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# Simulating growth, development, and yield of tillering pearl millet. III. Biomass accumulation and partitioning

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**Abstract**

Pearl millet landraces from Rajasthan, India, yield significantly less than improved cultivars under optimum growing conditions, but not under stressed conditions. To successfully develop a simulation model for pearl millet, capable of capturing such genotype × environment (G × E) interactions for grain yield, we need to understand the causes of the observed yield interaction. The aim of this paper is to quantify the key parameters that determine the accumulation and partitioning of biomass: the light extinction coefficient, radiation use efficiency (RUE), pattern of dry matter allocation to the leaf blades, the determination of grain number, and the rate and duration of dry matter accumulation into individual grains. We used data on improved cultivars and landraces, obtained from both published and unpublished sources collected at ICRISAT, Patancheru, India. Where possible, the effects of cultivar and axis (main shoot vs. tillers) on these parameters were analysed, as previous research suggested that G × E interactions for grain yield are associated with differences in tillering habit. Our results indicated there were no cultivar differences in extinction coefficient, RUE, and biomass partitioning before anthesis, and differences between axes in biomass partitioning were negligible. This indicates there was no basis for cultivar differences in the potential grain yield. Landraces, however, produced consistently less grain yield for a given rate of dry matter accumulation at anthesis than did improved cultivars. This was caused by a combination of low grain number and small grain size. The latter was predominantly due to a lower grain growth rate, as genotypic differences in the duration of grain filling were relatively small. Main shoot and tillers also had a similar duration of grain filling. The low grain yield of the landraces was associated with profuse nodal tillering, supporting the hypothesis that grain yield was below the potential yield that could be supported by assimilate availability. We hypothesise this is a survival strategy, which enhances the prospects to escape the effects of stress around anthesis.


*Keywords:* Biomass accumulation; Grain number; Grain size; Partitioning; Pearl millet; RUE; Stem growth

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## 1. Introduction

Pearl millet is traditionally grown in marginal environments, unsuitable to sustain growth of other cereal crops (FAO and ICRISAT, 1996). Although stress (low N, low water and high temperatures) is likely to occur (FAO and ICRISAT, 1996), the timing and intensity of stress occurrence are highly unpredictable (van Oosterom et al., 1996). There is a perception among subsistence farmers in the millet-based cropping systems of north-west India that high-tillering cultivars with small grains (similar to the local landraces) outperform low-tillering, improved cultivars with large grains under marginal conditions, but that the reverse is true under optimum conditions (Kelley et al., 1996; van Oosterom et al., 1996). This specific adaptation to stress environments of high-tillering, landrace-based cultivars was confirmed by Yadav and Weltzien (2000) and Bidinger et al. (1994) and supports observations for barley (van Oosterom and Ceccarelli, 1993) that cultivar types that are adapted to stress are often different from those adapted to high-input environments. The development of cultivars, adapted to stress conditions, is therefore a major challenge to breeding programs targeting variable stress environments (Richards, 1989). A crop simulation model for pearl millet, capable of simulating these genotype × environment (G × E) interactions for grain yield, could therefore be a valuable tool in matching genotypes to resource availability.

The successful development of a simulation model for pearl millet requires an understanding of the causes of these G × E interactions. Differences in grain yield can be caused by differences in either biomass accumulation or in partitioning to the grain and could be associated with genotypic differences in tillering habit, as landraces tend to be high-tillering. In the absence of stress, biomass accumulation is a function of the amount of radiation intercepted by the leaves and the efficiency with which this is converted into biomass (radiation use efficiency, RUE, g $MJ^{-1}$). The light extinction coefficient $k$ determines the fraction of incoming radiation that is intercepted by a canopy with a given leaf area index, with higher values for $k$ indicating an increased interception of radiation. Published values for $k$ for pearl millet, based on total radiation, range from 0.29 in a glass house study (Squire et al., 1984b) to 0.5 under field conditions at noon (Ong and Monteith, 1985) However, as the fraction of intercepted radiation at noon is lower than in the morning and afternoon (Muchow, 1985; Begue et al., 1991), it is likely the value of 0.5 is an underestimation. Similarly, published values for RUE (based on total radiation) during the pre-anthesis period of pearl millet, grown in the field under well-watered and well-fertilised conditions, range from 1.3 g $MJ^{-1}$ (Muchow, 1989) to 2.1 g $MJ^{-1}$ (Reddy and Willey, 1981), whereas Squire et al. (1984b, 1986) observed an RUE of 2.0–2.4 g $MJ^{-1}$ in a greenhouse study. While Sinclair and Muchow (1999) concluded in an overview that the highest RUE for C4-crops was close to 2.0 g $MJ^{-1}$, Ong and Monteith (1985) calculated that RUE of pearl millet would be in the range 2.0–2.5 g $MJ^{-1}$. However, this calculation was based on a $k$-value at noon and is thus likely to be overestimated. As many of the high (>2.0 g $MJ^{-1}$) RUE's for pearl millet that have been reported in literature were either based on LAI observations (Craufurd and Bidinger, 1988b) or on measurements taken at noon, without correction for variation during the day (Jarwal et al., 1990) there is a need to reconcile the apparently high RUE of pearl millet with the lower values of other C4-crops as reported by Sinclair and Muchow (1999).

The key parameter in the quantification of biomass partitioning before anthesis is the pattern of dry matter allocation between leaves and stems. In general, the fraction of current assimilates that is partitioned to the leaf blades is high early in the season, but declines gradually as stem elongation starts, until it is zero at the end of leaf growth (Jones and Kiniry, 1986; van Keulen and Seligman, 1987; Borrell et al., 1989). Although in some simulation models the onset of stem elongation occurs at panicle initiation (PI), e.g. CERES-Maize (Jones and Kiniry, 1986), results of Craufurd and Bidinger (1988a) indicate that in pearl millet there is no fixed relationship between apical development and onset of biomass accumulation to the stem. A comprehensive analysis of the differences among genotypes, axes (main shoot vs. tillers), and daylengths on the pre-anthesis dry matter allocation in pearl millet is required to quantify if there is any relationship between development stage and the onset of significant dry matter allocation to the stem.

Grain yield can be considered a function of grain number and grain mass. Grain number in cereals has been described as a function of the growth rate at

anthesis of either the crop (Edmeades and Daynard, 1979; Vega et al., 2001) or the panicle (Miralles et al., 1998, 2000). For pearl millet, Ong and Squire (1984) observed a linear relationship between grain number and the thermal interception rate (TIR, amount of radiation intercepted per plant per unit of thermal time) during the period from PI to anthesis, whereas Craufurd and Bidinger (1988a) observed under a range of photoperiods in the field a linear relationship between grain yield and shoot growth rate, which was independent of axis. Although both experiments point at a linear relationship between grain number and growth rate, the effect of plant type (high- vs. low-tillering) on this relationship has not been documented for pearl millet.

The grain filling period (GFP) of pearl millet can be divided into three phases (Fussell and Pearson, 1978; Bieler et al., 1993): (1) an initial lag phase between anthesis and the start of grain growth, (2) a period of near-linear increase in individual grain mass, and (3) a brief period just before physiological maturity of the grain during which the grain growth rate drops. The significant genotypic differences in grain mass which have been reported for pearl millet, were predominantly due to differences in the grain growth rate, rather than in the duration of the GFP (Fussell and Pearson, 1978; Craufurd and Bidinger, 1988b; Bieler et al., 1993).

This paper uses data from both published and unpublished sources, collected at ICRISAT, Patancheru, India, to better quantify some of the key parameters that determine biomass accumulation and partitioning in pearl millet: (1) the light extinction coefficient and RUE, (2) the pattern of dry matter partitioning between leaves and stems before anthesis, (3) grain number as determined by the crop growth rate at anthesis, and (4) the grain growth rate and duration of grain filling. Where possible, the effects of cultivar or axis (main shoot vs. tillers) on these relationships will be quantified. The analyses were part of the development of a pearl millet simulation module within the Agricultural Production Systems simulator (APSIM) framework (McCown et al., 1996). As the model is parameterised for optimum growing conditions, most data used were obtained from experiments without N or drought stress. This paper builds on the results of two previous papers in this series (van Oosterom et al., 2001a,b) that present a model to simulate the effects of plant type, photoperiod, and plant density on leaf area dynamics.

## 2. Materials and methods

### 2.1. Experimental details

Data used in the analyses were obtained from experiments conducted at Patancheru (17°45′N, 78°16′E) in central India and at Fatehpur-Shekawati (27°28′N, 81°22′E) and Jodhpur (26°30′N, 73°02′E) in north-west India. The experiments included both published and unpublished data (Table 1).

Details of the experiments conducted at Patancheru between 1977 and 1986 (Table 1) have been given by Gregory and Squire (1979), Squire et al. (1984a), Carberry et al. (1985) and Craufurd and Bidinger (1988a,b, 1989). In brief, the experiments were conducted under optimum water and nutrient conditions, except for PAT77, which included a fully irrigated treatment and one where the crop grew predominantly on stored moisture after crop establishment (Gregory and Squire, 1979). The experiments covered a range of plant densities (5–40 plants $m^{-2}$) and photoperiods at emergence (12.5–15.5 h). The cultivars used were BK 560 (PAT77), BJ 104 and its related hybrid 841A × J 104 (PAT82, PAT85, PAT86), and 81A × Souna B (PAT85, PAT86).

