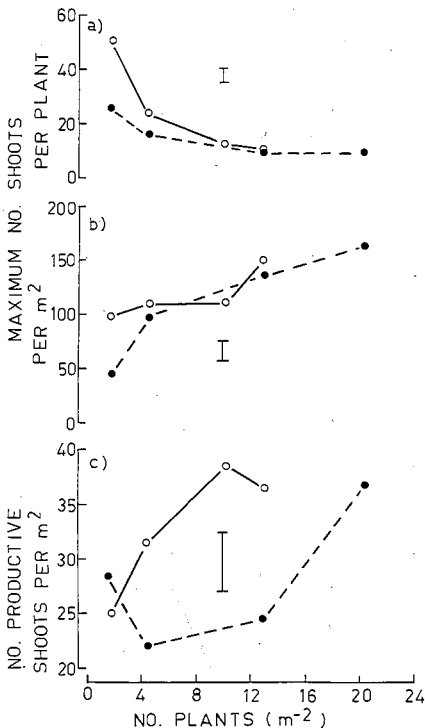


Fig. 1. Maximum number of shoots (a) per plant and (b) per m² and (c) number of productive shoots per m² in a range of plant population densities following short (open symbols) and long (closed symbols) photoperiods during GS1. Vertical bars are SE, for comparing means.

per plant compensated for the low plant population density and the maximum number of shoots produced per unit area was similar in all plant-population densities (Fig. 1b). In the long-GS1 treatment, shoot production plant⁻¹ was reduced in the 1.8 plants m⁻² treatment, compared with the short-GS1 treatment. Increased tiller production plant⁻¹ did not compensate for the lower plant-population density in the long-GS1 treatment, and the number of shoots m⁻² was reduced from 167 at 20.5 plants m⁻² to 47 at 1.8 plants m⁻² in this treatment.

The mean number of productive shoots m⁻² (i.e. having a grain-bearing panicle) was significantly (*P* < 0.01) less in the long-GS1 treatment, in agreement with other observations (Fig. 1c: cf. Alagarswamy and Bidinger, 1985; Craufurd and Bidinger, 1988b). The number of productive shoots was not correlated with maximum shoot number, shoot survival (number of productive shoots/maximum number of shoots) ranging from 65% at 1.8 plants m⁻² in the long-GS1 treatment to 21% at 12 plants m⁻² in the short-GS1 treatment.

Leaf-area production

Leaf area increased rapidly from 25 DAE, reaching a maximum between 45 and 50 DAE (Fig. 2). The main effect of the duration-of-GS1 treatment was to increase maximum leaf area index (*L*). Higher *L* was associated with a greater number of mainshoot leaves (mean of 18.6 and 24.4 in short- and long-GS1 treatment, respectively). Long leaf-area duration was associated with later flowering. In the short-GS1 treatment maximum *L* of 3.3 was reached at flowering, declining to 1.0 at maturity. In contrast, in the long-GS1 treatment, *L* reached a maximum of 6.4, 15 days before flowering (52 DAE), and declined to 2.3 at maturity.

There was an interaction between the effects of population and duration-of-

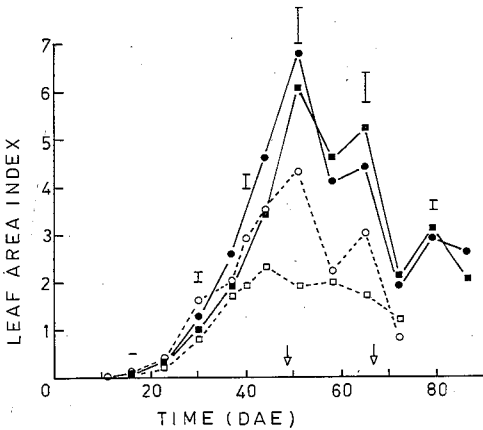


Fig. 2. Leaf-area index over time in 12 (○) and 4.5 (□) plants m⁻² population densities following short (open symbols) and long (closed symbols) photoperiods during GS1. ↓, flowering; vertical bars are SE of means.

