

## THE GROWTH AND DEVELOPMENT OF PEARL MILLET AS AFFECTED BY PLANT POPULATION

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### ABSTRACT

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Pearl millet (*Pennisetum americanum* (L.) Leeke) was grown at ICRISAT, Hyderabad, India at 20 densities ranging from 50 000 to 400 000 plants ha<sup>-1</sup> using a Nelder fan design. Studies were made on the effect of population on the distribution of plant dry weight, leaf area, grain yield and yield components throughout the season. The first effect of increasing population was evident at panicle initiation (<6% final dry weight produced) where dry weight accumulation in the main axis was unaffected but that in the tillers was reduced. Subsequently, the increased plant population resulted in reductions of 77% in total weight per plant, 66% in leaf area per plant and 59% in tiller number per plant at 50% anthesis. The development of green leaf area per plant followed the same trend over the range of populations, so that leaf area index ranged with increasing population from 2.9 to 6.7 at 50% anthesis; severe leaf senescence occurred in the latter part of grain filling. As population increased, the development of tillers terminated earlier in the growth of the plant, resulting in a reduced tiller survival rate and therefore reduced productive head numbers per plant. Grain yield per plant declined owing to the reduced head numbers and also to lower seed numbers per head. Seed size remained largely unchanged. Population influenced plant yield chiefly through the highly responsive yield fraction of tillers, as the yield of the main axis was relatively stable. Grain yield ha<sup>-1</sup> increased to a maximum at 150 000 plants ha<sup>-1</sup>, which was maintained through to 400 000 plants ha<sup>-1</sup> due to the large degree of plasticity in productive tiller number per plant.

### INTRODUCTION

Numerous experiments have defined the optimum plant population for pearl millet (*Pennisetum americanum* (L.) Leeke) in particular environments (Bhardwaj et al., 1971; Upadhyay and Nirval, 1976, Malik and Sharma, 1979; Singh and Singh, 1979). They have not, however, included details of how individual plants respond to population, e.g. by changes in partitioning of dry weight and morphology. These details are necessary if we wish to generalize and predict plant response to population. The present experiment

aimed to provide these details as part of a larger programme of predictive modelling of growth of pearl millet.

Grain yield versus density functions have been determined for sorghum (Fischer and Wilson, 1975), maize (Williams et al., 1968) and field crops collectively (Holliday, 1960; Donald, 1963). Intensified interplant competition reduced individual plant grain yield and was usually accompanied by reduced vegetative dry matter and head numbers at physiological maturity. When expressed on an area basis, these parameters increased sharply to a maximum and, as the competition increased further, grain yield per hectare declined slowly. The emphasis was on final grain yield; the effects of density on the development of leaf area and partitioning of dry matter into various components throughout the growth of the plant were not considered in detail in sorghum and maize.

We hypothesized that the response of pearl millet to increased density would result in an optimum density for grain yield per hectare, and that the optimum would be reflected in partitioning between the main axis and the tillers and their components throughout all the stages of growth.

This study evaluated the growth and morphological development of pearl millet as affected by density, using a series of growth analysis harvests taken at weekly intervals.

#### MATERIALS AND METHODS

An Indian hybrid of pearl millet, BJ 104, was grown on an alfisol soil at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India (lat. 18°N) during the 1982 kharif (monsoon) season.

A population treatment was imposed using the Nelder fan design (Fig. 1)

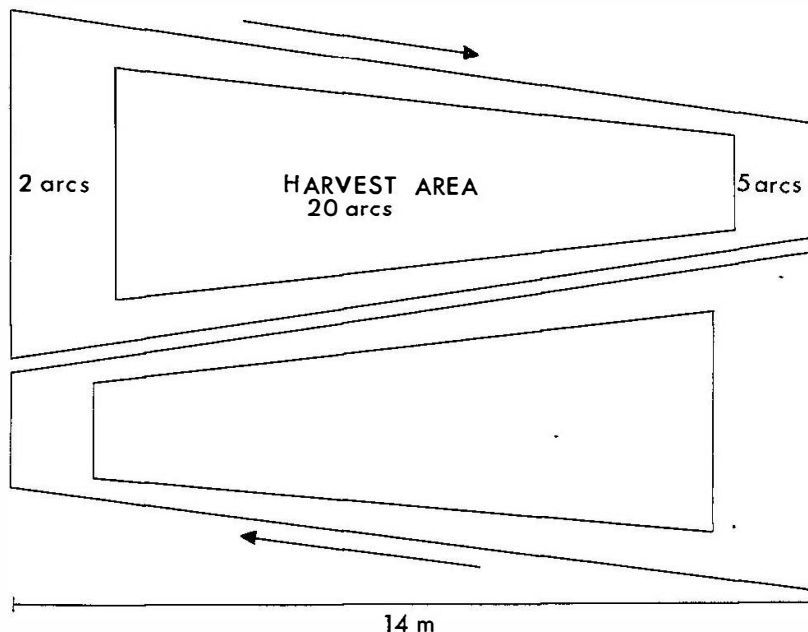


Fig. 1. The Nelder fan design. Arrows represent increasing density.

of 20 densities, ranging from 5 to 40 plants  $m^{-2}$  (Nelder, 1962). There was a 10.4% increment between densities, and the plants were spaced at a constant rectangularity of 1:4. There were 17 plants per density (arc) viz. 11 plants for harvest and three at each end for borders. Additionally, there were borders of five arcs (1.39 m) at the high density and two arcs (1.89 m) at the low density. There were two replicates, each with 16 fans, dove-tailed into each other and separated by 15 cm. The total area per fan was 36.3  $m^2$ .

