Paper 31

DURATION OF GRAIN FILLING AND YIELD OF GRAIN SORGHUM

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ABSTRACT

Sorghum grown in high-yielding environments tends to have source-limited grain yield; selecting for individual components may not cause a proportionate change in yield because of compensation effects. The source-limitation might be reduced by increasing the duration of the grain filling period (GFP), allowing more time for assimilate to accumulate in the grain. There is some evidence that long GFP is associated with high yield, and three experiments were conducted under irrigation at the Kimberley Research Station to provide further evidence of this effect. In each experiment, the relationships between grain yield, grain size, harvest index, and duration of grain filling were examined in a range of sorghum cultivars using multiple regression techniques.

Long duration of grain filling was generally associated with low mean temperature during that period, high yield, large grains, and high harvest index. The GFP's of cultivars were, however, not correlated between experiments, and it was not certain whether high yield was caused by long GFP. A more detailed investigation of the nature of these relationships, a search for long GFP germplasm and a study of its inheritance are advocated.

KEYWORDS

Sorghum bicolor, phenology, yield components, source-sink relationships, yield determinants, grain size, grain number.

INTRODUCTION

There is experimental evidence that grain sorghum (*Sorghum bicolor* L. Moench) grown under good conditions is source limited with respect to grain yield (Fischer and Wilson, 1975; Muchow and Wilson, 1976; A.A. Done and R.C. Muchow, unpub. data). Treatments which increased assimilate supply to developing grains increased grain size. Negative correlations between grain size and grain number occur frequently in grain sorghum (e.g. Heinrich *et al.*, 1983; Ross and Hookstra, 1983), and this is further (circumstantial) evidence that source limitation generally occurs. Selection for improved yield based on an individual yield component will be ineffective because of compensating effects on other components.

It should, however, be possible in source-limiting conditions to increase grain yield by partitioning a greater proportion of assimilate to the grain. One way in which this can be achieved is by increasing the duration of the grain filling period (GFP), as demonstrated by Eastin *et al.* (1971).

The relationships between GFP and grain yield, single grain weight (grain size), and harvest index are examined in this paper, to test the hypothesis that high grain yield is associated with long GFP.

MATERIALS AND METHODS

A range of F_1 hybrid and inbred grain sorghum cultivars was grown with furrow irrigation and liberal amounts of nutrients at the Kimberley Research Station (KRS) in the far northeast of Western Australia (15°39'S, 128°43'E). The region has a semi-arid climate with distinct wet (summer) and dry (winter) seasons; sorghum can be grown in both seasons. The soils and climate of the region are described in Williams *et al.* (1985).

Three experiments were conducted.

Experiment A

This experiment included 28 cultivars comprising 26 subtropical commercial or experimental F_1 hybrids, one commercial, and one experimental inbred line. These were sown on 12 January 1976 (wet season), at four seed rates on beds with four rows spaced 37 cm apart. There were three replicates. Anthesis was recorded as the day on which 50% of the total pollen had been shed, and maturity was judged subjectively as the day on which grain was dry (about 16% moisture). Grain yield was estimated from one 12 m^2 quadrat in each plot. A subsample was taken to determine harvest index and 200 grain weight.

Overall population density varied among cultivars. Cultivar means for a population of 195 000 seedling per ha were therefore obtained by regressing block residuals of variates on seedling density for individual plots.

Experiment B

This experiment was a duplicate of Experiment A, sown in the dry season on 31 May 1986 except that maturity was determined as the day on which 50% of the grains on a

Table 1. **Minimum, overall mean and maximum values for various plant characters in three experiments on grain sorghum. (There were 28 cultivars in experiments A and B, and 20 in Experiment C.)**

