

## Mechanisms of adjustment by different pearl millet plant types to varying plant population densities

F. R. BIDINGER\* AND D. S. RAJU

Genetic Resources and Enhancement Programme, International Crops Research Institute for the Semi-Arid Tropics, ICRISAT Patancheru PO, Andhra Pradesh 502 324, India

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### SUMMARY

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is commonly grown at a wide range of plant population densities, both by design and as a consequence of stand establishment problems. High tillering genotypes are known to compensate effectively for lower plant population densities through their tillering capacity; less is known about the ability of naturally low tillering genotypes to adjust to low plant population densities. This is a particular concern in the case of the *Iniadi* landrace materials which are currently widely used in breeding programmes in both India and Africa. This research was done to determine how effectively the low tillering *Iniadi* types adjust to low plant population densities and how their mechanism(s) of adjustment compares to those of higher tillering materials. Two high and two low tillering genotypes were grown over a period of 5 years at plant population densities ranging from 12 to 2 plants/m<sup>2</sup>, under both high and low fertility regimes at the ICRISAT Centre, India. Both the high and low tillering types adjusted equally well to the reduced plant population densities, as judged by grain yield, but differed in their mechanism of adjustment. The high tillering genotypes adjusted, as expected, primarily by increasing productive tiller numbers, with only small changes in individual tiller productivity. The *Iniadi* genotypes increased productive tiller numbers in response to decreasing plant population densities to a limited degree, but increased panicle productivity to a much greater degree than the high tillering types. There was no differential effect on adjustment ability between the two types as a consequence of increased fertility, despite the stimulating effect of fertility on productive tiller numbers. The results are discussed in terms of generalized mechanisms of response to changing individual plant environmental resources (fertility and space), and in terms of the use of *Iniadi* germplasm in pearl millet breeding programmes.

### INTRODUCTION

Plant population densities of pearl millet (*Pennisetum glaucum* (L.) R. Br.) in farmers' fields vary widely due to both planting method and to frequent failure of stand establishment. In the Sahelian and Sudanian zones of west Africa, planting is done primarily by hand, in widely spaced hills of multiple plants. The wide spacing of the hills allows farmers to plant as large an area as possible in the short time available following a rain, in which there is sufficient moisture in the seed zone for germination. The wide spacing of hills also allows for later interplanting of various other crops which are either too competitive to plant at the same time as the millet (e.g. cowpea), or whose

seed is too valuable to risk planting with the first rain (e.g. groundnut). Spacing of hills varies from less than 1 × 1 m to as much as 2 × 2 m (Spencer & Sivakumar 1987; Anand Kumar 1989). Hills are usually subsequently thinned, in conjunction with the first hoeing, to 3–5 plants per hill, giving intended plant population densities of the order of 10 000–30 000 plants/ha. In millet-growing areas in south Asia, sowing is done either with indigenous animal-drawn single row planters, or with modified, tractor-mounted, tine tillage implements. In both methods, seed is dropped by hand into funnel(s) connected to tube(s) which deposit the seed behind the opener/tines. Rows are closely spaced (0.30–0.50 m), and recommended plant population densities are of the order of 150 000–200 000 plants/ha (Harinarayana 1987; AICPMIP 1988). Thinning of fields is not customarily done, apart from localized areas where population densities are particularly high.

\* To whom all correspondence should be addressed.  
Email: f.bidinger@cgiar.org

Actual plant population densities in farmers' fields in both areas are frequently well below recommended population densities, however, due to losses from drought, blowing sand, downy mildew (*Sclerospora graminicola*) and soil insects. For example McIntire & Fussell (1989) reported results from on-farm experiments in Niger in which the actual number of viable hills (with at least one plant) ranged from 3200 to 7200/ha, compared to the expected (planted hills  $\times$  percentage emerged) number of hills (6300–10000/ha). Similarly, Soman *et al.* (1987) found that plant population densities at 15 d after sowing in one village in Rajasthan, in the arid zone of India, represented < 10% of the total number of seeds sown.