The seed was hand planted (approximately five seeds per hill) at 2 cm depth into moist cultivated soil and emergence occurred after 3 days. Emergence was assigned as day 0. Thinning to two plants per hill was done on day

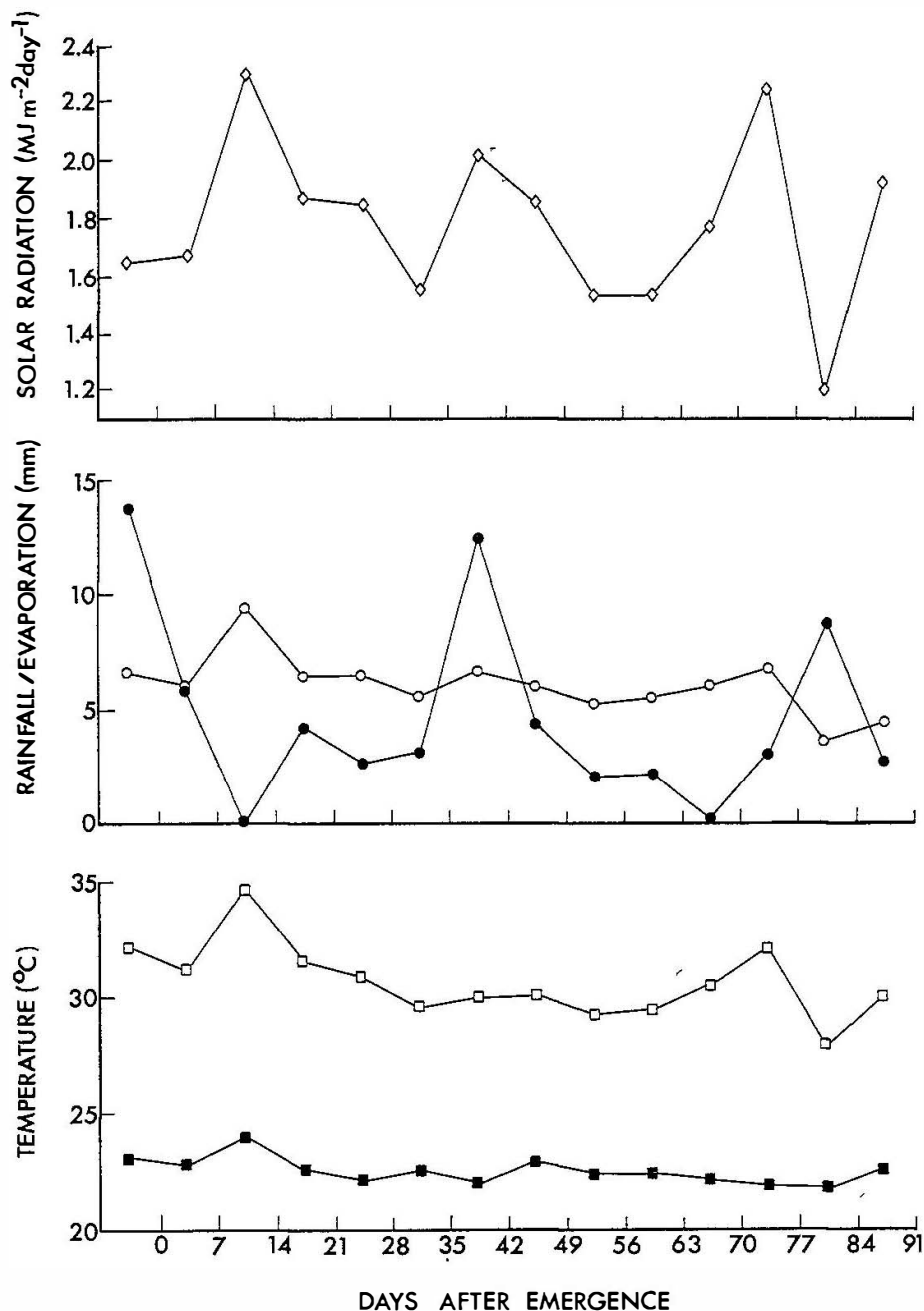


Fig. 2. Average daily maximum and minimum temperatures ( $\square$ ,  $\blacksquare$ ), rainfall and evaporation ( $\bullet$ ,  $\circ$ ) and solar radiation ( $\diamond$ ) at ICRISAT (Hyderabad, India) during the 1982 kharif season.