The experiments conducted at Patancheru between 1994 and 1996 were sown on an alfisol (clayey-skeletal mixed isohyperthermic Udic Rhodustalf) on ridges either 60 or 70 cm apart. Emergence was generally 3 days after sowing, but took a few days longer in PAT95s, where the crop only emerged after the first irrigation, which was applied after sowing. All crops were thinned to the desired plant density at around 10 days after emergence. They received a pre-sowing fertiliser application of 150 kg $ha^{-1}$ di-ammonium phosphate (DAP, 28:28:0 NPK) and a top dressing of 100 kg $ha^{-1}$ urea at the start of stem elongation. The PAT95s experiment was sprinkler irrigated about every 3 days during the first 4 weeks after emergence, at a rate of 10–15 mm each time. On 1 March, the crop was furrow irrigated up to field capacity and only one more furrow irrigation was applied afterwards (24 March, around flowering). As rainfall was negligible, this resulted in pre- and post-flowering drought, which

Table 1
Experiments included in the analyses of this paper, including their sowing date, plant density, number of cultivars, treatments included, plus an indication whether or not (+ and −, respectively) they were used in the analysis of RUE, dry matter AR to the leaf ($AR_{leaf}$), the thermal time from flag leaf to anthesis, the effect of growth rate per plant at anthesis on grain number or grain yield per plant at maturity, the duration of the grain growth rate (GGR) and the GFP and the relative dry weight of the panicle during grain filling (the original reference for each dataset is given in the last column)

| Experiment | Sowing date | Plant density ($m^{-2}$) | Number of cultivars | Treatments[a] | RUE | $AR_{leaf}$ | Flag to anthesis | Growth rate vs | | GGR GFP | Dry weight panicle | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Grain number | Grain yield | | | |
| Patancheru (17°45′N, 78°16′E) | | | | | | | | | | | | |
| PAT77 | 13 October 1977 | 26.7 | 1 | 2 w | − | + | − | − | − | − | − | Squire et al. (1984a), Gregory and Squire (1979) |
| PAT82 | 19 June 1982 | 5–40 | 1 | 4 den | − | + | − | + | + | − | + | Carberry et al. (1985) |
| PAT85 | 21 June 1985 | 9.0 | 2 | 3 dl | − | + | − | + | + | − | + | Craufurd and Bidinger (1988a,b) |
| PAT86 | 19 June 1986 | 4.5, 12 | 2 | 2 dl, 2 den | − | + | − | + | + | − | + | Craufurd and Bidinger (1989) |
| PAT94s | 25 January 1994 | 6.7 | 6 | 2 dl | − | − | − | − | + | − | − | This paper |
| PAT94 | 15 June 1994 | 6.7 | 6 | − | − | − | − | − | + | − | − | This paper |
| PAT95s | 26 January 1995 | 8.3 | 6 | − | + | + | − | − | + | − | − | This paper |
| PAT95 | 20 June 1995 | 6.7 | 6 | − | + | + | − | − | + | + | − | This paper |
| PAT96s | 29 February 1996 | 4–20 | 3 | 4 den | − | − | + | − | − | − | − | van Oosterom et al. (2001a) |
| PAT96 | 26 June 1996 | 4–20 | 4 | 4 den | − | − | + | − | − | + | − | van Oosterom et al. (2001a) |
| Fatehpur (27°28′N, 81°22′E) | | | | | | | | | | | | |
| FAT94 | 14 July 1994 | 5.6 | 6 | − | − | − | − | − | + | − | − | This paper |
| FAT95 | 20 July 1995 | 5.3 | 6 | − | − | + | − | − | + | − | − | This paper |
| Jodhpur (26°30′N, 73°02′E) | | | | | | | | | | | | |
| JOD94 | 03 July 1994 | 5.6 | 6 | − | − | − | − | − | + | − | − | This paper |
| JOD96 | 01 July 1996 | 5.3 | 2 | 3N | − | − | − | − | + | − | − | This paper |

[a] den, density; dl, daylength; N, nitrogen; w, water regime.

was temporarily relieved around anthesis. All other experiments were either fully irrigated or received sufficient rainfall to avoid significant drought stress.

The experiments at Fatehpur and Jodhpur were sown on a sandy soil (Psamment) in rows 60 cm apart and crops were thinned to the desired plant density about 1 week after emergence. At FAT94, the crop received a pre-sowing fertiliser application of 100 kg ha$^{-1}$ mono-ammonium phosphate (MAP: 18:46:0 NPK), whereas a top dressing of 40 kg ha$^{-1}$ urea was applied on 3 August 1994 at the start of stem elongation. At FAT95, a basal dose of 100 kg ha$^{-1}$ MAP was applied on 16 July 1995 and a topdressing of 32 kg ha$^{-1}$ urea on 7 August 1995. For JOD94, 40 kg ha$^{-1}$ MAP was applied on 1 July 1994 and 40 kg ha$^{-1}$ urea on 25 July 1994. The 1996 experiment at Jodhpur contained three nitrogen treatments. The crop received a pre-planting application of 125 kg ha$^{-1}$ single super phosphate (20 kg P ha$^{-1}$), whereas nitrogen was applied the same day as calcium ammonium nitrate at a rate of 0, 80.2 and 160.4 kg ha$^{-1}$, equivalent to 0, 20, 40 kg N ha$^{-1}$.

The 1994 and 1995 experiments consisted of two sub-experiments, which were laid out adjacent to each other. One sub-experiment was used for destructive biomass samples and had a plot size of 11–12 rows (Patancheru) or 18 rows (Fatehpur and Jodhpur) of 4 m long. The other sub-experiment was used for detailed yield component analyses, and plot size was two rows (Patancheru) or four rows (Fatehpur and Jodhpur) of 4 m length. Each sub-experiment was laid out as a randomised complete block design with three replications. However, due to poor establishment, only two replications were used in the biomass sampling sub-experiment of PAT95s and in the yield components sub-experiment of JOD94. Each experiment included six cultivars. Three of these produced many but small panicles and were based on landraces from Rajasthan: one pure landrace (Nokha Local) and two breeding populations (ERajPop and WRajPop). The other cultivars were not based on landrace material. Two of these (RCB-IC 911, WC-C 75) produced few but large panicles and one (CZ-IC 922) was intermediate. The six cultivars had a comparable phenology, although ERajPop tended to reach anthesis about 3 days earlier than average and WC-C 75 3 days later than average.

The 1996 experiments had a slightly different design. At Patancheru, the two experiments included four plant densities (4, 11, 15, 20 plants m$^{-2}$) and three (PAT96s) or four (PAT96) cultivars: WRajPop, RCB-IC 911 and BJ 104 in both experiments and HHB 67 (early hybrid) in PAT96 only. They were laid out in a split-plot design with density as the main plot; further details have been given by van Oosterom et al. (2001b). The JOD96 experiment contained three N-treatments and two cultivars, WRajPop and ICMH 451 (a relatively low-tillering hybrid). It was laid out as a randomised complete block design with three replications and a plot size of 20 rows of 8 m length.

### 2.2. Observations

#### 2.2.1. Meteorological data

Daily values for minimum and maximum temperature and rainfall were obtained from weather stations, located in close proximity to each experiment. Daily incident solar radiation was recorded at Patancheru only. The daily accumulation of thermal time was calculated from 3-hourly estimates of temperature between the daily minimum and maximum, using 10, 33, and 47 °C as the base, optimum, and maximum temperature, respectively, and assuming linear interpolations between these cardinal temperatures (Garcia-Huidobro et al., 1982; Mohamed et al., 1988; Ong, 1983a,b).

#### 2.2.2. Light interception

In the PAT95s and PAT95 experiments, the fraction ($f$) of photosynthetic active radiation (PAR) intercepted by the canopy was measured twice a week using a 90 cm long AccuPAR ceptometer (Decagon Devices, Pullman, Washington, USA). Measurements were taken within 2 h of noon. For each plot, five measurements were taken below the canopy at representative spots in the plot, by holding the ceptometer at such an angle between two adjacent rows, that the two ends of the sensor were located on two adjacent rows. Incoming radiation was measured for each plot by taking a reading above the canopy before and after the below-canopy measurements. After the onset of leaf senescence, the position of the ceptometer was adjusted vertically to discount interception by senescing leaves. Measurements were stopped around mid-grain filling, when lodging started and leaf senescence prevented accurate observations. An average $f_{PAR}$ was calculated for each plot at each sampling date, from

which means for the two groups of cultivars (landrace-based and improved cultivars) were derived.

#### 2.2.3. Biomass samples and grain yield data

In the experiments conducted from 1994 onwards (except PAT96 and PAT96s), weekly biomass samples were taken by harvesting a pre-determined area of four rows (only three rows in PAT95s) of 60–80 cm long, giving a sample size of about 12 plants (nine plants in PAT95s). In the experiments conducted during 1994, only total above-ground biomass was measured, but for PAT95, PAT95s, FAT95, and JOD96, samples were divided into green and dead leaf blades, stems (including leaf sheath), and panicles (stems and panicles were pooled at PAT95s). From the green leaf blades, a sub-sample was taken for leaf area measurements (PAT95, PAT95s only), using a LI300 leaf area meter (LI-COR Inc., Lincoln, Nebraska, USA). Plant parts were oven-dried for 2 days at 80 °C. At Fatehpur and Jodhpur, where oven capacity was limited, we first measured total fresh weight, and then took a subsample of two (JOD96) or three (FAT95) representative plants, for which we observed total fresh weight and dry weight of individual plant parts as described above. After drying, panicles where threshed for grain yield at PAT95 and JOD96, and yield components were measured at JOD96. In the other 1994–1996 experiments (except PAT96 and PAT96s), grain yield and yield components at maturity were obtained in the yield components sub-experiment (see Section 2.1). In these sub-experiments, entire plots (excluding parts with a poor stand) were harvested, but panicles were grouped for axis type (main shoot, basal tiller and nodal tiller) and anthesis date. For each axis × anthesis group of panicles, individual grain mass was calculated from three samples of hundred grains. Grain number was derived from total grain yield and grain mass. Stover yield of the entire plot was measured to allow calculation of harvest index.

In PAT96s and PAT96, biomass samples were only taken at physiological maturity. In PAT96s, an area of approximately 4–8 $m^2$ was harvested (depending on plant density), whereas in PAT96, three rows of 3 m length were harvested. After measuring fresh weight of the total sample, a subsample of 10–20% was taken, on which fresh weight was taken, plus dry weight of stover and grain yield. Grain mass was obtained from three samples of 100 grains, and grain number was derived from grain yield and grain mass.