The crop thus must adjust to extremely wide ranges in plant population, because of both design and failure to achieve target plant stands. There is ample experimental evidence that pearl millet has an impressive ability to adjust to varying plant population densities, mainly through its ability to tiller (Ramond 1968). Tiller contribution to crop biomass and grain yield can vary from < 25% to > 75% of the total, depending on plant population (Azam-Ali *et al.* 1984; Carberry *et al.* 1985). Grain yields frequently vary little, if at all, over ranges of plant population of two to fourfold around recommended population densities (Gautam 1970; Nirwal & Upadhyay 1979; Carberry *et al.* 1985; Craufurd & Bidinger 1989). Most of the plant population *v.* yield studies have, however, been done with genotypes with a capacity for considerable tillering (e.g. Carberry *et al.* 1985). There is some evidence that plant types with a limited tillering capacity may not have the ability to adjust as effectively to changing plant population as high tillering cultivars (Verma & Midha 1989). This concern is particularly relevant to the *Iniadi* landrace from Togo and Ghana, which has early maturity and large panicles and a large grain size, but a very low tillering capacity (Andrews & Anand Kumar 1996). Breeding materials derived from this source are presently being widely used in both the ICRISAT and national breeding programmes in India, and in national and regional breeding programmes in western and southern Africa (Andrews & Anand Kumar 1996). This type of material may be more sensitive to variation in plant population than the traditional, high tillering Indian cultivar (J. R. Witcombe, 1988, personal communication), and thus may be less adapted to production systems where plant population densities are low, either by design or due to stand loss. This study was conducted to determine (1) how effective the low tillering phenotype of millet derived from the *Iniadi* landrace type is in adjusting to low plant population densities, relative to higher tillering Indian plant types, and (2) to compare the mechanisms of adjustment in high and low tillering plant types.

## MATERIALS AND METHODS

The study was conducted during the rainy seasons of 1988–1992 at the ICRISAT Centre, Patancheru, India (17°30'N and 78°E) on a sandy alfisol (Udic Rhodustalf). It involved four genotypes of contrasting tillering ability, four different plant population densities and two different fertility regimes, in a split-split plot design with four replications. The basic plot size (sub-subplot) was 4 rows  $\times$  0.60 m  $\times$  9.0 m (21.6 m<sup>2</sup>), of which 2 rows  $\times$  7.0 or 8.0 m (8.4 or 9.6 m<sup>2</sup>) were harvested for comparison of treatments. All trials were completely rainfed, but were not subject to significant drought stress in any of the years they were grown.

Main plots were long-term (established many years before this study began) fertility environments: a high fertility (HF) regime receiving 80 kg N/ha and 18 kg P/ha and a low fertility (LF) regime receiving 20 kg N and 9 kg P/ha annually. All of the phosphorus in both regimes, all of the N in the LF regime and half of the N in the HF regime were banded into the ridges before seeding. The remaining N in the HF regime was side dressed at 15–20 days after crop emergence. The two fertility environments were intended to assess the effect of fertility on the ability to adjust to low plant population.

Subplots were four different plant population densities, achieved by varying the within-row plant spacing from 0.10 to 0.83 m: 167000, 79000, 40000 and 20000 plants/ha. Rows were machine sown and thinned by hand to the desired spacing between plants at 10–15 days after emergence. This method of varying plant population represents the situation of variable within-row plant stands, but does introduce differences in rectangularity among plant population treatments. The target range in plant population densities was chosen to represent *c.* 10–85% of the recommended plant population of 200000 plants/ha for the pearl millet zone in which the experimental site is situated (AICPMIP 1988).

Sub-subplots were two high tillering genotypes (ICMH 423 and HiTiP 88) and two low tillering genotypes (ICMH 501 and ICMV 87902); the first of the two genotypes in each pair was an F<sub>1</sub> hybrid and the other an open-pollinated variety or population. ICMH 423 (ICMA 841  $\times$  ICMP 423) is a released F<sub>1</sub> hybrid, of medium maturity and high tillering capacity. HiTiP 88 (High Tillering Population 1988) is a random-mating population made from very high tillering source lines. In the first year of the experiment, a high tillering hybrid HHB 67 (843A  $\times$  H77/833-2) was used, but was replaced by HiTiP 88, because it flowered well before the remaining three genotypes. It was considered the same as HiTiP 88 in the across-year analysis of variance, as it has a very similar phenotype. ICMH 501 (834A  $\times$  ICMP 501) is a released F<sub>1</sub> hybrid with a large panicle and large grain