7 and subsequently to single plants at day 12. Prior to planting, phosphorous ( $26 \text{ kg P ha}^{-1}$ ) was applied as single superphosphate; nitrogen ( $23 \text{ kg N ha}^{-1}$ ) as calcium ammonium nitrate was broadcast at 12 days and a further  $5 \text{ kg N ha}^{-1}$  at 19 days. Average daily rainfall, maximum and minimum temperatures, evaporation from a class A pan and solar radiation are given in Fig. 2 for the 1982 kharif season at ICRISAT. The soil water balance model follows that of Fitzpatrick and Nix (1969).

From 14 days after emergence to maturity, destructive harvests were made each week on one fan which was randomly selected from each replicate. Final grain yield was determined from two fans at maturity. From the harvest at 42 days onwards, measurements were taken on a subsample of five plants.

Weekly measurements included number of tillers (defined as visible leaf lamina  $> 3 \text{ cm}$ ), which were separated into productive and non-productive tillers on the basis of a fertile panicle, leaf areas and dry weights of leaves, stems, panicles and grains segregated into the main axis, productive tillers and non-productive tillers, as well as weight of dead material and 100 seed weights.

Analysis of the data was carried out for each harvest date and density, on a per plant basis and averaged over the replicates. Regressions of the components of yield with density were undertaken as proposed by Bleasdale (1967) using

$$\omega^{-\theta} = \alpha + \beta\rho$$

where  $\omega$  is the mean yield of a given component per plant;  $\rho$  the number of plants per unit area;  $\alpha$  and  $\beta$  parameters having a constant value for sets of data where  $\rho$  was the only variable; and  $\theta$  a parameter having a constant value for any one set of data.

## RESULTS

The hybrid BJ 104 took 16 days to panicle initiation, 42 days to 50% anthesis and 77 days to physiological maturity, which was consistent with unpublished field data at ICRISAT. Both temperature and solar radiation during the kharif season (Fig. 2) were favourable for millet growth. Moisture availability was considered using a simple soil water balance model (Table 1). The crop experienced slight moisture stress at around 28 days and again at 70 days; however, calculated rates of actual evapotranspiration did not fall below 70% of the potential evapotranspiration at either time.

Responses of the crop to plant density are shown in Fig. 3. Leaf area index (LAI) at 50% anthesis was the parameter most responsive to increased density (an increase of 170%). At physiological maturity, total above-ground dry weight per hectare also increased (by 58%) with increased density, although the response appeared to be levelling at the highest densities. Total grain yield per hectare increased by 17%, but most of this increase was

TABLE 1

The soil water balance model for the 1982 kharif season, showing both potential and actual evapotranspiration (ET and EA respectively) and the percent available moisture at the week's beginning and the actual available moisture at its end ( $M_i$ )

Days after emergence	Evapotranspiration <sup>a</sup>		Available moisture <sup>b</sup>	
	ET (mm)	EA (mm)	$(P+M_{i-1})/M_{\max}$ (%)	$M_i$ (mm)
0-7	20	20	100	74
7-14	31	31	100	43
14-21	32	32	97	40
21-28	33	30	80	29
28-35	38	34	69	17
35-42	46	46	100	58
42-49	30	30	100	58
49-56	26	26	99	47
56-63	28	28	84	34
63-70	32	22	49	14
70-77	37	26	49	10

<sup>a</sup>ET = (ET/EP). EP, where EP was pan evaporation (Fig. 2) and ET/EP was that for a 75-day millet (Dancette, 1980); and EA = (EA/ET). ET, where EA/ET was that for sorghum (Fitzpatrick and Nix, 1969).

<sup>b</sup>It was assumed the maximum water available ( $M_{\max}$ ) to millet with a 127 cm rooting zone on an alfisol soil was 74 mm (Russell, 1980);  $P$  was weekly rainfall (Fig. 2).

achieved prior to 150 000 plants  $\text{ha}^{-1}$  and thus grain yield remained relatively constant to 400 000 plants  $\text{ha}^{-1}$ . The ratio of grain yield to total top dry weight, i.e. harvest index, declined quadratically from a maximum of 0.39 as density increased above 62 000 plant  $\text{ha}^{-1}$  due to the continued increase in top weight without any change in grain yield.

Total dry weight and its components for four densities, as derived from single plant data, are shown in Fig. 4. At panicle initiation of the main axis only a small proportion (<6%) of total dry weight had been produced. Over the range of populations depicted, accumulation of plant dry weight followed a similar trend: initially leaf dry weights rose to a maximum, followed by stems and then panicles. Leaf senescence became important 14 days before maturity and some loss of stem weight occurred at low densities.

Plant leaf weights reached a plateau after 35 days and declined after 63 days, probably as a result of the onset of slight moisture stress. The increase in dead material was largely equated with leaf senescence late in the season. Stem elongation would have begun at panicle initiation at day 16 but it was not detected until after day 28. Stem weight was still increasing at 50% anthesis and reached a maximum at 49 days with the exception of 50 000 plants  $\text{ha}^{-1}$ , where stems continued to increase in weight until 63 days. At low densities, prolonged gains and subsequent large declines in stem weights