	Experiment								
	A (wet season)			B (dry season)			C (dry season)		
	min.	mean	max.	min.	mean	max.	min.	mean	max.
Time from planting to anthesis (days)	43	52.9	77	65	73.6	88	64	82.8	112
Time from planting to maturity (days)	69	81.0	97	111	115.6	124	103	117.8	142
Duration of grain filling (GFP) (days)	21	28.1	33	35	40.9	47	32	35.1	38
Mean daily temperature ((max + min)/2) during grain filling (°C)	27.6	27.96	28.8	24.6	25.20	26.3	26.3	27.82	30.8
Grain yield, oven dry basis ($kg.ha^{-1}$)	2010	3283	4020	5870	7066	8050	3870	6071	7630
Single grain weight (mg)	13.6	20.04	26.2	22.3	28.06	33.8	13.8	24.30	33.4
$Grains/ha^{-1} \times 10^{-6}$	119	166.0	216	195	256.1	349	167	257.0	324
Harvest index	0.24	0.366	0.44	0.41	0.487	0.54	0.26	0.485	0.58

range of panicles showed a well-formed black closing layer (Weibel *et al.*, 1982).

Experiment C

This experiment included 20 cultivars comprising eight subtropical F_1 hybrids, one sweet sorghum, one commercial inbred line, and ten experimental inbred lines. These were sown on 16 June 1980 in single rows on ridges 75 cm apart, with four rows to a plot, and replicated three times. Sixteen cultivars were thinned to about 200 000 seedlings per ha, but the seedling emergence of four cultivars was so poor that they were thinned to a population of 100 000 seedlings per ha. Anthesis and maturity were assessed as in Experiment B, and all measurements were taken from one 3 m^2 quadrat.

Five F_1 hybrids and the commercial inbred line were used in all experiments.

Standard screen air temperature was recorded about 1 km from the experiments.

Statistical analyses were done on the estimated (Experiments A and B) or actual (Experiment C) cultivar means from each experiment.

RESULTS AND DISCUSSION

The minimum, overall mean and maximum values for various plant characters, and associated temperature data for the three experiments are shown in Table 1.

Grain yield and grain size

There was variation in grain yield, size, and number in all experiments. Compensation was observed between number and size (r = −0.41*, −0.79*** and −0.63***), and grain yield and number were positively correlated (r = 0.57***, 0.62*** and 0.41^{NS}). The direct influence of GFP on yield would only be expected because of its effect on grain size; variation in grain number, and the correlations noted above, tended to obscure this anticipated relationship. The effect of variable grain numbers was counteracted using multiple regression analysis, and the hypothesis that high yield was associated with long GFP was tested by regressing grain size or yield on GFP and grain number simultaneously (Table 2). The relationship between grain yield and GFP could thus be interpreted for a given grain number. All results confirm the hypothesis that high yield is associated with long GFP for a given grain number. Furthermore, differences in yield and grain size between Experiments A and B were correlated with differences in GFP, for a given difference in grain number. The latter is a robust test of the hypothesis since it eliminates, to a considerable extent, any gratuitous genetic correlations.

Harvest index

Harvest index (HI) is frequently quoted as a measure of efficiency of crop production. Grain yield is mainly attributable to dry matter produced after anthesis in grain sorghum (Muchow and Wilson, 1976; Muchow *et al.*, 1982; A.A. Done and R.C. Muchow, unpub. data). HI should therefore be related to the relative amount of time spent in growth before anthesis and grain filling. This hypothesis was tested by regressing HI on time to anthesis and maturity (Table 3). Table 3 shows that Experiments B and C confirmed the hypothesis. The individual regressions of HI on time to anthesis or maturity were not significant in Experiment B, but the multiple regression yielded a negative coefficient for the former and a positive coefficient for the latter. High HI was therefore associated with late maturity date for a given anthesis date or early flowering for a given maturity date. A similar result was obtained in Experiment C, except that the individual regressions had negative coefficients, because of the