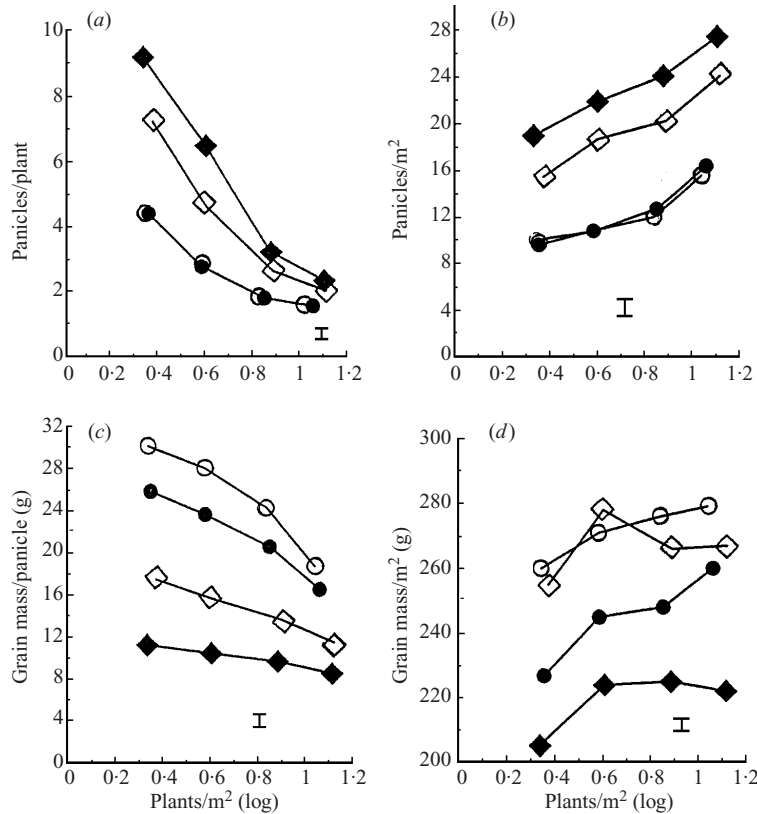


Fig. 1. Panicle number per plant (a), panicle number per m<sup>2</sup> (b), grain mass per panicle (c), and grain mass per m<sup>2</sup> (d), in relation to actual plant population for the high tillering (square) and low tillering (circle) genotypes. Solid symbols are open-pollinated varieties (HiTiP 88 and ICMV 87902); open symbols are hybrids (ICMH 423 and ICMH 501). The error bar is twice the S.E. (from the analysis of variance) for the genotype × log plant population density interaction means.

size. Its female parent, which was bred at ICRISAT from materials received from the Serere Research Station, Uganda, is almost certainly of *Iniadi* origin (Andrews & Anand Kumar 1996). ICMV 87902 is an unreleased open-pollinated variety, bred at ICRISAT from *Iniadi* germplasm from Togo.

At crop maturity, actual plant and panicle numbers in the harvest area of the plot were counted, panicles harvested, dried at 70 °C, threshed and the grain weighed. Panicles per plant and grain yield per panicle were calculated from these data. 100-grain mass for each plot was determined from triplicate 100 grain samples and the data used to calculate grain numbers per panicle. All data were analysed according to the experimental design, using the GLM procedure of SAS (SAS 1985), with the following exception: because of the lack of randomization of the fertility treatment across years, the ten combinations of year × fertility were considered as environments, each replicated four times. The effects of environment (partitioned into effects of fertility, year and their interaction) were tested against the replication within

environment mean square. Population effects were analysed for their linear, quadratic and residual components by single degree of freedom (S.D.F.) contrasts. The logs of the plant population densities (actual plant populations measured in the field) were used in order to have approximately equally spaced treatments to allow the use of standard S.D.F. comparison coefficients to test for linear and quadratic effects (Steele & Torrie 1981). Yield component data for the various genotypes were plotted against the log of the actual population densities, in order to present figures comparable to the S.D.F. analysis (Fig. 1). Genotype differences (high and low tillering habit, hybrid and open-pollinated cultivar and their interaction) and their interactions with fertility and plant population were also analysed by S.D.F. contrasts.