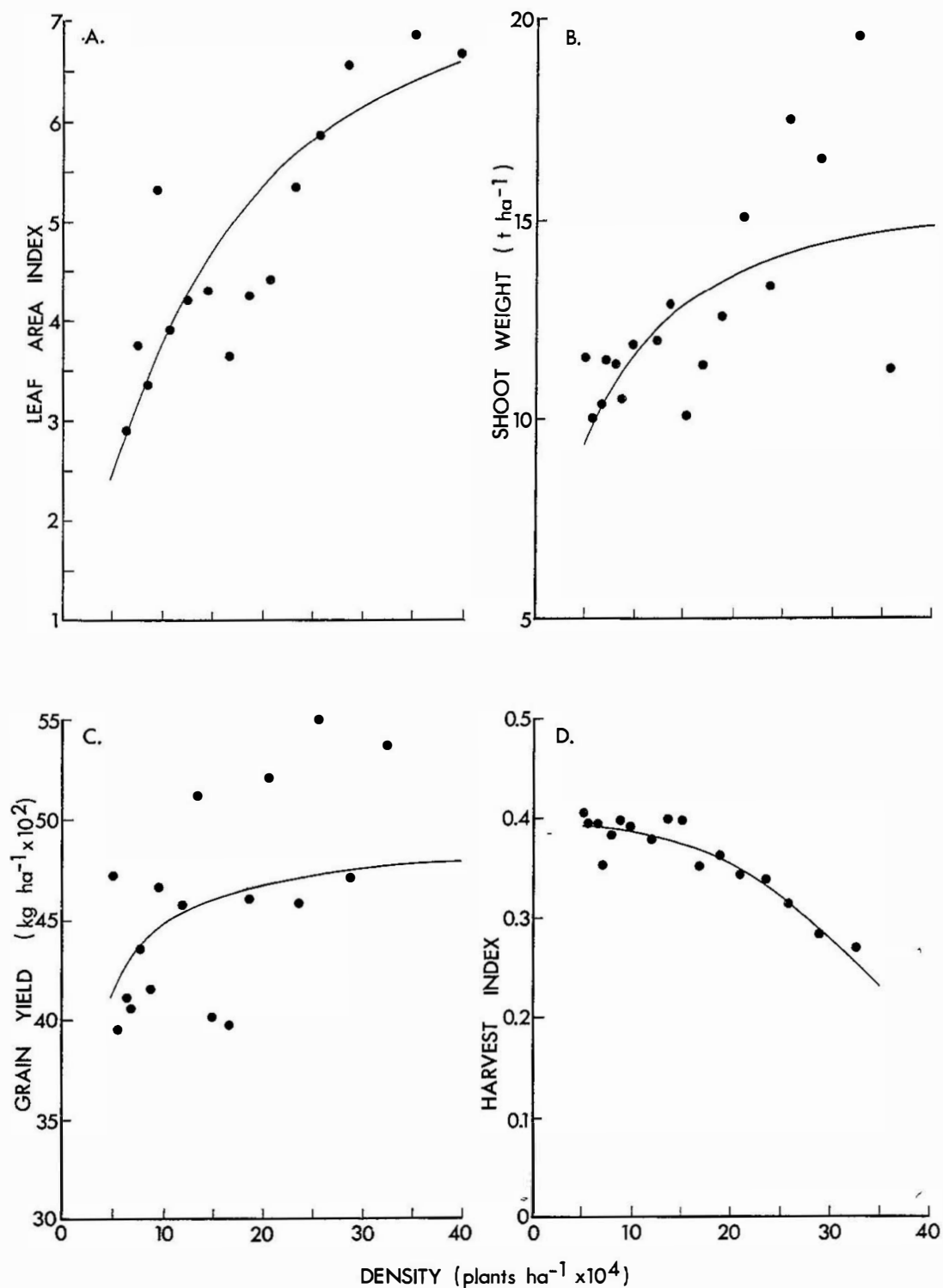


Fig. 3. The effect of population on A: leaf area index at 50% anthesis,  $\omega^{-1}=1.49 \cdot 10^{-4} + 1.10 \cdot 10^{-9} \rho$  ( $r^2=0.88$ ,  $P<0.001$ ); B: total above-ground dry weight per hectare at maturity,  $\omega^{-1}=2.23 \cdot 10^{-3} + 6.19 \cdot 10^{-8} \rho$  ( $r^2=0.82$ ,  $P<0.001$ ); C: total grain yield per hectare at maturity,  $\omega^{-1}=2.08 \cdot 10^{-3} + 2.03 \cdot 10^{-7} \rho$  ( $r^2=0.96$ ,  $P<0.001$ ); D: harvest index,  $Y=0.385 + 2.19 \cdot 10^{-7} \rho - 1.86 \cdot 10^{-12} \rho^2$  ( $r^2=0.88$ ,  $P<0.001$ ).