Our data were complemented by biomass samples from PAT77 (Gregory and Squire, 1979; Squire et al., 1984a), PAT82 (Carberry et al., 1985), PAT85 (Craufurd and Bidinger, 1988a,b), and PAT86 (Craufurd and Bidinger, 1989). In all these experiments, biomass samples were taken at intervals of 1 week or less and partitioned into plant parts. The original data of the individual sampling dates were available, except for grain yield and yield components at maturity, for which published data were used.

#### 2.2.4. Leaf number and anthesis date

In experiments PAT96s and PAT96, the number of fully expanded leaves (ligule visible) on each axis was counted twice a week throughout the pre-anthesis period on selected plants (van Oosterom et al., 2001a). On the same plants, the dates of anthesis (50% stigma's visible) and physiological maturity (black layer, PAT96 only) were recorded for each individual panicle.

### 2.3. Data analyses

#### 2.3.1. Light interception and biomass accumulation

The observations on the fraction of PAR intercepted at noon were transformed into an estimate of the fraction of total radiation intercepted throughout the day. Hereto, we first calculated the percentage intercepted total radiation at noon (Marshall and Willey, 1983):

$$\ln(1 - f_{\mathrm{PAR}}) = 1.34 \ln(1 - f_{\mathrm{TOTRAD}}) \quad (1)$$

where $f_{\mathrm{PAR}}$ and $f_{\mathrm{TOTRAD}}$ are the fraction of intercepted PAR and total radiation, respectively.

Next, we interpolated daily values of $f_{\mathrm{TOTRAD}}$ at noon from a fitted fifth-order polynomial function against time (days) through the observed data. The final step was to transform the noontime $f_{\mathrm{TOTRAD}}$ for each day to daily integrated data, as observations on light interception taken around solar noon tend to underestimate $f_{\mathrm{TOTRAD}}$ integrated over the day (Begue et al., 1991; Sinclair and Muchow, 1999). Hereto, we used the relationship presented by Muchow (1985):

$$\text{Underestimation of daily intercepted radiation (\%)} = 52.89 - 0.71F + 0.0018F^2 \quad (2)$$

where $F$ is the percentage of radiation intercepted at noon. As this relationship does not pass through the

origin, data could not be extrapolated below the lowest values of $f_{TOTRAD}$ at noon (0.2) observed by Muchow (1985). $RUE_{TOTRAD}$ was calculated for experiments PAT95s and PAT95, for the two types of cultivars (landrace-based and improved cultivars) by using data averaged over the three cultivars within each group. Daily intercepted radiation was obtained by multiplying $f_{TOTRAD}$ with the daily incident solar radiation. The extinction coefficient $k$ was calculated using Beer's law, and RUE (g $MJ^{-1}$) as the slope of the regression of total above-ground biomass on cumulative intercepted radiation. Because of errors associated with transformation of values for $f_{TOTRAD} < 0.2$, this relationship did not pass through the origin.

#### 2.3.2. Biomass partitioning to the leaves and onset of stem elongation

The partitioning of biomass to the different plant parts was analysed through the allocation ratio (AR), which is defined as (Borrell et al., 1989):

$$AR_{part} = \frac{\Delta dw_{part}/\Delta t}{\Delta dw_{total}/\Delta t} \quad (3)$$

where dw is the dry weight and $t$ the time.

Before the onset of stem elongation ($O_s$), the stem fraction predominantly contains leaf sheath, and the allocation of biomass between leaf blades and the stem fraction was assumed to represent the allocation of biomass between leaf blade and leaf sheath. As the AR during this period is relatively constant, it was estimated by plotting dry weight of the stem fraction as a function of dry weight of the leaf blade.

The $O_s$ was estimated by plotting the weight of the stem fraction as a function of thermal time after emergence. Hereto, stem weight was adjusted for the weight of the leaf sheath, using the observation in sorghum that the partitioning of dry matter between leaf blades and sheaths is relatively constant throughout the pre-anthesis period (van Oosterom, unpublished data). The linear increase in dry weight of the stem per sé was extrapolated to estimate the intercept with the $x$-axis. To avoid confounding effects due to tillers, the calculations were done on data from the main shoot only, using mean values across replications.

The dynamics of changes in $AR_{leaf}$ (green + dead leaf blades) during stem elongation where calculated according to Eq. (3) above. Only experiments where biomass samples were taken at least once a week were used and sampling intervals during which $\Delta dw_{total}$ was small were pooled with an adjacent interval.

#### 2.3.3. Time from flag leaf appearance to anthesis

The time from flag leaf appearance to anthesis was calculated for the PAT96s and PAT96 experiments. For each genotype × density × axis combination, data were pooled and fully expanded leaf number was regressed against thermal time after emergence. Only regressions where the slope was significant at $P < 0.001$ were used for further calculations. This linear regression was combined with the average leaf number to estimate the timing of full flag leaf emergence. The period from full flag leaf emergence to anthesis was calculated as the average for each genotype × axis combination, across densities, weighing the contribution of each density by the number of plants.

#### 2.3.4. Grain number and grain filling

The effect of assimilate flux at anthesis on grain number per plant at maturity was analysed for BJ 104 from experiments PAT82, PAT85, and PAT86 (Table 1). The dry matter flux at anthesis was calculated as the derivative of a logistic function, fitted through the observations on total above-ground dry matter:

$$DRY\_MATTER = a(1 + \exp(b - c\,TIME))^{-1} \quad (4)$$

where time is expressed as thermal time, $a$ is the asymptote (or dry matter at maturity) and $b$ and $c$ are constants. Hence, the assimilate flux at anthesis was calculated as g per °C day per plant. Grain number was obtained from the samples at maturity, except for PAT82, where it was derived from grain yield at maturity and mean grain mass; this was justified, as there was no correlation between density and grain mass (Carberry et al., 1985).

The effect of cultivar on this relationship was analysed by comparing results for BJ 104 with results for WRajPop and RCB-IC 911. A complication, however, was the fact that for the experiments conducted from 1994 onwards (which included WRajPop and RCB-IC 911), grain yield was obtained from an experiment conducted adjacent to the one from which

biomass samples were taken (except in JOD96). Assuming HI was similar for these experiments, we combined the HI of the grain yield experiment with the biomass at maturity of the biomass sampling experiment (taken as the asymptote of Eq. (4)) to estimate the grain yield at maturity for the biomass sampling experiment. Hence, cultivars were compared for the effect of growth rate at anthesis per plant on grain yield at maturity per plant.

The growth rate of individual grains during grain filling (mg per grain per °C day) was estimated for experiment PAT95 (biomass sampling experiment) from weekly observations on total grain yield. In the absence of data on yield components, grain mass was calculated from grain number at maturity, which was derived from the average grain yield of the last two samples and the grain mass obtained from the adjacent yield components experiment.

The duration of the GFP was defined as the period from anthesis to physiological maturity (defined as the presence of a black layer on the seed). For experiment PAT96, observations on the dates of anthesis and physiological maturity were available for individual panicles. To have an unbiased assessment of the effect of axis on the duration of GFP, only plants that produced a panicle on the main shoot and on the first two tillers (T3 and T4, produced from the axils of Leaf 3 and Leaf 4, respectively) were included in the analysis.

## 3. Results

### 3.1. Light interception and biomass accumulation

The extinction coefficient $k$ for the two 1995 experiments at Patancheru did not differ significantly between the two groups of cultivars (landrace-based vs. improved cultivars). Although there was a tendency towards a higher extinction coefficient in the rainy season (Fig. 1), the data were not sufficiently detailed to fit separate curves for the two experiments. Therefore, a common extinction coefficient across the two experiments was calculated. Assuming that pearl millet will intercept all incoming solar radiation, provided sufficient LAI is present, the common extinction coefficient we observed was 0.63 (Fig. 1).

Consistent with the absence of genotypic differences in $k$, there were no consistent differences in RUE between the two groups of cultivars. Under the optimal growing conditions of PAT95, the $RUE_{TOTRAD}$ (including 5% confidence interval) was $1.90 \pm 0.11$ g $MJ^{-1}$ (Fig. 2). Under drought stress at PAT95s, the $RUE_{TOTRAD}$ was $1.12 \pm 0.09$ g $MJ^{-1}$.

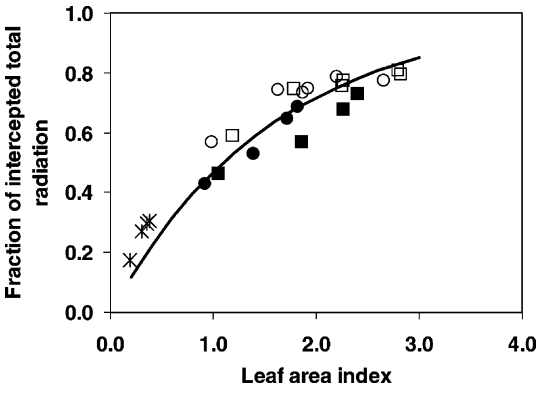


Fig. 1. Calculated fraction of intercepted total radiation (integrated over the day) as a function of LAI, averaged over three landrace-based cultivars grown at PAT95s (●) and PAT95 (○) and three improved cultivars, grown at PAT95s (■) and PAT95 (□). Stars represent observations not included in the fitted curve, because of likely overestimation of intercepted radiation. Fitted regression is $f_{TOTRAD} = 1 - \exp(-0.63\text{LAI})$. $n = 20$; $R^2 = 0.76$.