## RESULTS

### *Plant population, fertility and year effects*

Actual plant population densities achieved in the experiment were close to the target population

Table 1. Main treatment effects means and S.E. for plant numbers per m<sup>2</sup> (PLNOM2), panicle numbers per plant (PNNOPL), panicle numbers per m<sup>2</sup> (PNNOM2), grain mass per panicle (GRMAPN) and grain mass per m<sup>2</sup> (GRMAM2). Data are means of trials conducted between 1988 and 1992

Main effect	PLNOM2 (no./m <sup>2</sup> )	PNNOPL (no./pl)	PNNOM2 (no./m <sup>2</sup> )	GRMAPN (g/pn)	GRMAM2 (g/m <sup>2</sup> )
Fertility					
High	6.5	4.2	19.2	18.8	297
Low	6.5	3.0	14.4	16.9	204
S.E.	0.05	0.05	0.18	0.16	1.8
Population					
16.7 plants/m <sup>2</sup> *	12.4	1.8	20.9	13.8	257
7.9 plants/m <sup>2</sup> *	7.5	2.3	17.3	17.1	254
4.0 plants/m <sup>2</sup> *	4.0	3.9	15.5	19.5	254
2.0 plants/m <sup>2</sup> *	2.3	6.3	13.5	21.2	237
S.E.	0.07	0.07	0.26	0.22	2.6
Genotype					
HiTiP 88	6.8	5.0	23.1	10.0	219
ICMH 423	6.9	4.1	19.6	14.6	267
ICMV 87902	6.3	2.6	12.4	21.6	245
ICMH 501	6.1	2.6	12.1	25.2	272
S.E.	0.07	0.07	0.26	0.22	2.6
Mean high tillering	6.9	4.6	21.4	12.3	243
Mean low tillering	6.2	2.6	12.2	23.5	258
S.E.	0.05	0.05	0.18	0.16	1.8
Grand mean	6.5	3.6	16.8	17.9	251
S.E.	0.04	0.03	0.13	0.11	1.3
D.F.	360	356	358	356	360

\* Intended plant population densities, actual population densities are given in the Table.

densities for the three lower population densities, but fell below the target for the highest population (mean of 12.4 plants/m<sup>2</sup> compared to a target of 16.7 plants/m<sup>2</sup> (Table 1)). Plant population density effects were significant for both yield ( $P < 0.002$ ) and all yield components ( $P < 0.001$ ). The effect on yield was due only to the lowest population, however, as grain yields did not differ between 4 and 12 plants/m<sup>2</sup> (Table 1).

Mean panicle number per plant increased more than threefold across the range of plant population densities, from 1.8 at 12 plants/m<sup>2</sup> to 6.3 at 2 plants/m<sup>2</sup>. However the sixfold difference in plant numbers over the population treatments resulted in a net decline in panicle numbers from 20.9 to 13.5/m<sup>2</sup> between 12 and 2 plants/m<sup>2</sup> (Table 1). Mean grain yield per panicle increased, as panicle numbers declined, by approximately the same magnitude as the decreases in panicle numbers/m<sup>2</sup> (13.8 to 21.2 g/panicle), however, resulting in full compensation in grain yield at all but the lowest plant population, which yielded 7% less than the three higher ones (Table 1). Single degree of freedom comparisons of the effects of population density means (log transformation) indicated significant linear and quadratic effects of plant population density on grain yield

and on all yield components (analysis not presented, but see Fig. 1).

Fertility had highly significant effects ( $P < 0.001$ ) on grain yields and all yield components, as expected. Grain yields were 46% higher in the high fertility regime (Table 1). The yield component primarily affected by higher fertility was productive tiller number/m<sup>2</sup> (33% increase), with a secondary effect on panicle productivity (13% increase). Increased fertility thus had the expected greater promotive effect on productive tiller number than on panicle productivity. Interactions of fertility regime and plant population density were not significant (except for panicle number/plant), indicating that the relationship of plant population density and grain yield was not different in the two fertility environments used in this experiment. Therefore our original hypothesis that higher fertility would improve the ability of pearl millet to adjust to low population densities was not supported by the grain yield data.