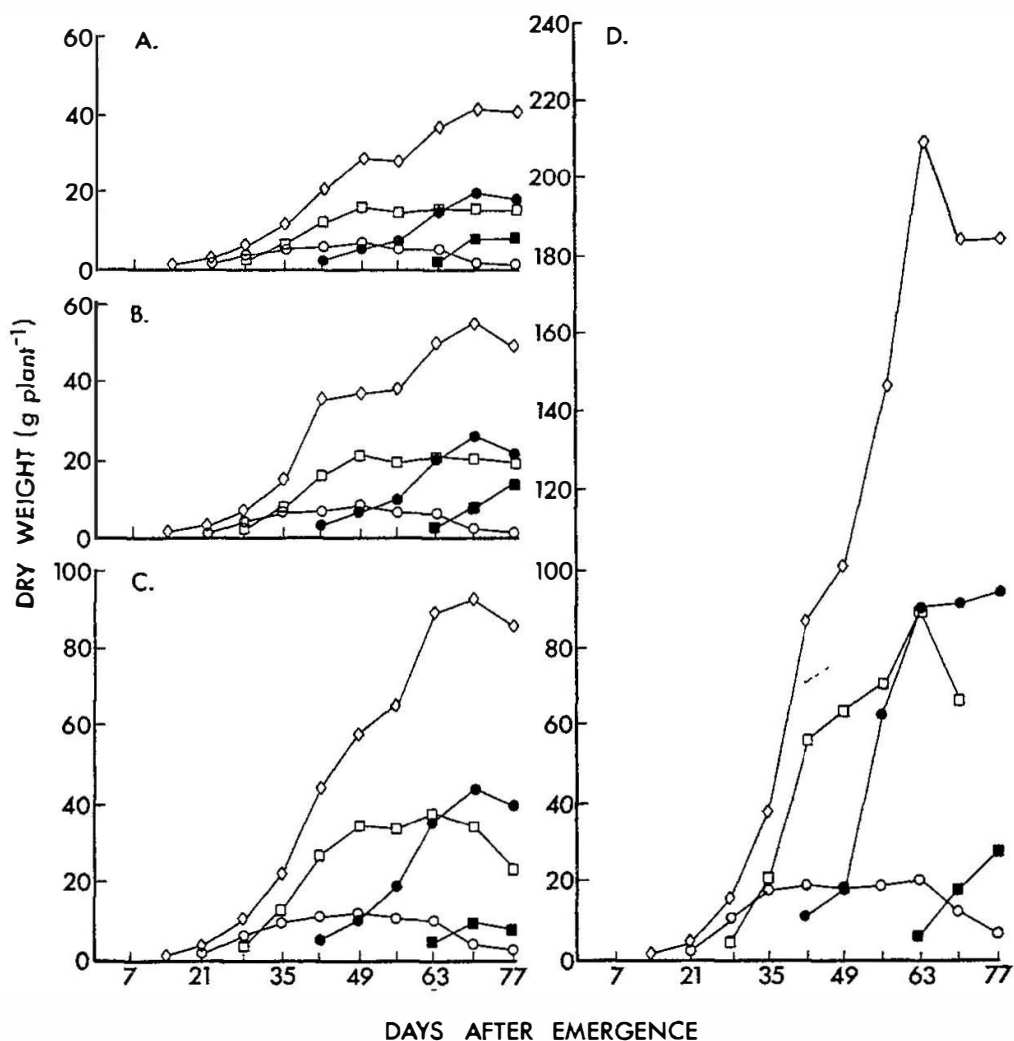


Fig. 4. The time course of accumulation of dry weight (total ◇; leaf ○; stem □; panicle ●; dead material ■) during the growing season at four populations: A: 400 000; B: 288 000; C: 149 000; and D: 50 000 plants ha<sup>-1</sup>.

occurred because of continued growth of tillers, of which a high proportion failed to become productive.

Panicle weights initially increased slowly after 50% anthesis, indicating a short lag period in grain filling. Rapid accumulation of dry weight in the panicles followed and ended just prior to physiological maturity.

The partitioning of dry weight between the main axis and tillers is shown in Table 2. At 21 days after emergence, population effects were already evident in terms of increased partitioning into tillers at low densities. The dry weight of the main axis was unaffected by density; partitioning to leaf and stem favoured the leaf 2:1. At 50% anthesis (42 days), tillers, when contrasted with the main axis, had lower stem but comparable leaf weight at higher densities; conversely at low densities, tiller stem weights constituted the major fraction of dry matter produced. The difference in the distribution of leaf and stem weights between the main axis and tillers was due to a relatively high number of tillers, and therefore numbers of leaves, over the whole density range, but a proportionately lower fraction of these elongating

TABLE 2

The effect of developmental stage and population on the dry weight partitioning per plant. Observed values (mean of two replicates) are presented

Days after emergence	Density (plants ha <sup>-1</sup> × 10 <sup>4</sup> )	Partitioned dry weight (g/plant)					
		Main axis			Tillers		
		Leaf	Stem	Panicle	Leaf	Stem	Panicle
21	40.0	0.7	0.4	—	0.6	0.3	—
	28.8	1.0	0.5	—	0.8	0.4	—
	14.9	0.8	0.4	—	1.2	0.8	—
	5.0	1.0	0.5	—	2.2	1.2	—
42	40.0	3.0	10.4	2.6	2.9	2.5	0.6
	28.8	3.2	10.7	2.7	5.3	7.3	0.7
	14.9	3.2	12.9	3.5	8.4	15.2	2.0
	5.0	6.4	20.0	5.9 <sup>a</sup>	26.2 <sup>a</sup>	54.8	12.6 <sup>a</sup>
77	40.0	0.6	9.7	11.9 <sup>a</sup>	0.2	6.0	5.5 <sup>a</sup>
	28.8	1.3	14.2	14.3	0.3	5.4	8.0
	14.9	1.3	9.4	14.9	1.5	14.4	18.5
	5.0	1.6	19.0	26.5	5.6	63.8	87.6

<sup>a</sup>Values for a single replicate consisting of five to eleven plants.