GS1 treatment on L . In the short-GS1 treatment, where development (time to flower) was rapid, L was about 50% less at 4.5 plants m^{-2} ($L=2.3$) than 12 plants m^{-2} ($L=4.3$). In the long-GS1 treatment, the L was the same at all population densities.

Radiation interception and dry-matter accumulation

The radiation intercepted during all phases was greater in the long-GS1 than in the short-GS1 treatment. It was also greater during GS2 at the higher population (Table 3) in line with the observed effects of treatments on L . Thus in the short-duration crops, Q_i was very low during GS1, but rose rapidly during GS2 with development of the canopy, and was maintained at about the same level during GS3. In the long-GS1 treatment (relative to the short-GS1 treatment), Q_i increased approximately 800%, 100% and 50% in GS1, GS2 and GS3, respectively. The large increase in interception in GS1 was nonetheless only a small proportion of the total seasonal interception (Table 3).

Dry-matter production in millet has been linearly related to the amount of Q_i (Squire et al., 1984; Ong and Monteith, 1985; Craufurd and Bidinger, 1988b). The slope of this relationship is the conversion efficiency, E , calculated from linear regression of dry-matter on Q_i over the period from emergence to maximum dry-matter. Maximum dry-matter was 7-10 days before maturity: after this time dry-matter either did not change in the short-GS1 treatment, or declined in the long-GS1 treatment (Table 3). The conversion efficiencies, 2.34–2.61 $g\ MJ^{-1}$, were similar to other values reported for millet (Squire et al., 1984; Ong and Monteith, 1985) and were not significantly affected by photoperiod or population density (Fig. 3). There was, nonetheless, a reduction in E as Q_i increased, but the decline in E of 0.09 $g\ MJ^{-1}$ per 100 MJ of Q_i was very small. Thus dry-matter production before flowering was greatly increased in the long-GS1 treatment because Q_i was greater (Table 3). However, during the later stages of grain-filling there was considerable loss of dry-matter in the

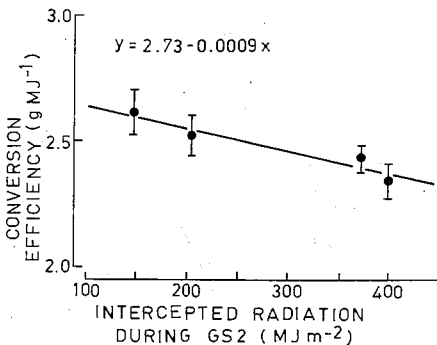


Fig. 3. Relationship between conversion efficiency and intercepted radiation during GS2: vertical bars are SE.

long-GS1 treatment, around 350 g m^{-2} , as a result of rapid senescence and loss of lower leaves and secondary tillers. Therefore, differences in dry-matter between the plots given two GS1 treatments were less at maturity than at flowering.

Stem and panicle growth-rates

Stem and panicle growth-rates (Table 4) were calculated from linear regressions of stem and panicle dry-weight against time to determine the partitioning

TABLE 4

Stem and panicle growth-rates, and panicle growth-rate expressed as a proportion of stem + panicle growth-rates over the period-flowering (FL) - 10 days to FL + 10 days (stem) or to maturity (panicle), and the duration of panicle growth in millet hybrid 841A × J104 grown at two plant populations and following short (13.5-h) and long (15.5-h) photoperiods during GS1

Photoperiod during GS1	Population (plants m^{-2})	Stem dry-matter at FL - 10 days (g m^{-2})	Growth-rate ($\text{g m}^{-2} \text{ day}^{-1} \pm \text{SE}$)		Panicle/ stem + panicle (%)	Duration of panicle growth (days)
			stem	panicle		
13.5 h	12	168	12.2 ± 1.68	10.3 ± 0.47	46	32.0
	4.5	96	11.7 ± 0.89	11.1 ± 0.78	49	29.5
15.5 h	12	352	20.9 ± 0.52	15.4 ± 0.90	42	29.0
	4.5	404	23.3 ± 1.82	13.1 ± 0.67	35	28.0
SE*		30.5				

*SE for comparing means.