Year effects were significant for all variables measured ( $P < 0.001$ ). Grain yields ranged from a low of 226 g/m<sup>2</sup> in 1989 to 293 g/m<sup>2</sup> in 1990; but there was no evident trend over the years (data not presented). Mean panicle numbers per m<sup>2</sup> were similar (13–16) for all years except 1991, in which they

averaged 23 per m<sup>2</sup>, for unknown reasons. This did affect grain yields in that year, however (mean of 253 g/m<sup>2</sup>).

#### *Genotype differences*

Genotypes differed significantly for all variables measured ( $P < 0.001$ ), as expected from the objectives of the experiment. Genotype effects on grain yield were due to significant ( $P < 0.001$ ) differences between high and low tillering types, between hybrids and open-pollinated varieties, and the interaction of the two. Differences between the high and low tillering types were significant ( $P < 0.001$ ) for all yield components. Mean panicle numbers per plant (4.6 v. 2.6) and m<sup>2</sup> (21.4 v. 12.4) were *c.* 75% greater in the high tillering genotypes than in the low tillering ones (Table 1, Fig. 1*a, b*). Conversely, mean grain mass per panicle was 90% greater in the low tillering genotypes (23.5 g) than in the high tillering ones (12.3 g, Fig. 1*c*). This greater difference in panicle productivity between the low and high tillering genotypes resulted in a statistically ( $P < 0.001$ ), if not agronomically, greater mean grain yield in the low (258 g/m<sup>2</sup>) than in the high tillering (243 g/m<sup>2</sup>) genotypes (Table 1, Fig. 1*d*).

The open-pollinated varieties (HiTiP 88 and ICMV 87902) had a greater ( $P < 0.001$ ) mean panicle number per m<sup>2</sup> than the hybrids (17.8 v. 15.9), due mainly to the high tillering habit of HiTiP 88 (Table 1 and Fig. 1*b*). However, the hybrids (ICMH 423 and ICMH 501) had a considerably greater ( $P < 0.001$ ) mean grain mass per panicle than the open pollinated varieties (19.9 g v. 15.8 g, Fig. 1*c*) and a consequently greater ( $P < 0.001$ ) mean grain yield (270 g/m<sup>2</sup> v. 232 g/m<sup>2</sup>, Fig. 1*d*). These specific differences are probably largely a consequence of the individual genotypes used, but the yield advantages of hybrids over open-pollinated varieties are well documented in the crop (Mahalakshmi *et al.* 1992).

#### *Interactions of genotype with fertility*

Genotype × fertility interactions were significant for all yield component variables ( $P < 0.001$ ) and for grain yield itself ( $P < 0.028$ ), due to two different interactions: (1) significant differences in the response to fertility regime between the high and low tillering types in all yield components ( $P < 0.001$ ), but not final grain yield, and (2) differences between the hybrid and variety types in final grain yield ( $P < 0.004$ ), but not in individual yield components. The high tillering genotypes responded to increased fertility primarily by an increase in productive tiller numbers, increasing on average 1.6 panicles/plant (equivalent to an average increase of 6.8 panicles/m<sup>2</sup>), compared to an average increase of only 0.8 panicles/plant (equivalent to an average increase of only 1.7 panicles/m<sup>2</sup>) by the low tillering genotypes. In contrast, the increase in mean grain yield per panicle

in the high tillering genotypes in response to an increase in fertility was only 0.9 g (11.9 to 12.8 g/panicle), where the low tillering types increased grain yield per panicle by an average of 2.7 g (22.1 to 24.8 g/panicle). The net result of this was a similar increase in mean grain yield of 93 g/m<sup>2</sup> in response to increased fertility in both the high tillering types (197 to 290 g/m<sup>2</sup>) and the low tillering types (212 to 305 g/m<sup>2</sup>).

The hybrids and varieties did not differ significantly in response to fertility regime in terms of the increase in mean productive tiller number (5.0 m<sup>2</sup> for the hybrids v. 4.5 m<sup>2</sup> for the varieties), or in mean panicle productivity under higher fertility than the varieties (2.1 v. 1.5 g/panicle). The combination of small differences in response to higher fertility in the hybrids and varieties in the individual yield components did result in a significantly ( $P < 0.004$ ) greater increase in mean grain yield in the hybrids than in the varieties (101 v. 86 g/m<sup>2</sup>) under the higher fertility regime, however.