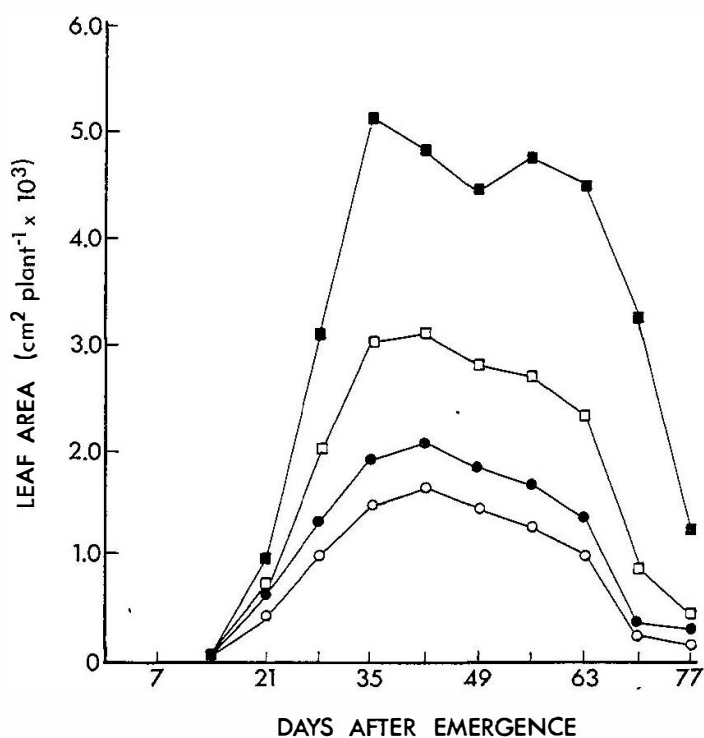


Fig. 5. The time course of development of green leaf area per plant at four populations, 400 000 (○), 288 000 (●), 149 000 (□) and 50 000 (■) plants ha<sup>-1</sup>.



as the plant density increased. At maturity, leaf weights of tillers declined relatively more severely than for the main axis due to senescence of non-productive tillers.

Green leaf area per plant followed the same incremental pattern for all four densities (Fig. 5), and corresponded to the changes in leaf dry weight. Maximum leaf area per plant was attained about 50% anthesis, declined gradually to 63 days and fell off sharply thereafter. Table 3 demonstrates the importance of the tillers for maximum leaf area at all densities. At the time of maximum leaf area per plant, tiller leaf area was equal to that of the main axis at the highest density and almost four times greater at the lowest density. By maturity, leaf area per plant was reduced greatly, with tillers retaining a higher leaf area than the main axis only at the lower densities. The maximum leaf area index of 6.7 was recorded for 400 000 plants ha<sup>-1</sup> and declined with density to 2.9 at 50 000 plants ha<sup>-1</sup> where the canopy failed to close.

TABLE 3

The effect of developmental stage and population on component leaf areas (LA) per plant and leaf area indices (LAI). Observed values (mean of two replicates) are presented

Days after emergence	Density (plants ha <sup>-1</sup> × 10 <sup>4</sup> )	LA/plant (cm <sup>2</sup> )		
		Main axis	Tillers	LAI
21	40.0	213	247	1.8
	28.8	350	303	1.9
	14.9	256	462	1.1
	5.0	292	704	0.5
42	40.0	770	898	6.7
	28.8	754	1523	6.6
	14.9	674	2469	4.7
	5.0	1201 <sup>a</sup>	4610 <sup>a</sup>	2.9
77	40.0	155	40	0.8
	28.8	295	72	1.1
	14.9	189	285	0.7
	5.0	241	1066	0.7

<sup>a</sup>Values for a single replicate consisting of five to eleven plants.

The number of productive tillers per plant at maturity was between 15–40% of the maximum tiller number per plant which was achieved at 50% anthesis (Fig. 6). At lower populations, both tiller production and survival rate increased. Above 270 000 plants ha<sup>-1</sup> tiller number per plant fell below unity, i.e. some plants produced a panicle only on the main axis. However, head numbers per hectare increased as the number of plants per hectare increased.

Increased plant competition decreased total grain yield per plant (Fig. 6)

with the relative contributions of the main axis and tillers varying in relation to density. The tillers rapidly overtook the main axis as the principal determinant of plant yield as the density declined below 140 000 plants ha<sup>-1</sup>, above which the main axis dominated.