Table 2. **Multiple regression of grain yield (kg. ha^{-1}) and single grain weight (grain size/(mg)) on grain number and duration of grain filling (GFP) in three grain sorghum experiments. The regressions are of the form $y = a + b_1 x_1 + b_2 x_2$. 't' refers to Students t. The proportional change is the b_2 regression coefficient obtained if y and x_2 are transformed to y/y and x_2/x_2 respectively.**

y-variate	n	a, constant	t	b_1, x_1 = grains. ha^{-1}	t	b_2, x_2 = GFP	t	Proportional change (y:x_2)
Expt A, wet season	28							
Grain yield		-73	0.12^{NS}	10.6	3.56**	57.0	3.39**	0.48
Grain size		21.1	4.93***	-0.0615	3.00**	0.325	2.80**	0.46
Expt B, dry season	28							
Grain yield		142	0.08^{NS}	13.8	5.07***	80.5	2.50*	0.48
Grain size		30.5	4.15***	-0.0051	4.65***	0.251	1.95^{NS}	0.38
Expt C, dry season	20							
Grain yield		-5306	2.86*	4.7	1.97^{NS}	289.5	5.43***	1.67
Grain size		1.9	0.24^{NS}	-0.0614	6.03***	1.091	4.87***	1.57

Table 3. **The regression of harvest index (HI) on time between planting and anthesis (x_1), and planting and maturity (x_2) in three grain sorghum experiments. Individual ($y = a_1 + b_1 x_1$ and $y = a_2 + b_2 x_2$) and multiple ($y = a_3 + b_1 x_1 + b_2 x_2$) are shown. 't' refers to Students t.**

		Constant		Time from planting to anthesis, days, x_1		Time from planting to maturity, days, x_2	
y-variate	n	a	t	b_1	t	b_2	t
HI, Experiment A	28	0.711	14.14***	-0.0065	6.91***	-	-
		0.727	7.36***	-	-	-0.0045	3.67**
		0.637	8.68***	-0.0084	5.01***	0.0021	1.36^{NS}
HI, Experiment B	28	0.608	7.91***	-0.0016	1.58^{NS}	-	-
		0.473	2.16*	-	-	0.0001	0.06^{NS}
		-0.063	0.26^{NS}	-0.0057	3.37**	0.0084	2.86**
HI, Experiment C	20	0.943	16.47***	-0.0055	8.14***	-	-
		1.1735	10.75***	-	-	-0.0058	6.35***
		0.257	1.40^{NS}	-0.0189	5.38***	0.0152	3.84**

association of late anthesis (or maturity) with more vegetative growth and a lower HI. Experiment A also gave individual negative correlations, for the same reason. The effect of varying maturity was, however, not significant for a given anthesis date in Experiment A , and therefore high HI was not associated with long GFP.

Causes of variation in duration of grain filling

The results described above indicated that high yield and high HI were generally associated with long GFP. It is pertinent to ask, from the plant breeding viewpoint, what were the causes of variation in GFP, and particularly, whether there was any detectable genotypic component of variation.

One possible source of variation in GFP could be variation in the prevailing temperature during GFP, since others (Chowdhury and Wardlaw, 1978; Reddy *et al.*, 1985) have demonstrated that high temperature shortens GFP. In the experiments described above, mean daily temperatures during grain filling differed according to season and also as a consequence of variation in time to anthesis. Late anthesis coincided with lower temperature in Experiment A and higher temperature in Experiments B and C. This was expected on the basis of seasonal changes in temperature.

The relationship between GFP and temperature in the three experiments is illustrated in Fig. 1. Distributions in Experiments B and C (dry season) could represent part of the same curvilinear relationship. Individually, these two experiments had significant but different linear regression coefficients for GFP on temperature. When the two data sets were combined, good fits giving virtually identical curves were obtained with:

