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Studies of Grain Production in *Sorghum bicolor* (L. Moench). IV* Some Effects of Increasing and Decreasing Photosynthesis at Different Stages of the Plant's Development on the Storage Capacity of the Inflorescence

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Abstract

Sorghum plants (cv. RS610) grown in field stands at two population densities were manipulated to increase the supply of assimilates (by removing neighbouring plants) at one of three developmental stages—10–15 days after floral initiation, 1 week prior to three-quarters anthesis, and 1 week after three-quarters anthesis.

Post-initiation exposure increased the number of grains per inflorescence 1·8-fold and 3·5-fold in medium and high density populations respectively, but had relatively less effect on grain size. Higher grain number resulted largely from more grains per secondary branch in the lower part of the inflorescence.

Neither of the post-heading exposure treatments influenced grain number, but the higher supply of assimilates resulted in larger grains at both densities. Differences at one density only between yield characteristics of plants exposed at the two times provide evidence of inter-plant competition for assimilates to the extent that the potential size of the grain may be affected.

Shading (10% light transmission) of plants grown in a glasshouse, whether for 1 week at anthesis or during grain filling, reduced grain yield at maturity by the same amount as the immediate reduction at the end of the shading period. The experiment was unable to demonstrate changes in the potential size of grains resulting from the loss of assimilates at anthesis. There was substantial compensation for the loss by translocation from other plant parts.

Introduction

Fischer and Wilson (1975) reported that grain yield in *Sorghum bicolor* is correlated with grain number and not with the leaf area of the upper four leaves, which are the major source of material for the grain during grain filling (Fischer and Wilson 1971*b*). Notwithstanding the association of yield with an index of storage capacity, they also reported (Fischer and Wilson 1975) that grain yield was affected by changes in the supply of grain-filling assimilates and that the size of individual grains could be increased. Similar difficulties in interpreting evidence of limitation on yield in wheat have been reported (Fischer and Kohn 1966; Welbank *et al.* 1968; Rawson and Evans 1970) but may be resolved by Wallpole and Morgan's (1970) suggestion that both processes, i.e. the supply of assimilates and the storage capacities of the grain, limit yield, but at different stages of grain development.

The experiments reported here were designed to measure the effect of altering the supply of assimilates during different stages of reproductive development on grain size and yield.

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Materials and Methods

Experiment 1 was aimed at increasing photosynthesis at three stages of reproductive development in plants grown at medium (143,500 plants ha^{-1}) and high (645,800 plants ha^{-1}) densities. The planting arrangement and culture of these stands (designated medium (S), and high density of trial 2) were described by Fischer and Wilson (1975). At three stages, the first 10–15 days after floral initiation (post-initiation), the second 1 week before anthesis, i.e. pre-anthesis (anthesis defined as three-quarters of florets with anthers visible), and the third 1 week after anthesis (post-anthesis), single plants from the two populations were isolated by the removal of neighbouring plants (exposure treatment).

The sample units of 10 plants in each of four replicate blocks were harvested at grain maturity.

The object of experiment 2 was to determine whether a reduction in the current supply of assimilates during the developmental stages of the grain (in the sense of cellular growth) had the same effect on grain yield as a reduction in assimilate supply during the later grain-filling phase.

Eighty plants were grown singly in a glasshouse in 5-gallon pots arranged in five randomized blocks of 16 plants. In each block the following treatments were applied. Plants were shaded (10% light transmission) for a period of 1 week either from half anthesis or from 1 week later. Harvests of whole plants (roots included) were made at the beginning and end of the shade periods and at maturity. Control plants were also harvested at the commencement and finish of the shade treatments as well as at maturity. The early and later shading coincided with periods of grain development and grain filling respectively. Dry matter yields were measured and these data provided estimates of loss of dry matter production of the plant and its parts (including the roots) during the shading periods as well as indicating the residual effects at maturity. The 'grain' yield at the initial harvest (half anthesis) included unfertilized florets, which are not grains in the botanical sense. Recovery of all florets from the inflorescence in order to measure 'grain' yield would have been too time-consuming as would the recovery of the young grains at the second and third harvests. Estimates of grain yield in these harvests were made from the weights of 100 'grains' carefully separated from the inflorescence on the assumption that the number of these per inflorescence would not differ from the mean number of grains in the control plants at grain maturity.