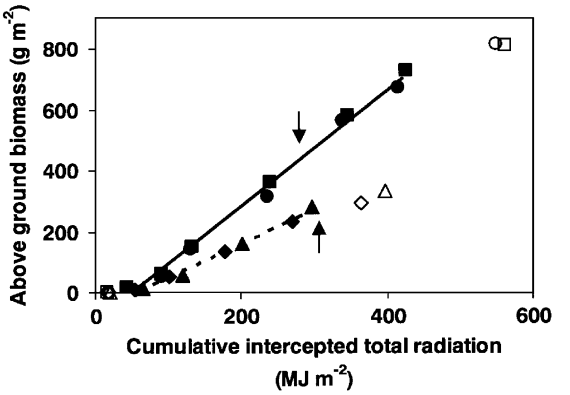


Fig. 2. Total above-ground biomass as a function of cumulative intercepted solar radiation for landrace-based (●, ○, ◆, ◇) and improved cultivars (■, □, ▲, △), grown at Patancheru under well-watered conditions in the rainy season (—) and under drought during the dry season (. . .) of 1995. Open symbols are not included in the regression. Arrows indicate average date of anthesis. Regression lines are: rainy season: $y = 1.90x - 96.65$, $n = 12$, $R^2 = 0.99$; dry season: $y = 1.12x - 62.21$, $n = 8$, $R^2 = 0.99$.

### 3.2. Allocation of biomass before anthesis

Before the onset of stem elongation ($O_s$), $AR_{leaf}$ was independent of cultivar, density, or photoperiod. On a whole plant basis, the amount of dry matter in the stem fraction (leaf sheath) was half the amount allocated to the leaf blade irrespective of cultivar type (Fig. 3a). Similarly, across a range of photoperiods and densities, both main shoots and tillers allocated twice as much biomass to the leaf blade than to the stem fraction before $O_s$ (Fig. 3b). None of the regression slopes in Fig. 3 were significantly different from 0.5 ($P > 0.05$). Therefore, before $O_s$, $AR_{leaf} = 0.67$, and, by definition, we assumed that all biomass in the stem fraction represented leaf sheath.

The occurrence of $O_s$ was estimated from the intercept of the regression of stem dry weight (excluding leaf sheath) on time. Using the results of Fig. 3, the leaf sheath component of each stem fraction sample was estimated as half the dry weight of the corresponding leaf blade sample. Within individual experiments, there was no consistent effect of water supply (1977), plant density (1982, 1986), or cultivar (1985, 1986) on $O_s$, but there was a distinct effect of photoperiod. Therefore, for each experiment observations on $O_s$ were pooled across treatments within each photoperiod. To avoid bias due to differences in tillering, only main shoot data were considered.

As $AR_{leaf}$ was constant prior to $O_s$ (Fig. 3), exclusion of the leaf sheath component from the stem weight resulted in a distinct timing of $O_s$ (data not shown). Daylength affected the timing of $O_s$ and of PI differently. If time was expressed as a percentage of the time from emergence to anthesis, PI occurred later as daylength increased (Fig. 4). This reflects the increase in time from emergence to PI for daylength between 13 and 15.5 h, while the period between PI and anthesis is relatively constant (van Oosterom et al., 2001a). The timing of $O_s$ varied to nearly the same

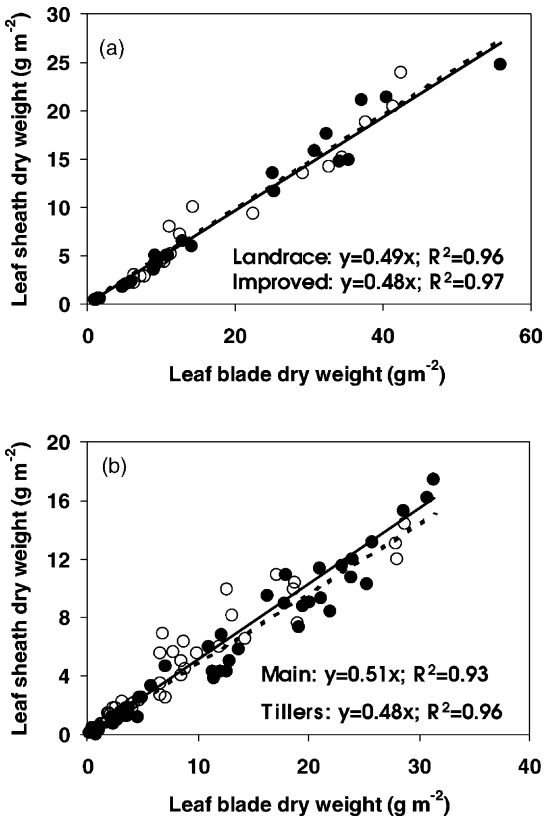


Fig. 3. Dry weight of the stem fraction (g $m^{-2}$) as a function of the dry weight of the leaf blade for biomass samples of pearl millet taken before the onset of stem elongation for (a) landraces (○- - -○) and improved cultivars (●—●), and (b) main shoots (○—○) and tillers (●- - -●). Data for figure (a) from experiments PSS95, PAT95, FAT95, and JOD96, and for figure (b) from PAT77 (Gregory and Squire, 1979; Squire et al., 1984a) PAT82 (Carberry et al., 1985), PAT85 (Craufurd and Bidinger, 1988a,b) and PAT86 (Craufurd and Bidinger, 1989).

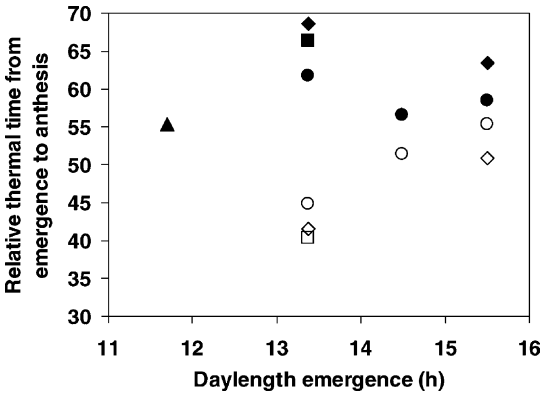


Fig. 4. Relationship between relative thermal time from emergence to PI (open symbols) and the onset of dry matter accumulation to the stem (closed symbols) as a function of daylength at emergence for experiments PAT77(▲), PAT82 (□, ■), PAT85 (○, ●), and PAT86 (◇, ◆). Time is expressed as a fraction of the time from emergence to anthesis. Individual data points are means per daylength treatment. Data from Gregory and Squire (1979), Squire et al. (1984a), Carberry et al. (1985), and Craufurd and Bidinger (1988a,b, 1989).

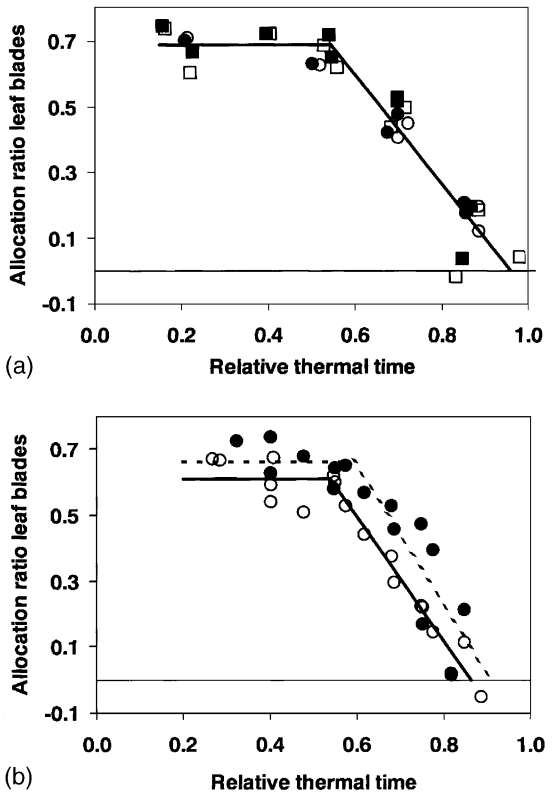


Fig. 5. (a) AR of the leaf blades as a function of relative thermal time from emergence to anthesis for the entire crop, averaged for landraces grown at PAT95s, PAT95 (○) and FAT95, JOD96 (□) and for improved cultivars grown at PAT95s, PAT95 (●) and FAT95, JOD96 (■). (b) AR of the leaf blades as a function of relative thermal time from emergence to anthesis for main shoots (○—○) and tillers (●- - -●) of crops grown at Patancheru under normal daylength in 1982 (Carberry et al., 1985), 1985 (Craufurd and Bidinger, 1988a,b) and 1986 (Craufurd and Bidinger, 1989). Within experiments, data have been averaged across densities and cultivars. For equations of the piecewise regressions, see Table 2.

extent as timing of PI, but this variation was not related to daylength (Fig. 4).

During stem elongation, there were no obvious effects of cultivar (Fig. 5a) and plant density (data not shown) on $AR_{leaf}$. Therefore, data were pooled across cultivars and densities for the calculation of $AR_{leaf}$ during stem elongation. Initially, $AR_{leaf}$ was about 0.67 (Table 2, Fig. 5), in accordance with Fig. 3. After $O_s$, $AR_{leaf}$ declined linearly with relative thermal time (fraction of the thermal time from emergence to anthesis that had elapsed) and approached zero when relative thermal time was approximately 0.9 (Fig. 5; Table 2). The decline in $AR_{leaf}$ started slightly earlier in main shoots than in tillers (Fig. 5b), but the difference was not significant at $P = 0.05$ (Table 2). There was, however, a significant effect of daylength on the onset of decline in $AR_{leaf}$, both for main shoots and tillers (Table 2), but this was predominantly due to PAT85, as daylength had no effect on the onset of decline in $AR_{leaf}$ in PAT86. In addition, in FAT95 and JOD96, the pattern of $AR_{leaf}$ was similar to that in PAT95s and PAT95 (Fig. 5a), despite a difference in daylength of about 2.5 h.

The cessation of dry matter allocation to the leaves ($AR_{leaf} = 0$), when 90% of the time from emergence to anthesis had elapsed, heralded the flag leaf stage. Data from PAT96s and PAT96 showed that the time from flag leaf stage to anthesis was on average 60–65 °C d (close to 10% of the time from emergence to anthesis of the main shoot), irrespective of axis (Table 3). Although we observed consistent genotypic differences, with RCB-IC 911 having a short and HHB-67 a long period between flag leaf and anthesis (Table 3), these differences were small in absolute terms.