#### *Interactions of plant population density and genotype*

##### *Interactions of plant population density and tillering phenotype*

Genotype × population density interactions were significant for all yield components ( $P < 0.06$  to  $< 0.001$ ), but not for yield itself. Single degree of freedom comparisons indicated that most of the yield component interactions were due to differences between the high and low tillering genotypes in both the linear and the quadratic components of their response to changing plant population density ( $P < 0.044$ – $P < 0.001$ ). High tillering genotypes responded more effectively to declining plant population density in terms of panicle numbers per plant than did the low tillering genotypes (Fig. 1*a*), particularly at the lower plant population densities. For example, as plant population density declined from 8 to 2 plants/m<sup>2</sup>, the high tillering types increased the number of productive panicles per plant by an average of 5.3 (from 2.9 to 8.2), compared to the low tillering genotypes which increased the number of productive panicles per plant by an average of only 2.6 (from 1.8 to 4.4). This allowed the high tillering genotypes to maintain virtually the same numeric superiority in panicle numbers per m<sup>2</sup> over the low tillering genotypes at all plant population densities (Fig. 1*b*).

The opposite response was evident in productivity per panicle, where the low tillering types increased productivity per panicle at a greater rate than did the high tillering types as plant population density declined. For example, the high tillering types increased panicle productivity by only 4.4 g/panicle (10.0 to 14.4 g/panicle) as population density declined from 12 to 2 plants per m<sup>2</sup>, where the low tillering types increased panicle productivity by 10.4 g/panicle

(17.6 to 28.0 g/panicle) over the same range of plant population densities (Fig. 1c). The net result was that the ability of the two types to compensate for declining plant population density was effectively the same, despite the marginal significance ( $P < 0.056$ ) of the high v. low tillering type by linear population density effect single degree of freedom comparison. The yield difference between the low and high tillering types was 25 g/m<sup>2</sup> (270 v. 245 g/m<sup>2</sup>) at the highest plant population density, compared to 14 g/m<sup>2</sup> (244 v. 230 g/m<sup>2</sup>) at the lowest population density. This is not sufficient to favour one type over the other for specific plant population density situations.

#### *Interactions of plant population density and cultivar type*

The hybrids and varieties also differed significantly in the linear response of panicle number per plant ( $P < 0.001$ ) and in panicle productivity ( $P < 0.001$ ). The adjustment by the hybrids in terms of panicle numbers per plant as plant population density declined was slightly less than that of the varieties, due to the strong tillering response of HiTiP 88 to declining plant population density (Fig. 1a). This difference in response in terms of panicles per plant did not translate into a significant difference in response in panicles per m<sup>2</sup>, however ( $P > 0.10$ ). The hybrids had a significantly greater response to declining plant population density in terms of grain mass per panicle (15.1 to 23.8 g/panicle) than the varieties (12.5 to 18.6 g/panicle), but again, this did not translate into a significantly different response in overall yield. Therefore there was no evidence in this experiment that the normal yield superiority of hybrids over varieties has any important consequences for the ability to adjust to declining plant population densities.

#### *Interactions of plant population density × fertility × genotype*

Genotype × population × fertility interactions were significant for panicle numbers ( $P < 0.004$ ) but not for panicle productivity or for grain yield. It was our original hypothesis that the expected greater promotive effect of increased fertility on panicle number than on panicle productivity (Table 1) might favour high tillering lines over low tillering ones in adjusting to lower plant population densities under well-fertilized conditions. The expected interaction of plant type, plant population and increased fertility did occur in terms of panicle numbers (data not presented). However this advantage of the higher tillering types under higher fertility was offset by a lesser increase in grain yield per panicle with declining plant population density under higher fertility in the high tillering types than in the low tillering, negating any advantage of the higher tillering types in adjusting to low plant population densities under higher fertility.

## DISCUSSION

### *Yield – plant population response of the low tillering genotypes*

The low tillering *Iniadi* genotypes were able to adjust to declining plant population densities equally as well as the high tillering types, as judged by their grain yields. Not only was there no genotype × population interaction for grain yield, but there was also no interaction of genotype × population with either year, fertility regime or year × fertility regime, suggesting that the adjustment ability of the *Iniadi* types should be equal to that of the higher tillering types across environments, at least within the ranges of the treatments used in this experiment. The absence of an effect of fertility regime on genotype response to population should probably not be extrapolated to other (lower) fertility environments than those used in this experiment, however. Although our low fertility regime received only 20 kg N and 9 kg P/ha, the yields of 2.0 t/ha were more than twice national yield averages for most millet growing countries.