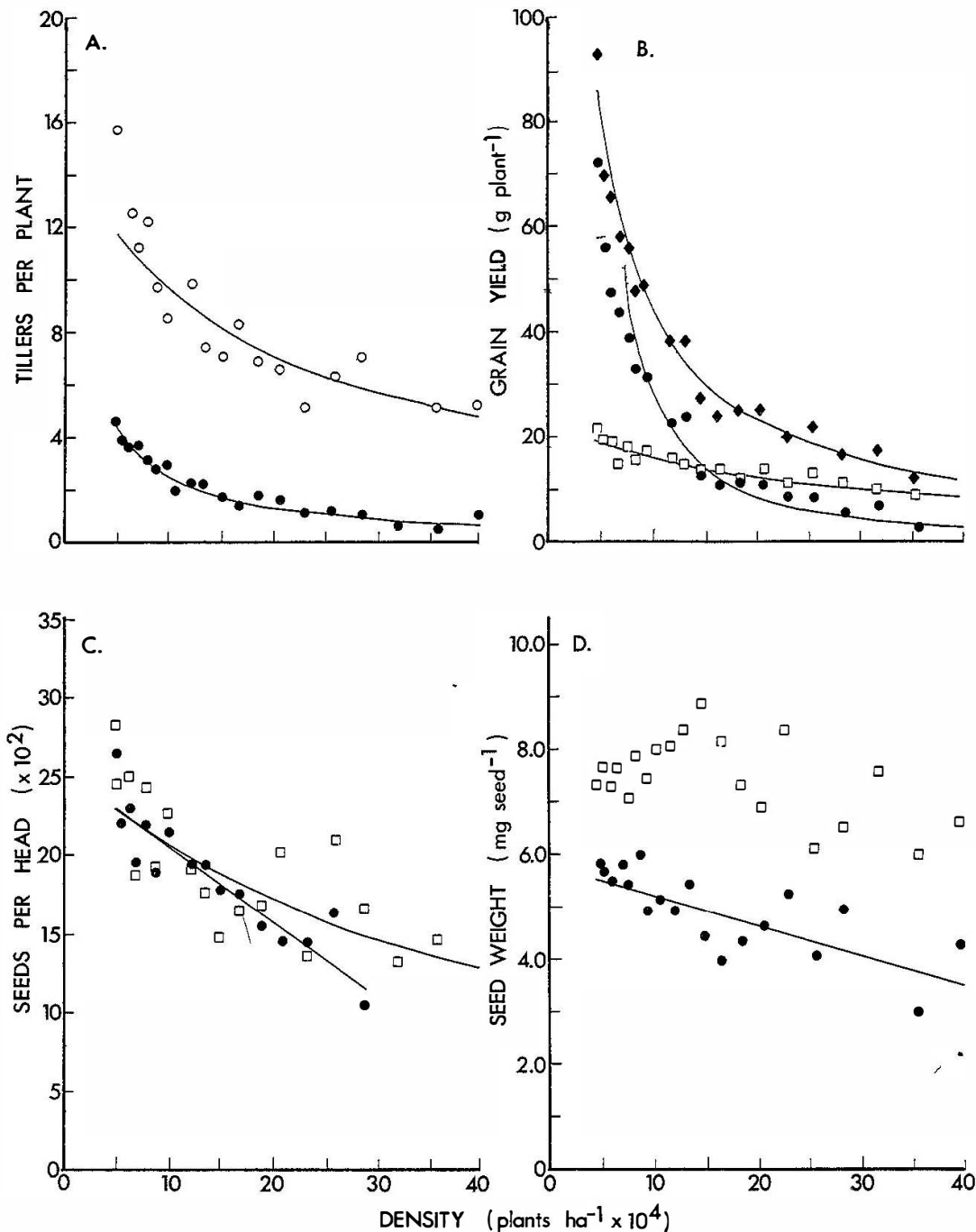


Fig. 6. The effect of population on A: number of tillers (excluding the main axis) at 50% anthesis and maturity (○, ●),  $\omega^{-1}=6.81 \cdot 10^{-2}+3.46 \cdot 10^{-7} \rho$  ( $r^2=0.82$ ,  $P<0.001$ ) and  $\omega^{-1}=3.26 \cdot 10^{-2}+3.60 \cdot 10^{-6} \rho$  ( $r^2=0.79$ ,  $P<0.001$ ) respectively; B: total grain yield and the contributions from the main axis and tillers (◆, □, ●),  $\omega^{-1}=2.08 \cdot 10^{-3}+2.04 \cdot 10^{-7} \rho$  ( $r^2=0.95$ ,  $P<0.001$ ),  $\omega^{-1}=4.45 \cdot 10^{-2}+1.67 \cdot 10^{-7} \rho$  ( $r^2=0.88$ ,  $P<0.001$ ) and  $\omega^{-1}=-4.31 \cdot 10^{-2}+7.94 \cdot 10^{-7} \rho$  ( $r^2=0.82$ ,  $P<0.001$ ) respectively; C: seed number per head from the main axis and tillers (□, ●),  $Y^{-1}=4.00 \cdot 10^{-4}+9.19 \cdot 10^{-10} \rho$  ( $r^2=0.55$ ,  $P<0.001$ ) and  $Y=2540-0.0047 \rho$  ( $r^2=0.84$ ,  $P<0.001$ ) respectively; D: seed weight from the main axis (no correlation) and tillers (□, ●),  $Y=5.95-5.87 \cdot 10^{-6} \rho$  ( $r^2=0.58$ ,  $P<0.001$ ).