### 3.3. Determination of grain number

Grain number per plant increased with the dry matter flux per plant at anthesis. For BJ 104 (experiments PAT82, PAT85, and PAT86), the observations fitted a linear regression, with about 4300 grains produced if dry matter accumulation rate increased by 0.1 g per °C day per plant above a minimum of 0.044 g per °C day per plant (Fig. 6a). One medium density data point in PAT82 did not fit the regression, but as grain yield per square meter in this density was considerably lower than in all other densities in the same experiment, this data point was considered to be unrepresentative.

For RCB-IC 911 and WRajPop, no data on grain number were available, but if grain yield was plotted as a function of the dry matter accumulation rate at anthesis, the results for RCB-IC 911 were similar to those of BJ 104 (Fig. 6b). Given the significantly higher grain mass of RCB-IC 911 than BJ 104 (Table 4), it is likely that BJ 104 produced more grains per unit of dry matter flux at anthesis. WRajPop generally produced a lower grain yield per unit of dry matter flux at anthesis than the other two cultivars

Table 2
Piecewise regression of dry matter allocation ratio to the leaves ($AR_{leaf}$) as a function of the relative thermal time (relTT) between emergence and anthesis, intial $AR_{leaf}$, onset of dry matter allocation to the stem (including 5% confidence interval), end of dry matter allocation to the leaves, number of observations on which the piecewise linear regression is based, and the $R^2$, for experiments conducted at Patancheru under extended (ED) and normal (ND) daylength and at Rajastan[a]

| Group | Piecewise regression equation[b] | Initial $AR_{leaf}$ (%) | Onset stem allocation[c] (relTT) | End leaf allocation[d] (relTT) | $n$ | $R^2$ |
|---|---|---|---|---|---|---|
| Total crop | | | | | | |
| Patancheru-ED | $AR_{leaf} = 1.35 - 1.59^{*}relTT + 1.59^{*}(relTT - 0.43)$ | 66.9 | $0.43 \pm 0.055$ | 0.85 | 28 | 0.92 |
| Patancheru-ND | $AR_{leaf} = 1.56 - 1.66^{*}relTT + 1.66^{*}(relTT - 0.55)$ | 64.3 | $0.55 \pm 0.047$ | 0.94 | 23 | 0.92 |
| Rajasthan | $AR_{leaf} = 2.24 - 2.54^{*}relTT + 2.54^{*}(relTT - 0.61)$ | 68.5 | $0.61 \pm 0.099$ | 0.88 | 7 | 0.95 |
| All | $AR_{leaf} = 1.48 - 1.64^{*}relTT + 1.64^{*}(relTT - 0.50)$ | 65.0 | $0.50 \pm 0.044$ | 0.90 | 85 | 0.84 |
| Main shoot | | | | | | |
| Patancheru-ED | $AR_{leaf} = 1.13 - 1.32^{*}relTT + 1.32^{*}(relTT - 0.36)$ | 66.1 | $0.36 \pm 0.064$ | 0.86 | 25 | 0.94 |
| Patancheru-ND | $AR_{leaf} = 1.62 - 1.87^{*}relTT + 1.87^{*}(relTT - 0.54)$ | 60.9 | $0.54 \pm 0.041$ | 0.87 | 18 | 0.96 |
| All | $AR_{leaf} = 1.27 - 1.47^{*}relTT + 1.47^{*}(relTT - 0.43)$ | 63.7 | $0.43 \pm 0.050$ | 0.87 | 43 | 0.91 |
| All tillers | | | | | | |
| Patancheru-ED | $AR_{leaf} = 1.38 - 1.58^{*}relTT + 1.58^{*}(relTT - 0.43)$ | 70.3 | $0.43 \pm 0.054$ | 0.88 | 25 | 0.92 |
| Patancheru-ND | $AR_{leaf} = 1.86 - 2.04^{*}relTT + 2.04^{*}(relTT - 0.59)$ | 66.3 | $0.59 \pm 0.096$ | 0.91 | 15 | 0.82 |
| All | $AR_{leaf} = 1.45 - 1.59^{*}relTT + 1.59^{*}(relTT - 0.48)$ | 68.8 | $0.48 \pm 0.058$ | 0.91 | 40 | 0.83 |

[a] Source of data: Carberry et al., 1985; Craufurd and Bidinger, 1988a,b, 1989.
[b] Last term of equation only incorporated if relTT < breakpoint.
[c] Onset of stem elongation taken as break point of peicewise regression.
[d] Estimated as moment that $AR_{leaf} = 0$.

Table 3
Thermal time from flag leaf stage to anthesis for the main shoot and Tillers 3–5, time from emergence to anthesis for the main shoot, and time from emergence to flag leaf stage for the main shoot, expressed as a percentage of the time from emergence to anthesis, for four cultivars, grown in two experiments at Patancheru in 1996

| | Time from flag leaf to anthesis (°C d) | | | | Emergence to anthesis (°C d) | Emergence to flag leaf (%) |
|---|---|---|---|---|---|---|
| | Main | T3 | T4 | T5 | | |
| Patancheru 1996 dry season | | | | | | |
| BJ 104 | 65 | 50 | 68 | 42 | 675 | 90.4 |
| HHB 67 | 92 | 77 | 81 | 82 | 593 | 84.5 |
| RCB-IC 911 | 59 | 23 | 24 | 52 | 659 | 91.1 |
| WRajPop | 67 | 56 | 58 | 55 | 666 | 90.0 |
| Overall | 68 | 56 | 62 | 56 | 656 | 89.7 |
| Patancheru 1996 rainy season | | | | | | |
| BJ 104 | 71 | 58 | 64 | 49 | 731 | 90.3 |
| HHB 67 | 74 | 78 | 87 | 88 | 637 | 88.3 |
| RCB-IC 911 | 40 | 17 | 12 | 122 | 734 | 94.6 |
| WRajPop | 61 | 70 | 64 | 72 | 728 | 91.6 |
| Overall | 62 | 62 | 67 | 65 | 708 | 91.3 |

(Fig. 6b). As its grain mass is comparable to that of BJ 104 (Table 4), this indicates a lower number of grains produced per unit of dry matter flux at anthesis than for BJ 104. These differences between cultivars in the relationship between grain number and dry matter flux can be due either to a difference in the number of florets produced per unit of dry matter flux, or to a difference in the fraction of florets that sets grains.

The low grain yield of WRajPop as compared with RCB-IC 911 and BJ 104 (Fig. 6b) suggests that

Table 4
Plant density, panicle number, grain yield, total above-ground biomass, non-grain biomass, 100 grain weight, harvest index, panicle harvest index, and grain number, averaged across plant density treatments and cultivars, for pearl millet grown under well-watered conditions during the dry season at Patancheru in 1996

| | Plant density ($m^{-2}$) | Panicle number ($m^{-2}$) | Grain yield (g $m^{-2}$) | Biomass yield (g $m^{-2}$) | Non-grain biomass (g $m^{-2}$) | 100 grain weight (g $m^{-2}$) | Harvest index | Panicle harvest index | Grain number ($m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| Density treatment | | | | | | | | | |
| D1 | 4.6 | 23.9 | 336 | 1255 | 919 | 0.83 | 0.27 | 72.3 | 41,718 |
| D2 | 10.7 | 30.4 | 316 | 1204 | 888 | 0.80 | 0.26 | 68.0 | 41,541 |
| D3 | 14.6 | 32.1 | 293 | 1240 | 947 | 0.75 | 0.24 | 65.9 | 39,883 |
| D4 | 16.5 | 33.9 | 296 | 1262 | 966 | 0.78 | 0.24 | 66.1 | 38,044 |
| Density effect | *** | ** | ns | ns | ns | + | + | ** | ns |
| Cultivars | | | | | | | | | |
| BJ 104 | 11.6 | 31.7 | 348 | 1283 | 935 | 0.67 | 0.27 | 70.3 | 52,228 |
| RCB-IC 911 | 11.2 | 19.2 | 342 | 1254 | 912 | 0.99 | 0.27 | 70.5 | 34,373 |
| WRajPop | 12.2 | 39.3 | 241 | 1184 | 942 | 0.70 | 0.21 | 63.4 | 34,288 |
| Cultivar effect | ns | *** | *** | + | ns | *** | *** | *** | *** |
| Interaction | ns | ** | * | + | ns | ** | ns | + | ns |

+ Significant at $P < 0.10$.
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.
*** Significant at $P < 0.001$.

WRajPop does not reach its potential grain yield, given its growth rate at anthesis. In PAT96s, where BJ 104, WRajPop, and RCB-IC 911 were compared across four plant densities, WRajPop tended to accumulate less above-ground biomass than BJ 104 and RCB-IC 911 (Table 4). This difference, however, was entirely due to a reduction in grain yield. BJ 104 had a similar grain yield as RCB-IC 911, as its lower grain mass was compensated by an increased grain number, associated with more profuse tillering. WRajPop, however, combined the low grain mass of BJ 104 with the low grain number of RCB-IC 911. Moreover, the low grain yield of WRajPop was accompanied by a profuse production of nodal tillers under optimum conditions. In four experiments at Patancheru, nodal tillers consistently accounted for >10% of the grain yield of WRajPop (Table 5). Across the six cultivars in these four experiments, there was a significant negative correlation between the grain yield per plant (excluding nodal tillers) and the number of nodal tillers ($R^2 = 0.43$, $P < 0.01$). Profuse production of nodal tillers thus represents a surplus of assimilates, likely to be caused by a limited sink size of the grains. The regression line in Fig. 6b therefore represents an upper boundary for the relationship between grain yield and growth rate.