It would seem, intuitively, that high tillering would be the more effective compensation mechanism for low plant population densities. Greater tillering should result in a greater pre-flowering leaf area and radiation interception and therefore the potential for greater compensation in the form of an increase in grain numbers per unit area, which are directly linked to intercepted radiation (Ong & Squire 1984; Craufurd & Bidinger 1989). No measurements were made of radiation interception, but there was a significant interaction of tillering habit and plant population for grain numbers per m<sup>2</sup>. The high tillering types had a decline in grain numbers per unit area of only 17% ( $3.55 \times 10^3$  to  $2.95 \times 10^3$  grains/m<sup>2</sup>) between the highest and lowest plant population densities, compared to a decline of 27% ( $2.92 \times 10^3$  to  $2.13 \times 10^3$  grains/m<sup>2</sup>) in the low tillering genotypes. But this advantage was offset by a similar, but opposite, interaction of tillering and plant population for individual grain mass. The high tillering types increased the 1000 grain mass by only 14% (7.06 to 8.04 g) between the highest and lowest population densities, compared to an increase of 26% (9.38 to 11.83 g) in the low tillering genotypes. Thus, although the high tillering types appear to possess a potentially more effective compensation mechanism for declining plant population, in their greater ability to maintain grain numbers per unit area, they were not able to realize this advantage in terms of grain yield. Apparently there are limits to increasing grain size in the higher tillering types that are not operating in the lower tillering ones – either a genetic maximum in grain size or insufficient availability of assimilates for grain filling, due either to inadequate radiation interception post-flowering or lesser stored (pre-

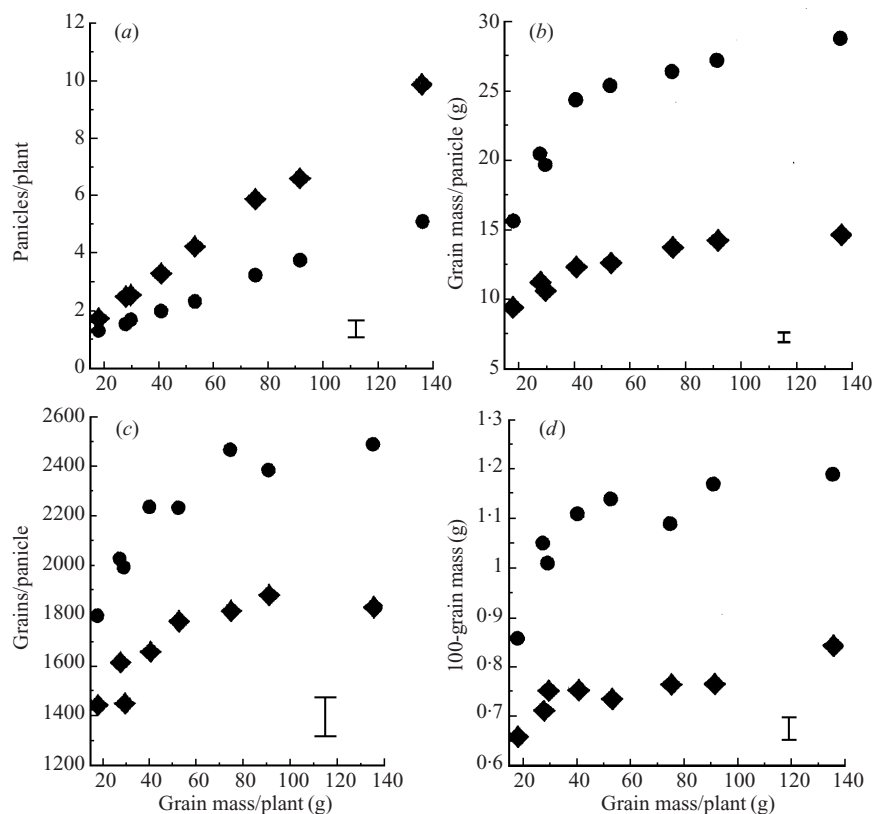


Fig. 2. Panicle number per plant (a), grain mass per panicle (b), grain number per panicle (c), and 100-grain mass (d), in relation to the single plant environmental resource index (estimated as the mean grain yield per plant, over years and genotypes) for the eight fertility  $\times$  population environments, for the high tillering (square) and low tillering (circle) genotypes. The error bar is twice the s.e. (from the analysis of variance) for the tillering type  $\times$  log plant population density  $\times$  fertility treatment interaction means.

flowering) assimilates available for grain filling (Craufurd & Bidinger 1989).