$$GFP = 32.0 + (14.88 \times 10^6)e^{-0.565x} \quad (1)$$

$$GFP = 27.5 + 35.8/(x - 22.7) \quad (2)$$

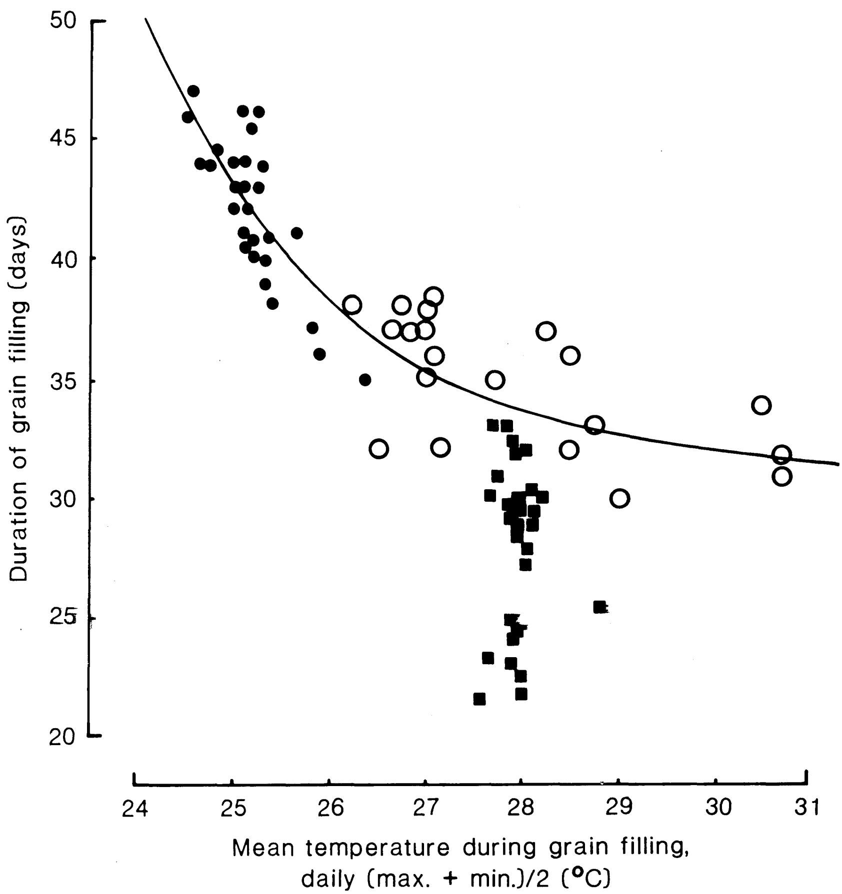

Figure 1. The relationship between duration of grain filling and mean temperature during grain filling in three experiments (A = ■, B = ●, C = ○) on grain sorghum grown under irrigation at the Kimberley Research Station (15°39'S, 128°43'E). The curve represents the relation: duration of grain filling, days = 27.5 + 35.8/(x − 22.7) where x is mean temperature (daily (max. and min.)/2 (°C)) during grain filling, fitted to Experiments B and C only.

where x is the mean temperature during grain filling. Both of these equations incorporate the concept of a minimum GFP, of 32.0 and 27.5 days respectively, as temperature tends to infinity. Equation 1 is based on the biological model that duration of a growth stage changes proportionately with linear change in temperature. In this instance it is proportionate change in 'excess' GFP above the minimum. Equation 2 is a modified day-degree model, and indicates that there were 35.8 day-degrees of growth between anthesis and maturity above the minimum GFP and critical temperature, 22.7°C. The conventional day-degree relation, $GFP = k/(x-c)$, and the simple logarithmic relation $\log GFP = a + bx$, resulted in poorer fits which were almost linear with respect to GFP and temperature. The former, however, indicated a critical temperature of 12°C, and the latter a Q_{10} value of 1.83. It is conjectural whether the relationships observed in Experiments B and C indicate that low temperatures cause long GFP in the manner described in Equations 1 and 2; the relationships might reflect an association with another factor related to anthesis date.

Much of the variation in GFP in Experiment B might have been caused by variation in temperature (Fig. 1). No significant correlation was found between high yield and long GFP when grain yield was regressed simultaneously on GFP, grain number, and temperature. This compares with the significant correlation obtained if only GFP and grain number were used as x variates (Table 2). Thus, even if there is little genotypic variation in GFP, long GFP could be obtained by altering flowering date so that lower temperatures would prevail during that period. This could be done by selecting cultivars with appropriate phenology, or by changing planting date. The effect on yield might not, however, be predictable, since altering flowering date also alters plant morphology and many features of the crop environment. In Experiment B, for example, although early flowering was associated with long GFP, it was not directly associated with higher grain yield because of a correlation between early flowering and low grain number.