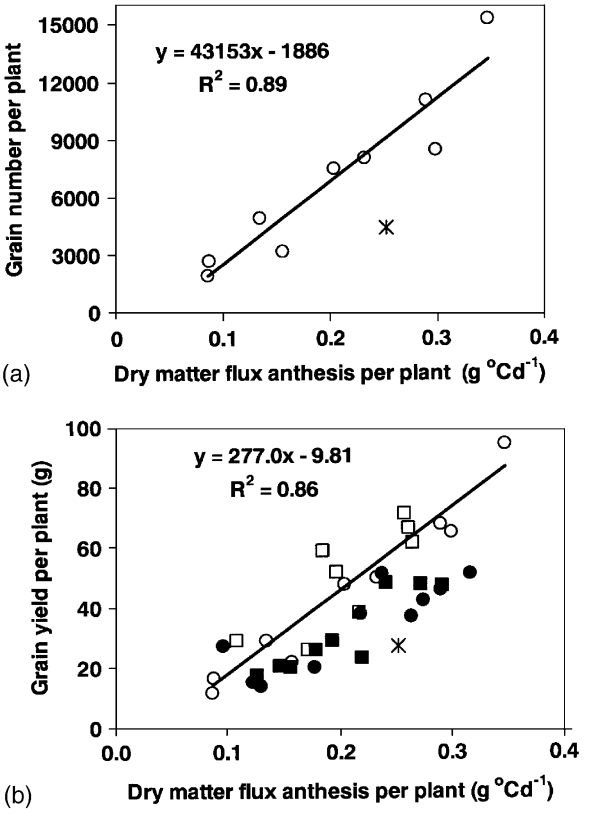


Fig. 6. (a) Grain number per plant at maturity and (b) grain yield per plant at maturity as a function of the rate of dry matter accumulation per plant at anthesis for BJ 104 (○), RCB-IC 911 (□), and WRajPop (●). Data for sorghum hybrid CSH 13 (■), with a stature comparable to pearl millet, have been added for comparison (van Oosterom, unpublished data). Regression equations include all open symbols. In (b), the regression equation represents an upper boundary of the relationship between grain yield and dry matter flux. Star symbol represent an outlier for BJ 104, not included in the analyses. Data for BJ 104 from Carberry et al. (1985) and Craufurd and Bidinger (1988a,b, 1989).

### 3.4. Dry matter partitioning to grains

The significant genotypic differences in grain mass in PAT96s (Table 4) were related to differences in the grain growth rate. A piecewise regression of grain mass (based on sample grain yield and grain number at maturity) on thermal time after anthesis for PAT95 indicated that the grain growth rate of improved cultivars ($0.0344 \pm 0.0076$ mg per grain per °C day) was 30% higher than that of landraces ($0.0267 \pm 0.0100$ mg per grain per °C day) (Fig. 7), although the difference was not significant at $P < 0.05$. In both

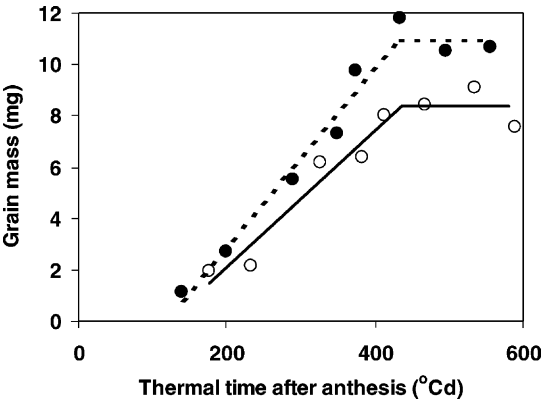


Fig. 7. Grain mass as a function of thermal time after anthesis for ERajPop and WRajPop landraces (○) and RCB-IC 911 and WC-C 75 improved cultivars (●), grown at Patancheru during the rainy season of 1995. Equations for the piecewise regressions are: Landraces: grain mass $= -3.23 + 0.0267T - 0.0267(T - 435)$ $(T > 435)$, $n = 8$, $R^2 = 0.94$. Improved cultivars: grain mass $= -3.97 + 0.0344T - 0.0344(T - 434)$ $(T > 434)$, $n = 8$, $R^2 = 0.98$.

Table 5
Number of productive basal and nodal tillers per plant, grain yield and percentage of grain yield produced by main shoot, basal tillers, and nodal tillers, above-ground biomass and grain number for RCB-IC 911 and WRajPop, grown in four experiments at Patancheru under well-watered and well-fertilised conditions

| | Tiller number | | Grain yield | | | | Biomass ($g\ m^{-2}$) | Grain number | |
|---|---|---|---|---|---|---|---|---|---|
| | Basal (per plant) | Nodal (per plant) | Total ($g\ m^{-2}$) | Main (%) | Basal (%) | Nodal (%) | | Total ($m^{-2}$) | Main + basal ($m^{-2}$) |
| Patancheru dry season 1994 | | | | | | | | | |
| RCB-IC 911 | 1.91 | 1.19 | 465 | 39.4 | 56.1 | 4.5 | 897 | 45,196 | 42,562 |
| WRajPop | 4.42 | 8.93 | 310 | 19.6 | 63.0 | 17.5 | 936 | 42,600 | 33,759 |
| Patancheru dry season 1994 extended daylength | | | | | | | | | |
| RCB-IC 911 | 1.11 | 2.07 | 457 | 53.6 | 40.0 | 6.4 | 1141 | 44,246 | 39,720 |
| WRajPop | 3.08 | 5.89 | 321 | 25.8 | 55.3 | 19.0 | 1198 | 43,601 | 33,967 |
| Patancheru rainy season 1994 | | | | | | | | | |
| RCB-IC 911 | 1.43 | 1.18 | 488 | 44.0 | 49.5 | 6.5 | 1035 | 42,563 | 38,629 |
| WRajPop | 3.78 | 6.62 | 418 | 20.7 | 58.4 | 20.9 | 1070 | 54,998 | 40,462 |
| Patancheru rainy season 1995 | | | | | | | | | |
| RCB-IC 911 | 2.12 | 1.34 | 488 | 42.9 | 50.8 | 6.3 | 1094 | 43,506 | 39,375 |
| WRajPop | 2.99 | 3.10 | 387 | 29.5 | 57.9 | 12.6 | 984 | 45,428 | 37,926 |

cases, grain growth started around 115–120 °C d after anthesis, and maximum grain mass was reached at 435 °C d after anthesis (Fig. 7). These results compare well with the results the of the PAT96 experiment, where physiological maturity occurred around 460 °C d after anthesis, irrespective of the axis (Table 6). Although differences between cultivars in the duration of the period between anthesis and physiological maturity were consistently significant across axes, the absolute differences were small and rarely exceeded 2.5 days.

Productive axes within a plant generally had similar patterns of dry matter accumulation to the grain. For BJ 104, grown across a range of daylength treatments at Patancheru, the fraction of dry matter present in the panicle generally increased linearly with time after anthesis, and patterns were similar for the main shoot

Table 6
Time from anthesis to physiological maturity for the main shoot, Tiller 3 and Tiller 4 of individual cultivars, grown during the rainy season at Patancheru in 1996[a]

| Cultivar | *n* | Main shoot (per °C day) | Tiller 3[b] (per °C day) | Tiller 4 (per °C day) |
|---|---|---|---|---|
| BJ 104 | 20 | 445 a | 451 a | 455 b |
| HHB 67 | 20 | 482 b | 466 b | 469 c |
| RCB-IC 911 | 7 | 472 b | 474 b | 476 c |
| WRajPop | 13 | 439 a | 433 a | 434 a |
| Mean | | 459 | 456 | 459 |

[a] Data are means of observations on individual plants. Means followed by the same letter are not significantly different at $P < 0.05$ according to a *t*-test, assuming unequal variances between groups and using Satterthwaite's approximation for calculating the effective degrees of freedom.

[b] Tiller 3 is generally the first tiller to appear (van Oosterom et al., 2001b).

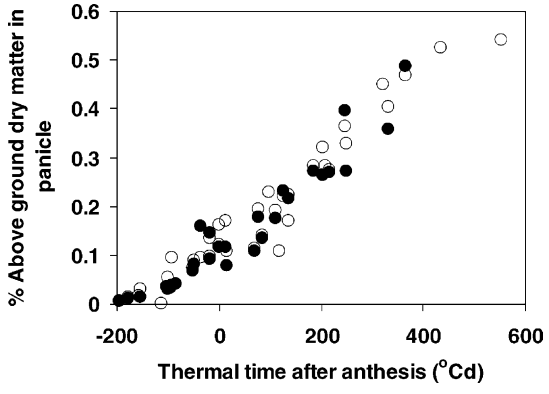


Fig. 8. Fraction of above-ground dry matter, present in the panicles, as a function of thermal time after anthesis for main shoots axes (○) and Tiller 3 axes (●) of crops of BJ 104, grown at Patancheru under a range of daylengths. Data are averaged across densities. Sources: Carberry et al. (1985) and Craufurd and Bidinger (1988a,b, 1989).

and Tiller 3 (Fig. 8). The results also indicate that biomass accumulation to the panicle ceases soon after 400 °C d after anthesis. The similarity between axes in dry matter allocation to the grain was supported by the results of the PAT96s and PAT96 experiments, where the HI at maturity of the first three tillers was on average within 5% of the HI of the main shoot (data not shown).

## 4. Discussion

### 4.1. Light interception and biomass accumulation

We estimated an $RUE_{TOTRAD}$ of $1.90 \pm 0.11$ g $MJ^{-1}$ under optimal conditions. This value compares well with the values of 1.96 g $MJ^{-1}$ (Squire et al., 1984a) and 2.0 (Reddy and Willey, 1981) for pearl millet grown in the field at Patancheru. However, values of 2.1–2.4 g $MJ^{-1}$ have been reported by Squire et al. (1984b) and Craufurd and Bidinger (1988b). The value of Squire et al. (1984b) was obtained from glass house experiments, where the observed extinction coefficient was low ($k = 0.3$). Similarly, the high RUE of Craufurd and Bidinger (1988b) was obtained from calculated light interception, based on observed LAI in the field and an extinction coefficient of 0.3. Our estimate for the extinction coefficient was considerably higher ($k = 0.63$), but compared well with results of Ong and Monteith (1985), who reported a value of 0.5 for field measurements taken at noon. It is likely this value is an underestimation though, as light interception at noon is relatively low (Muchow, 1985; Begue et al., 1991). The high RUE observed by Squire et al. (1984b) and Craufurd and Bidinger (1988b) could thus have been associated with the low $k$, as negative correlations between RUE and $k$ have been reported for wheat (Green, 1989) and pigeonpea (Robertson et al., 2001). Our RUE of 1.90 g $MJ^{-1}$ compares well with the maximum RUE of sugarcane of 2.0 g $MJ^{-1}$ (Muchow et al., 1997; Sinclair and Muchow, 1999). It is also close to the RUE of 1.7–1.8 g $MJ^{-1}$ that has been observed for sorghum cultivars with a crop stature comparable to pearl millet (Hammer et al., unpublished data) in an experiment where standard dwarf sorghum hybrids had an RUE of 1.2–1.4 g $MJ^{-1}$, similar to the maximum RUE for sorghum quoted by Sinclair and Muchow (1999). Although our RUE for pearl millet during the pre-anthesis period is slightly higher than the maximum RUE of maize, which is typically around 1.6–1.7 g $MJ^{-1}$ (Sinclair and Muchow, 1999), our values are consistent with maximum RUE's reported for pearl millet, sorghum, and sugarcane.