TABLE 5

Grain-yield and number of grains m^{-2} at maturity in millet hybrid 841A × J104 grown in a range of plant populations following short (13.5-h) and long (15.5-h) photoperiods during GS1

Photoperiod during GS1	Actual plant population (no. m^{-2})				
	20.5	12	10.2	4.5	2
Grain yield (g m^{-2})					
413.5 h	— ¹	262	290	292	291
15.5 h	387	349	—	304	319
SE*			34.4		
No. of grains (10^3 m^{-2})					
13.5 h	—	37.37	42.07	37.75	40.35
15.5 h	70.76	58.59	—	49.36	50.18
SE*			6.225		

*SE for comparing means.

¹—, not measured.

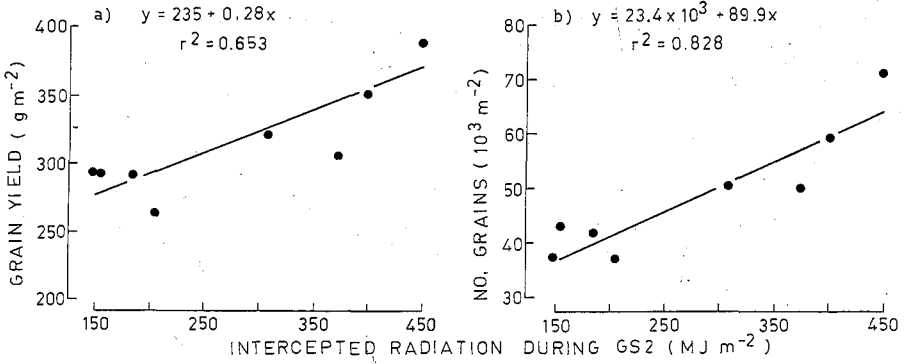


Fig. 4. Relationship between (a) grain-yield (g m^{-2}) and (b) number of grains m^{-2} and intercepted radiation (MJ m^{-2}) during GS2.

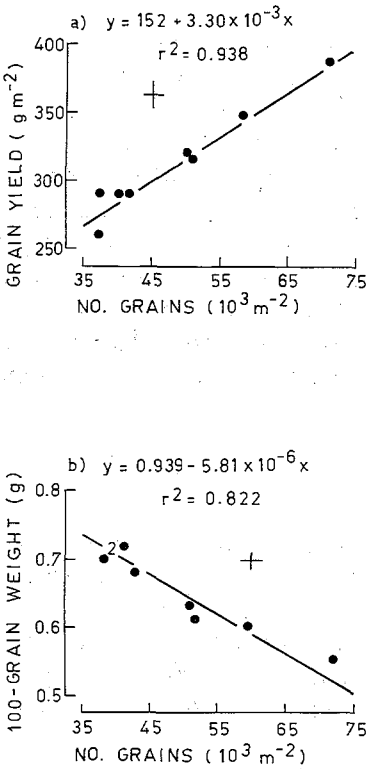


Fig. 5. Relationship between (a) grain-yield (g m^{-2}) and number of grains m^{-2} and (b) 100-grain weight (g) and number of grains m^{-2} . +, SE for comparing means.

of dry-matter during the phase when yield potential and grain-yield are determined. Regressions were calculated from 10 days before flowering to either 10 days after flowering, when stem growth ceased, or maturity, when panicle growth ceased.

At the start of panicle growth, stem dry-matter was significantly greater in the long-GS1 than the short-GS1 treatment. Both stem and panicle growth-rates were significantly increased in the long-GS1 treatment, but the increase in stem growth was approximately twice that in panicle growth. Thus the ratio panicle: stem + panicle growth was reduced in the long-GS1 treatment.

Variation in yield-potential and in grain-yield

The range of treatments imposed resulted in significant variation in yield-potential (from 37 to 71×10^3 grains m^{-2}) and in grain-yield (from 262 to 387 $g m^{-2}$) among the treatment combinations (Table 5). The variation in both number of grains ($r^2=0.83$) and, to a lesser extent, grain yield ($r^2=0.65$) was closely related to Q_i during GS2 (Fig. 4). An increase in Q_i of 10 MJ during GS2 was associated with an increase in the number of grains of 900 m^{-2} and in grain-yield of 2.8 $g m^{-2}$.