#### *Mechanisms of adjustment to changing environmental resources*

Changes in soil fertility and in plant population density can be considered as changes in environmental resources available to the individual plant (nutrients, radiation and, in some cases, water). As one or more environmental factors almost invariably limit the productivity of pearl millet in the semi-arid, subsistence agricultural systems in which the crop is primarily grown, the ability of individual plants to respond to improvements in environmental resources, on even a local scale (i.e. within-field areas of greater land area per plant or higher fertility) can be important to overall crop productivity. If this ability to respond were influenced by plant type, then plant type differences would be important in breeding pearl millet cultivars for these environments.

Although both high and low tillering types responded similarly, as judged by grain yield, to an increasing space resource (decreasing plant population density), and only marginally differently to an increasing fertility resource, the mechanisms by which they responded to improving environmental resources differed. These differences in mechanisms of response to changing environmental resources can be summarized by plotting changes in tiller numbers and panicle productivity against an index of plant available environmental resources, which can be approximated by the average (over years and genotypes) grain yield per plant for each of the eight combinations of fertility regime and plant population in the experiment (Fig. 2). This index ranged from a low of  $< 20$  g grain/plant (low fertility, high plant population) to  $> 130$  g grain/plant (high fertility and low population).

Panicle numbers per plant increased linearly over the whole range of the environmental resource index, for both high and low tillering genotypes, but the rate

of increase in the former was significantly greater than that in the latter (Fig. 2*a*). In contrast, the average panicle productivity increased in a curvilinear fashion, but in this case the low tillering types were much more responsive to increasing environmental resources than the high tillering ones (Fig. 2*b*). The increase in the average panicle productivity in both genotypes was due primarily to an increase in grain number per panicle (Fig. 2*c*); a response to improving environmental resources in terms of 100-grain mass was evident only at the lowest resource environments (Fig. 2*d*). The low tillering types demonstrated a greater ability to adjust panicle productivity through both grain numbers per panicle and individual grain mass than did the high tillering types.

*Use of low tillering Iniadi germplasm in pearl millet breeding*

The results of this experiment do not indicate that the low tillering/large panicle *Iniadi* germplasm is likely to have any disadvantages in low plant population situations, or in different fertility environments (within the range of those used in this experiment). Decisions to use or not use this type of material in a breeding programme can thus be based on farmer preferences for specific plant or panicle types, and/or aspects of crop management, straw use, and so on, which would favour one type over the other. For example, a farmer survey along a declining rainfall gradient in western Rajasthan, India (van Oosterom *et al.* 1996) indicated

a changing preference from larger panicle, lower tillering types in the wetter part of the gradient to high tillering, thin stemmed types in the driest part. This changing preference reflected the changing importance of grain *v.* fodder yield (farmers considered the low tillering types to have greater grain yields, but at the expense of fodder yield and fodder quality) and the increasing importance of unpredictable drought stress (to which farmers felt the higher tillering types were better adapted due to greater developmental plasticity). Other considerations may be important elsewhere. For example, in many areas of west Africa only panicles are harvested, and the plants left in the field for animals to graze, in contrast to India where the entire crop is harvested and the straw is chopped and stall-fed to animals. In west Africa, lower tillering types with fewer panicles reduce the harvest labour requirement, and the thicker stems do not increase the labour required for chopping the straw, as is the case in India. Similarly, where stems are used for fencing, thatching or weaving mats, different diameter stems will be preferred, which will again influence choice of plant type.

This research indicates that, at least within the yield range reported in this experiment, these choices can be made without a penalty in ability of the plant type to either adjust to sub-optimal plant stands or to respond to improving environmental resources. Whether or not this conclusion also holds for more marginal areas, with yields between 100 and 1000 kg/ha, would probably need to be confirmed.

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