Landraces and improved cultivars had similar RUE in our experiments. Although genotypic differences in RUE have been reported for pearl millet (Craufurd and Bidinger, 1988b; Jarwal et al., 1990), it is possible that some of these were a consequence of the fact that light interception was estimated from LAI. In the results of Craufurd and Bidinger (1988b), the cultivar with a low RUE produced only few fertile tillers; consequently, a large proportion of its LAI was at the bottom of the canopy, what could have caused an overestimation of light interception and hence an underestimation of RUE. The absence of significant genotypic differences in RUE and extinction coefficient in our experiments indicates that the low grain yield of the landraces is not a consequence of low light attenuation or conversion efficiency.

In the absence of genotypic differences in RUE, differences in biomass accumulation early in the season were associated with differences in light interception. As the cultivars in our experiment did not differ in the rate of leaf and tiller appearance (van Oosterom et al., 2001a), cultivars with big leaves (RCB-IC 911) have a high LAI early in the season (van Oosterom et al., 2001b) and tend to intercept more radiation than landraces with smaller leaves (Fig. 1a). The large leaves of RCB-IC 911 could be a consequence of the large seed size at sowing, as differences in grain size at sowing can have a significant effect on the dry matter accumulation of the subsequent crop early in the season (Manga and Yadav, 1995; López-Castañeda et al., 1996).

### 4.2. Onset of stem elongation

The onset of stem elongation was not related to apical development, as the difference in occurrence between $O_s$ and PI decreased with increasing daylength (Fig. 4). The absence of an association between $O_s$ and PI is in accordance with results for sorghum (Morgan and Finlayson, 2000), but contrasts the situation of $C_3$-cereals, where $O_s$ is related to the double ridge stage of the apex (Gomez-Macpherson et al., 1998). Although $O_s$ can occur before PI in late

flowering sorghum (Morgan and Finlayson, 2000), it always occurred around or after PI in our analyses, which covered a wide range in daylength (Fig. 4). As time to anthesis for an axis in APSIM-millet is calculated from the final leaf number on that axis, which is known at PI (van Oosterom et al., 2001a), timing of anthesis can generally be calculated when $O_s$ occurs. As the timing of $O_s$ was relatively constant if expressed as a fraction of the time from emergence to anthesis (Fig. 4), this could provide a better approximation of $O_s$ when modelling biomass partitioning in pearl millet than expressing $O_s$ relative to the occurrence of PI.

The effect of axis on the occurrence of $O_s$ was minor, as judged from the small and non-significant effect of axis on the change in $AR_{leaf}$ (Table 2). On average, the delay in decline of $AR_{leaf}$ in tillers as compared to the main shoot was about 5% of the time from emergence to anthesis, equivalent to 35 °C d if time from emergence to anthesis is 700 °C d. As tiller appearance in pearl millet typically does not start until 150 °C d after emergence, $O_s$ is thus well synchronised across axes within a plant. This is consistent with the observed synchrony between axes for phenology and leaf senescence (Craufurd and Bidinger, 1988a; van Oosterom et al., 2001a).

### 4.3. Dry matter partitioning

Before the onset of stem elongation, the allocation of dry matter between leaf blade and stem fraction (sheath) was not affected by daylength, plant density, or axis (Fig. 3). Our results, with 67% of dry matter allocated to the leaf blades, were consistent with results for maize (Birch et al., 1999), wheat (van den Boogaard et al., 1996), and sorghum (van Oosterom, unpublished data). Elliott et al. (1997), however, reported for wheat seedlings that up to 80% of shoot dry matter was allocated to the leaf blades, whereas Gomez-Macpherson et al. (1998) reported a fraction of 62% for wheat. A reason for this discrepancy could be the existence of small genotypic differences in allocation patterns (van den Boogaard et al., 1996).

After the onset of dry matter accumulation in the stem, $AR_{leaf}$ generally declined linearly with relative thermal time. This is in agreement with results for wheat (Borrell et al., 1989) and maize (Birch et al., 1999). Our observation that daylength had little effect on the pattern of $AR_{leaf}$ is supported by results of Birch et al. (1999) who found for maize no effect of maturity type on the fraction of dry matter present in leaves if time was expressed as the relative number of visible leaves. Genotypic differences in maturity are generally associated with differences in leaf number, similar to the effect of daylength extension on leaf number for individual cultivars (van Oosterom et al., 2001a).

The cessation of dry matter allocation to the leaves ($AR_{leaf} = 0$) heralds the appearance of the flag leaf. The results of Fig. 5, where $AR_{leaf}$ dropped to zero when approximately 90% of the time from emergence to anthesis had elapsed, were consistent with the results of Table 3, where the period from flag leaf stage till anthesis constitutes 10% of the period from emergence to anthesis. Combined with the approximation that the onset of decline in $AR_{leaf}$ (or the timing of $O_s$) can be expressed relative to anthesis, daily values for $AR_{leaf}$ can be calculated, assuming a linear decline from 0.67 at $O_s$ to 0.0 at the flag leaf stage.

### 4.4. Determination of grain number

Grain number per plant for BJ 104 was a linear function of the dry matter accumulation rate at anthesis (Fig. 6a). The slope we observed (4300 grains per 0.1 g per °C day, Fig. 6) is comparable to the results of Ong and Squire (1984) who observed in a greenhouse study a slope of 99,000 grains per MJ per °C day. Combined with an RUE of 2.5 g $MJ^{-1}$ (Squire et al., 1984b), this is equal to approximately 4000 grains per 0.1 g per °C day. Our results, however, cover a much wider range of data. The linear relationship we observed is in agreement with results observed for sorghum (van Oosterom and Hammer, unpublished data) and wheat, where a linear relationship between grain number and panicle weight around anthesis has been widely reported (Fischer, 1993; Miralles et al., 1998, 2000; Demotes-Mainard et al., 1999). For maize, however, curvilinear relationships between plant growth rates around anthesis and grain number per plant have been reported (Edmeades and Daynard, 1979; Vega et al., 2001). Several reasons might explain this difference. Firstly, maximum crop growth rates for maize are considerably higher than those we observed. The maximum of 0.35 g per plant per °C day in our data (Fig. 6) is equivalent to approximately

3 g per plant per day, which is within the linear part of the relationship reported by Vega et al. (2001). Secondly, the curvilinear relationship in maize might reflect morphological restrictions to the production of new sinks, caused by a limited capacity to produce tillers (Vega et al., 2001). Pearl millet responds to an increased assimilate availability per plant through an increase in the number of productive tillers (Bidinger and Raju, 2000). Craufurd and Bidinger (1988a) observed a linear relationship between grain yield and growth rate across individual axes within plants, grown under a range of photoperiods. Such a linear relationship between grain number (or grain yield) and growth rate in pearl millet could indicate a high level of reproductive plasticity.

The relationship between grain yield and growth rate at anthesis (Fig. 6b) suggests a consistent effect of cultivar on the relationship between grain number and crop growth rate at anthesis. This can be caused by genotypic differences in the fraction of dry matter that is allocated to the growing panicle around anthesis and by differences in the relationship between grain number and non-grain panicle weight (van Oosterom and Bidinger, unpublished data). The importance of the non-grain panicle weight in determining grain number was also noted by Bindraban et al. (1998), who observed for wheat that the relationship between grain number and non-grain spike weight at anthesis was conservative across genotypes. Similarly, genotypic differences in the relationship between grain number and crop growth in sorghum, caused by differences in crop stature, could be accounted for by expressing grain number as a function of the panicle growth rate at anthesis (van Oosterom and Hammer, unpublished data). The relationship between grain yield and growth rate for the landraces (Fig. 6b) was similar to that of sorghum hybrid CSH 13, a tall hybrid from India (Fig. 6b), whereas dwarf sorghum hybrids developed in Australia had a relationship that was close to that of BJ 104 and RCB-IC 911 (data not shown). This similarity across species in the relationship between grain yield at maturity and growth rate at anthesis suggests that differences between pearl millet and sorghum in the relationship between grain number and growth rate could be related to differences in grain size. An upper limit for the relationship between grain yield and growth rate may exist (Fig. 6b), which could be common across species. The extent to which individual cultivars do not reach this maximum could then reflect a limitation on sink capacity, which could reflect their relative stage of genetic improvement.

The positive intercept with the *x*-axis of the relationship between grain number and growth rate reflects a minimum growth rate, below which the crop will not produce any grain yield. In our results this was 0.04 g per plant per °C day (Fig. 6), or 0.6 g per plant per day. This value is in agreement with results of Ong and Squire (1984) for pearl millet, but is considerably lower than the 1.0 g per plant per day reported for maize by Vega et al. (2001). This difference might well reflect the better adaptation of pearl millet to harsh growing conditions. Within this context, it is worthwhile noting that the only instance in Fig. 6b where the grain yield of WRajPop was above the regression line of the grain yield–growth rate relationship of BJ 104 and RCB-IC 911 was in experiments PAT95s, where the crop experienced mid-season drought stress which was temporarily relieved around anthesis, a pattern of drought stress which is not uncommon in the environments where the landraces have evolved (van Oosterom et al., 1996).