Seed number per head on the main axis declined asymptotically as density increased (Fig. 6). Seed number for tiller heads was almost comparable to that for the main axis at low populations and declined linearly as density increased. Seed number per head, averaged over all heads per plant, decreased linearly with increases in population ( $r = -0.80$ ,  $P < 0.001$ ).

The weight of individual grains on main heads did not correlate with density; the mean seed weight was  $7.6 \pm 0.3$  mg. The weight per seed harvested from tillers decreased as density increased to 400 000 plants  $\text{ha}^{-1}$  (Fig. 6). The weight of individual grains averaged over all heads did not correlate with density and had a mean weight of  $6.2 \pm 0.1$  mg.

## DISCUSSION

Grain yield per hectare ranged from 4080 to 4790  $\text{kg ha}^{-1}$  over the population range, which was considerably higher than the yield of 2490  $\text{kg ha}^{-1}$  for BJ 104 in the 1977 kharif season at ICRISAT (ICRISAT, 1979). Also, in contrast to our original hypothesis, there was a plateau in grain yield per hectare over a wide range of populations, from 150 000 to 400 000 plants  $\text{ha}^{-1}$ , which demonstrated the large degree of plasticity within the millet plant BJ 104. The high, broad plateau in grain yield was associated with a combination of several factors, of which tillering is considered as the most important.

At 400 000 plants  $\text{ha}^{-1}$ , tillers contributed 25% of the grain yield as there were still 1.7 heads per plant. As population declined, the sharp increase in tiller yield, combined with the relative stability of the yield of the main axis, largely compensated for the reduced plant numbers per unit area. At the lowest population, tillers contributed 77% of the grain yield, which resulted in a range of tiller yield contribution considerably higher than that of the 15–50% found by Ayyanger and Hariharan (cited by Rachie and Majmudar, 1980).

Tillering caused seed numbers to increase slightly (6%) from 65 000 to 69 000  $\text{m}^{-2}$  as population declined (88%). In fact, pearl millet can tolerate extremely high populations, above 20 million plants  $\text{ha}^{-1}$ , by becoming a unicum (Pearson et al., 1977). This tolerance was also associated with individual seed weight being relatively constant (in the present study 6.2 mg; unpublished data, ICRISAT). It contrasts with other cereals, e.g. wheat and rice, where seed number  $\text{ha}^{-1}$  and individual seed weight vary substantially (and compensate each other) with increasing plant population (e.g. Evans and Wardlaw, 1976).

In addition to yield compensation, tillers were the major contributors to leaf area index at low populations (Table 3 and Gregory and Squire, 1979), as in sorghum (Fischer and Wilson, 1975). At high populations also, tillers were a significant component of leaf area index, in that the partitioning ratio between the leaf component and the stem component of tillers was high. Tiller and leaf area survival depended on population, e.g. tiller survival in-

creased from 14% to 42% of total tillers produced as population declined from the high to the low extreme. The increased survival of tillers at low population was due partly to the continued development of tillers during early grain filling. With other millet varieties, Ramond (1968) reported that about 25% of tillers produce viable heads.

LAI's reached a maximum at 50% anthesis and declined gradually during grain filling until severe leaf senescence near physiological maturity. LAI's were high relative to some other wet season and dry season BJ 104 millet crops at ICRISAT (e.g. 3 and 1.7 respectively; ICRISAT, 1979) and were maintained through most of grain filling in contrast to the early and rapid decline of LAI in wheat (Allison, 1964).

Grain filling within the plant proceeded according to sigmoid pattern at all populations (Fig. 4), although the rate of filling (the slope of the linear period of panicle weight increase) increased with decreasing population due to the higher number of heads per plant and therefore grains involved.

The above-ground dry weight was greater than that recorded for BJ 104 in 1977 of 6550 kg ha<sup>-1</sup> at ICRISAT (ICRISAT, 1979) and it increased markedly with increased population to reach an optimum or plateau beyond 400 000 plants ha<sup>-1</sup>. Therefore the decline in harvest index, which began at 62 000 plants ha<sup>-1</sup>, was due mostly to a constant grain yield with increased top weight in contrast to the depressed grain yield with constant top weight with increased population in most maize and wheat crops (Donald and Hamblin, 1976).

The results suggest that the population optimum or plateau of yield of pearl millet in the semi-arid tropics will depend on the extent to which moisture stress accelerates senescence: population, the effects of which were already evident within the plants after panicle initiation, determines the number of potential grain sites but moisture stress will determine how many of these and to what extent they are filled and what proportion of grain yield comes from tillers. In this case, moisture stress presumably initiated the severe leaf senescence which occurred at 63 days: the effect on grain yield of the plant was negligible due to (i) high seasonal yield, (ii) high individual grain weights and (iii) no decline in yield at high populations where moisture stress should be more severe.

In conclusion, these results provide further support for the judgement that pearl millet has become adapted to, and selected for, growing in conservative, traditional farming systems: populations may commonly be about 10 000 plants ha<sup>-1</sup> in the African Sahel (Pearson and Hall, 1984) and may range up to 175 000 plants ha<sup>-1</sup> in the semi-arid tropical regions of India (ICRISAT, 1982).

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