The range of GFP's in Experiment A was similar to that in the other experiments, but the range of temperatures was narrow (Fig. 1), and no significant relationship between the two was detected. The mean GFP was also lower in Experiment A than in the other experiments. Stresses caused by pests and diseases which are absent in the dry season may have been responsible. The difference in methods of measuring maturity would, however, have favoured higher estimates of GFP in Experiment A.

The genotypic contribution to variation in GFP over experiments was examined by analysing GFP as a randomised block with experiments as blocks, cultivars as treatments and temperature (with quadratic and cubic terms) as covariates. This gave two analyses, 28 cultivars in two seasons and six cultivars in three seasons. In both analyses the covariate effect of temperature was significant, and thus the difference in GFP between seasons could be partly attributed to difference in temperature, but in neither analysis was there any cultivar effect. Variance ratios (cultivars v. cultivars x experiments) were, in fact, less the 1.0 with or without covariates. There was therefore no detectable genotype component in GFP variation over experiments.

CONCLUSION

The results support the hypothesis that high grain yield is associated with long grain filling period. However, the failure to detect a genotype effect over experiments, and the relatively short GFP and its lack of association with harvest index in Experiment A, cast considerable doubt on the possibility that long GFP causes high yield. It is quite feasible that factors contributing to high yield could also cause long GFP. The results were, however, encouraging and further investigation of the relationship between GFP and yield is advocated. Two main topics are suggested:

- The association between GFP and grain yield should be examined in greater detail. Examples include the use of different criteria for measuring the duration of grain filling, and the relationship of yield and GFP to other plant characters, agronomic practices, and environmental factors.
- A search should be made for both long GFP and short GFP germplasm, as an aid to (a) above, and the inheritance of duration of grain filling should be investigated.

Phenological manipulation might profitably be employed to improve yield in any crop species in which selection for desirable individual components is frustrated by compensation effects, and merits investigation as a plant breeding technique in these species.

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SYMPOSIUM DISCUSSION

Professor R.H.M. Langer, Lincoln College

Could you explain again the definition of the grain filling period? When did you start measuring?

Done

At anthesis.

Langer

Do the grains fill simultaneously or does grain 1 fill, then grain 2, grain 3, etc.

Done

There is a tendency for the tops of the heads to flower and shed pollen first. Pollen shedding then proceeds down the head over a 3-day period. It seems that the length of grain filling tends to be the same in all parts of the head. It follows the typical sigmoid growth curve for grain filling.

Langer

Is there sufficient synchronisation between grains not to have to worry about that aspect?

Done

It seems so, but could be further investigated.

Langer

It seems that with the growth habit of sorghum there is a possibility of considerable lag between the filling of the first and last grains.

Done

There is a difference between the north and the south sides of heads due to the effect of sunlight and temperature, but not between the tops and bottoms other than can be accounted for by variation in anthesis date.

Dr P. Jamieson, Crop Research Division, DSIR

It seems that what you have really shown is that the length of grain filling period is entirely determined by the date of anthesis. In other words if you had knowledge beforehand of what the climate was going to be, and planted such that anthesis occurred at the same time for all the varieties, then they would all mature at the same time.

Done

No. An effect of grain filling upon yield can be detected in Figure 1.

Mr A.K. Hardacre, Plant Physiology Division, DSIR

You mentioned your problem is due to assimilate limitation. One way to lessen this is to increase leaf area duration, what about increasing your leaf area per se? Can you do that?

Done

My personal view is that excessive leaf area is bad. I've been using tropical sorghums for which the rate of leaf production and initiation is very high under high temperatures. I think there are the competitive effects that Dr Kirby (Paper 30) referred to between leaves and panicles, if the plant has too large a leaf area. There is no evidence at all in the tropics that a leaf area index greater than 3 is of any benefit, and sorghums have this level of leaf area under good cropping conditions.

Mr S.K. Roy, Lincoln College

Did you study any relationship between number of grains and grain size.

Done

Yes, grain size and number were negatively correlated in all 3 experiments. The actual values were −0.41, −0.79 and −0.63. This would suggest that in all situations there was source limitation for grain yield.