### 4.5. Duration and rate of grain filling

The GFP can be split up into an initial lag phase (before the onset of grain growth), a period of linear increase in individual grain mass (the effective grain filing period, EGFP), and a period from the end of EGFP until physiological maturity. The duration of the lag phase we observed (115–120 °C d) was only slightly higher than the value of approximately 80 per °C day reported by Fussell and Pearson (1978), but was within the range of 30–127 °C d observed by Bieler et al. (1993) in a comprehensive analysis of grain growth in West Africa. Our EGFP was about 320 °C d and the period from end grain filling until physiological maturity appeared to be short, as judged from a comparison of the end of the EGFP in PAT95 (420–430 °C d after anthesis, Fig. 7) and the GFP in PAT96 (460 °C d, Table 6). This confirms the result of Fussell and Pearson (1978) that the attainment of black layer in pearl millet is a reliable indicator of the attainment of maximum seed size, and that this stage is preceded by only a brief period during which the grain growth rate declines from its linear value. Our value for the GFP was within

Table 7
Overview of previously published data on the duration of the GFP (anthesis to maturity) in pearl millet, including temperature regime during grain filling and duration of GFP, expressed in either days or degree days[a]

| Reference | Location | Daylength sowing | Temperature (°C) | GFP | | Cardinal temperatures (°C) |
|---|---|---|---|---|---|---|
| | | | | Days | °C d | |
| Fussell et al. (1980) | Glasshouse | na[b] | 21/16 | 30–33 | 255–281 | 10, 33, 47 |
| Fussell et al. (1980) | Glasshouse | na | 27/22 | 23–26 | 334–377 | 10, 33, 47 |
| Fussell et al. (1980) | Glasshouse | na | 30/25 | 21–24 | 368–420 | 10, 33, 47 |
| Fussell et al. (1980) | Glasshouse | na | 33/28 | 21–23 | 431–472 | 10, 33, 47 |
| Lambert (1983) | Bambey, Senegal | na | na | 24–26 | na | na |
| Ong (1983b) | Glasshouse | 12.0 | 19.0 | 32.0 | 288 | 10 |
| Ong (1983b) | Glasshouse | 12.0 | 21.9 | 23.3 | 277 | 10 |
| Ong (1983b) | Glasshouse | 12.0 | 24.9 | 21.0 | 313 | 10 |
| Ong (1983b) | Glasshouse | 12.0 | 27.7 | 20.5 | 363 | 10 |
| Ong (1983b) | Glasshouse | 12.0 | 31.0 | 20.3 | 426 | 10 |
| Carberry et al. (1985) | Patancheru | 13.5 | na | 35 | na | 10, 33, 47 |
| Coaldrake and Pearson (1985) | Australia | 15.4 | na | 35 | 400 | 10 |
| Coaldrake and Pearson (1985) | Australia | 15.4 | na | 41 | na | 10 |
| Craufurd and Bidinger (1988b) | Patancheru | 13.5 | na | 28–29 | 464–481 | 10, 33, 47 |
| Craufurd and Bidinger (1988b) | Patancheru | 14.5 | na | 28 | 466 | 10, 33, 47 |
| Craufurd and Bidinger (1988b) | Patancheru | 15.5 | na | 28 | 466 | 10, 33, 47 |
| Craufurd and Bidinger (1989) | Patancheru | 13.5 | na | 26 | 397 | 10, 33, 47 |
| Craufurd and Bidinger (1989) | Patancheru | 15.5 | na | 22 | 372 | 10, 33, 47 |
| Bieler et al. (1993) | Niamey, Niger | na | na | na | 265–422 | 10, 33, 45 |
| Bieler et al. (1993) | Niamey, Niger | na | na | na | 231–459 | 10, 33, 45 |

[a] Cardinal temperatures (minimum, optimum, and maximum) used for the calculation of degree days are given in the last column.
[b] Not available.

the range observed in the literature (Table 7). Overall, our results are in agreement with those of Fussell and Pearson (1978) that the lag phase constitutes 20–25% of the GFP, the EGFP 65–70% and the period from end grain filling to physiological maturity 5–10%.

Differences in grain mass between landraces and non-landraces were predominantly due to a difference in the grain growth rate, as differences in the duration of the GFP were small (Fig. 7; Table 6). This confirms results of Lambert (1983), who found for pearl millet grown in West-Africa that the duration of GFP was similar across cultivars with vastly different phenology. Bieler et al. (1993), however, observed significant genotypic differences in GFP across 45 pearl millet cultivars grown in Niger (Table 7). Yet, 51% of the variation in grain mass in their experiments (Bieler et al., 1993) could be attributed to variation in grain growth rate, compared with 37% to variation in the duration of the EGFP and only 9% to variation in the lag phase. Similarly, Fussell and Pearson (1978) observed that differences in grain mass between pearl millet hybrids and their parents were predominantly due to differences in grain growth rate, rather than duration of the EGFP. Most of the variation in grain size in pearl millet thus appears to be associated with differences in the grain growth rate.

The grain growth rate can be considered as the balance between the demand for carbon by the sink or growing grain, and the supply of carbon by the source, through assimilation and translocation. The grain growth rates which we observed (0.027–0.034 mg $g^{-1}$ per °C day, or 0.4–0.5 mg $g^{-1}$ per °C day) are within the range of 0.017–0.039 (mean 0.027) mg $g^{-1}$ per °C day reported by Bieler et al. (1993), but are higher than the 0.25 mg $g^{-1}$ per day reported by Fussell et al. (1980). Heiniger et al. (1997) expressed the grain growth rate of sorghum as a function of the total dry matter accumulation rate per grain during grain filling. The slope of this relationship was about 0.4 (Heiniger et al., 1997), suggesting that the rate of grain growth is relatively constant across environments. This is supported by observations for pearl millet that individual grain mass is relatively insensitive to the availability of resources (light, nutrients)

per plant, particularly in case of high-tillering cultivars with small grains like the landraces (Bidinger and Raju, 2000). Under N-stress, the demand for carbon by the grains can be met through increased translocation of carbon from stems, as the fraction of water-soluble or non-structural carbon in the plant increases with decreasing N% of the vegetative parts (Batten et al., 1993; van Herwaarden et al., 1998). The theory of Heiniger et al. (1997) would predict a higher grain growth rate for RCB-IC 911 than for BJ 104, as the former has less grains to fill while total dry matter is comparable (Table 4). The substantial difference in grain mass (Table 4) between the two cultivars, despite a small difference in GFP (Table 6), is indirect evidence of such a difference in grain growth rate. The differences in grain growth rate between WRajPop and RCB-IC 911 might not be explained that way, as both cultivars had similar grain numbers (Table 5). The small grain size of the landraces could therefore be a sign of a genetic limitation to grain size.

### 4.6. Potential advantages of genetic limitations of grain size under stress

A possible genetic limitation to grain size of the landraces could be a key component of a strategy that enhances adaptation to variable stress environments. Compared with RCB-IC 911 and BJ 104, WRajPop has a significantly lower grain yield under optimum growing conditions, despite a similar stover weight (Table 4). As we did not observe genotypic differences in RUE or $k$, there is no apparent reason for such a difference in grain yield. The significantly lower panicle harvest index of WRajPop (Table 4) also indicates that the potential grain yield of WRajPop has not been met. This hypothesis is supported by the observation that particularly under optimum growing conditions, landraces produce an abundance of nodal tillers in comparison with improved cultivars (Table 5). As these tillers are positioned in the top of the canopy, where leaves are most actively photosynthesising (Jacquinot, 1970), their appearance suggests carbon supply exceeds demand. Indeed, nodal tiller production was negatively correlated to the grain yield of the main shoot and basal tillers. A strategy to promote nodal tillering through a low sink size in the panicles of the main shoot and basal tillers would be a useful survival mechanism in environments where stress is likely to occur, but its timing and intensity are unpredictable. The desert margins where the landraces have evolved are characterised by such conditions (van Oosterom et al., 1996). Developmental plasticity has been advocated as a mechanism to ensure drought escape in environments where the timing of stress (drought) is unpredictable (Ludlow and Muchow, 1988). Recent results for pearl millet, however, suggest a high level of synchrony in the development of main shoots and basal tillers, with successive primary basal tillers on a single plant reaching anthesis within 1–2 days of each other (van Oosterom et al., 2001a). As the effects of stress on grain yield in cereals are particularly strong around anthesis (Roberston and Giunta, 1994), when grain number is determined (Edmeades and Daynard, 1979), it is unlikely that prolific tillering per sé is an adequate mechanism to escape drought stress. Nodal tillers, by contrast, reach anthesis about 3 weeks later than their subtending main shoot or primary basal tillers (van Oosterom, unpublished data), and thus provide a better mechanism to ensure some grain yield and hence survival of the species. The low grain yield of landraces under optimum conditions would thus not be a consequence of low potential biomass accumulation, but rather of restrictions in partitioning to the grain, brought about through lower grain growth rates and aimed to increase adaptation to variable stress environments.

## 5. Conclusions

This paper quantifies the effects of genotypes and axis type (main shoot vs. tiller) on parameters that determine biomass accumulation and partitioning in pearl millet. Landraces and improved varieties did not differ in the light extinction coefficient and the RUE, and hence did not differ in their ability to accumulate biomass. In the absence of genotypic differences in the fraction of biomass allocated to the leaves before anthesis, there were no differences in yield potential. Nevertheless, grain yield of landraces under high-yielding conditions was significantly lower than that of improved varieties. This was due to a lower grain yield produced per unit of dry matter accumulation per °C d at anthesis, associated with a combination of low individual grain growth rate and low grain number. As

the low grain yield was accompanied by an abundance of nodal tillers, which are a sign of assimilate surplus, it is hypothesised the low grain yield of landraces was the result of a low rate of dry matter partitioning to grains in the main shoot and basal tillers, which enables stress escape around anthesis by stimulating the production of nodal tillers.

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