From the above relationship it was to be expected that grain-yield and number of grains were closely correlated (Fig. 5a). However, increased yield-potential did not result in a proportionate increase in grain-yield: doubling numbers of grain from 37 to $71 \times 10^3 m^{-2}$ only increased yield from 262 to 387 $g m^{-2}$, i.e. by 48% (Table 5). This occurred because of an inverse relationship of number of grains and individual grain weight (Fig. 5b), such that grain weight declined from 7.35 mg per grain at 35×10^3 grains m^{-2} to 5.32 mg per grain at 70×10^3 grains m^{-2} . As a consequence, grain-yields were similar at all population densities in the short-GS1 treatment (Table 5), where grain numbers varied from only 37.4 to $42.1 \times 10^3 m^{-2}$. Yields were increased only in the 12 and 20.5 plants m^{-2} population densities in the long-GS1 treatment, where grain numbers were above $55 \times 10^3 m^{-2}$.

DISCUSSION

In most cereals, variation in grain-yield caused by agronomic treatments is strongly correlated with variation in the number of grains m^{-2} (e.g. wheat: Fischer, 1985; millet: Mahalakshmi et al., 1985) and hence to crop growth and intercepted radiation during GS2, the phase when floret differentiation and growth occurs (Ong and Squire, 1984; Fischer, 1985). This was true for pearl millet hybrid 841A \times J104 also, where number of grains and grain-yield were correlated with Q_i during GS2.

The only other published data for millet on the relationship between number of grains and Q_i is from the glasshouse studies of Ong and Squire (1984), who grew millet in Great Britain at temperatures of 19–31 °C with a solar radiation

of $7\text{--}10 \text{ MJ m}^{-2} \text{ day}^{-1}$. To eliminate the variation in GS2 caused by the different temperature treatments, they expressed Q_i per plant on an accumulated-temperature basis, i.e. MJ per $^{\circ}\text{Cd}$ (cf. fig. 1c of Ong and Squire, 1984). The data presented in Fig. 4b were recalculated to give number of grains plant $^{-1}$ $^{\circ}\text{Cd}^{-1}$; the relationship observed is presented in Fig. 6. The slope from the glasshouse studies of Ong and Squire (1984), 9.9×10^4 grains plant $^{-1}$ MJ $^{-1}$ $^{\circ}\text{Cd}^{-1}$ over the range 2500–7000 grains per plant, compares well with the slope of 8.5×10^4 grains plant $^{-1}$ MJ $^{-1}$ $^{\circ}\text{Cd}^{-1}$ over the much greater range of 3000–30 000 grains plant $^{-1}$ from the field in India. Allowing for some uncertainty in the field data because of the few points having a large number of grains and high Q_i , these data confirm that variation in number of grains can largely be accounted for in terms of intercepted radiation and accumulated temperature.

From the above analysis it is apparent that the yield-potential (number of grains m^{-2}) of short-duration crops may be limited by low radiation interception, particularly if the plant population is low. Increasing the population density or delaying panicle initiation slightly are two ways to increase radiation interception and yield-potential in short-duration crops. Whether there is useful variation in seedling size or in canopy architecture, which might also increase Q_i and E , or differences between genotypes in conversion efficiency, has not been investigated.

In longer-duration crops, the prolific tillering ability of millet (over 65 tillers per plant in one plot in the $1.8 \text{ plants m}^{-2}$ treatment; see also Ramond, 1968), and the resultant high L ensures that even at low populations Q_i and yield-potential are high. Indeed, in the 1.8 and $4.5 \text{ plants m}^{-2}$ treatments, tiller leaves accounted for 80–90% of the total leaf area. Although some of the treatments had L 's greater than 3.5, when maximum interception is reached (Squire

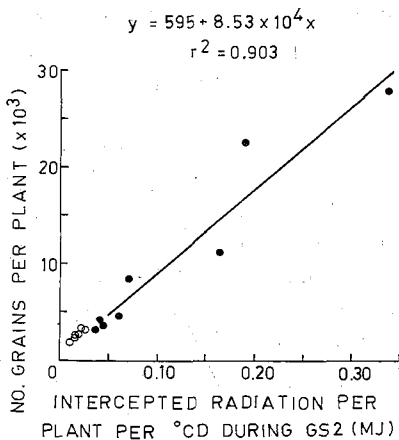


Fig. 6. Relationship between number of grains plant $^{-1}$ and intercepted radiation plant $^{-1}$ $^{\circ}\text{Cd}^{-1}$ during GS2. \circ ; data from Ong and Squire (1984).

et al., 1984; Craufurd and Bidinger, 1988b), there was no strong evidence that increased shading or increased maintenance cost associated with higher L reduced conversion efficiency. Furthermore, an additional advantage of prolific tillering is that vegetative tillers can relocate significant amounts of dry-matter to fertile tillers, at least in barley (Chafai-Elalaoui and Simmons, 1988; see also Khan and Kassam, 1984).

Although there was considerable variation in yield-potential, at maturity grain-yield was only increased in the higher-population/long-duration crops, due to the reduction in grain size that occurred with high numbers of grains. There would appear to be several reasons why this occurs. In the long-duration crops there was a considerable loss of dry-matter during GS3, and net accumulation during GS3 was only around 200 g m^{-2} , compared with 400 g m^{-2} in the short-duration crops. This was due to rapid leaf senescence and the death of secondary tillers during GS3, which may have been associated with the pattern of L development. In the short-duration crops, maximum L occurred at flowering, and dry-matter accumulation and Q_i were similar in GS2 and GS3, i.e. there was a balance between the potential and the realized yield. In the long-duration crops, L and Q_i reached maximum 10 days before flowering. This led to a large imbalance in Q_i and dry-matter accumulation between GS2, when yield potential was determined, and GS3, when grain-filling occurred. If grain-yield in longer-duration crops of millet is to be increased, we need to see if there is any genetic variation in L /development (flowering) relationship that would allow maximum yield-potential and grain-yield.

The small amount of dry-matter accumulated during GS3 in the long-duration crops, while perhaps preventing the full attainment of yield-potential, did not result in a significant reduction of grain-yield. This may have been due to the relocation of assimilates from the stem, a mechanism known to make significant contributions to grain-yield in other cereals (e.g. Austin et al., 1980). Differences between maximum stem dry-matter and stem dry-matter at maturity were $0\text{--}90 \text{ g m}^{-2}$ in the short-duration treatment, and $200\text{--}300 \text{ g m}^{-2}$ in the long-duration treatment.

A second possible reason why yield-potential was not realised is that competition from stem growth was increased in the long-GS1 treatment (Table 4: Craufurd and Bidinger, 1988a,b). Furthermore, the duration of panicle growth was also reduced. Such competition, occurring in the critical period for floret and grain-growth (flowering – 10 days to flowering + 10 days; Fischer, 1985) may limit grain growth directly or limit the potential size of the grain (Brooking and Kirby, 1981; Fischer and Stockman, 1987).

A third possible reason why grain-yield was not increased is that individual grain size may be limited by space for grain expansion, i.e. by the number of grains per unit panicle surface area (Alagarswamy and Bidinger, 1985). Comparison of Fig. 1 (number of productive shoots) and Table 5 (number of grains

m^{-2}) shows clearly that increased number of grains m^{-2} , particularly in the long-GS1 treatment, is due to an increase in the number of grains panicle $^{-1}$ rather than an increase in the number of panicles m^{-2} , without any marked change in panicle length or volume (see also Alagarswamy and Bidinger, 1985).

CONCLUSION

This study has shown that variation in the number of grains in millet hybrid 841A \times J104 can be largely accounted for in terms of intercepted radiation and accumulated temperature. This approach has shown that the yield of short-duration crops may be limited by a small yield-potential, i.e. by low L 's and low Q_i . In contrast, long-duration crops may not realise their much greater yield-potential because of increased competition from the stem and low rates of dry-matter accumulation during grain-filling.

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