Results

Exposure at all three stages of growth increased grain yield significantly at both densities in the field (Table 1). Grain yield of plants exposed at post-initiation was highest owing to a considerable increase in the number of grains per plant at both densities (3·5-fold and 1·8-fold at the high and medium densities respectively). Although exposure at each stage significantly increased grain size, exposure at pre- and post-anthesis was more effective. The mean effect of the treatment on both densities was to increase grain size 25% when the plants were exposed following post-initiation, 53% following pre-anthesis and 46% following post-anthesis. However, it was only at medium density that exposure at pre-anthesis resulted in a significant increase in grain size compared with exposure at post-anthesis. In all treatments except the post-anthesis treatment, the grain size of the high density plants

was greater than that of the medium density. There was no significant difference between the stem plus leaf weights of plants exposed at pre- and post-anthesis, but in both treatments these weights were significantly greater than for the control plants (Table 1).

The effect of the post-initiation exposure treatment on the inflorescence structure for each density was examined by measuring the number of whorls on the rachis, the number of primary branches at each whorl, secondary branches per primary branch, and grains per secondary branch in the upper and lower sections of the rachis at maturity.

Table 1. The effect of removing neighbouring plants (exposure) at (*a*) 10–15 days after initiation, (*b*) 1 week prior to, and (*c*) 1 week after, three-quarters anthesis, on yield of plants grown at medium (143,500 plants ha^{-1}) and high (645,800 plants ha^{-1}) densities in the field

Yield characteristic (per plant)	Density	Control	Exposure following		
			Post-initiation	Pre-anthesis	Post-anthesis
Grain dry matter (g)	Medium	54·0d*	114·7a′	85·7b′	79·3c
	High	18·0c	78·2a′	25·4b	27·6b
Grain number	Medium	2596b	4742a′	2572b′	2616b′
	High	792b′	2690a′	776b′	826b′
1000 grain weight (g)	Medium	†20·7d′	24·2c′	33·4a	30·2b
	High	†22·8c′	29·2b	32·7a	33·4a
Total shoot dry matter (g)	Medium	107·8c′	202·6a′	160·3b′	150·9b′
	High	36·6c′	142·6a′	60·3b′	59·8b′
Stem plus leaf dry matter (g)	Medium	32·9c′	63·9a′	44·1b′	42·3b′
	High	14·0c′	44·2a′	24·1b′	22·0b′

* Values indicated by the same letter do not differ significantly. a, b, c, d indicate significant differences along rows only at $P = 0{\cdot}05$; a′, etc. indicates differences at $P = 0{\cdot}01$.

† 1000 grain weight for high density significantly larger than for medium density in all treatments except pre-anthesis exposure.

The treatment significantly affected the number of grains per secondary branch in the lower part of the rachis at both densities (grain numbers were 72 and 116 respectively in the control and exposed plants at medium density, and 30 and 125 at high density). The number of branches, both primary and secondary, was not affected by the exposure treatment, nor did it differ markedly between population densities.

In experiment 2, the immediate effect of early shading was to reduce total dry matter per plant by a significant 11·0 g and grain yield by 2·3 g (Table 2). At maturity there was still a difference of 9·7 g in total dry matter while the difference in grain yield was 2·6 g. A modified *t*-test showed that these differences were similar at each harvest. Thus the reduction in grain yield brought about by shading at anthesis may have been caused simply by a reduction in the amount of assimilates used for grain filling rather than for structural development of the grain. Corresponding data for late shading show that its immediate effect was to reduce dry matter production by 13·1 g and grain production by 6·7 g. At maturity the corresponding figures were 10·8 g and 5·0 g and, as in the previous case, these reductions did not differ between the initial and final harvests.

It is not known to what extent the distribution of the current assimilates was indicated by the dry weight changes in the different parts of the plants. An increase

in the dry weight of a certain part of a plant may be brought about by a gain from current assimilate or by translocation of material stored in another site. Decreases in dry weights may result from translocation to other parts of the plant or from respiratory loss. Notwithstanding this lack of information, net photosynthesis in the first week after anthesis for the control plants was 15·9 g (Table 2) which was attributed to increases of 4·9, 2·9, 6·7 and 1·4 g in the grain, root, stem plus leaves, and inflorescence structure respectively. These values represent 30·6, 18·3, 42·3 and 8·8% of net photosynthesis respectively. In the next week, net photosynthesis was 15·8 g and grain weight increased by 15·3 g. There was a loss in stem plus leaf weight over this period and it is not known to what extent material was translocated to other parts of the plant, e. g. the grain, or lost in respiration.

Table 2. Weights and weight gains (g per plant) of plants and parts shaded to 10% of incident radiation for periods of 1 week from either half anthesis (1/2A) or half anthesis plus 1 week (1/2A+1) (shade 1), or half anthesis plus 1 week to half anthesis plus 2 weeks (1/2A+2) (shade 2), and harvested at the commencement and end of each treatment and at grain maturity (glasshouse experiment)

Yield characteristic	Harvest time	Weights			Weight gains		
		Control	Shade 1	Shade 2	Control	Shade 1	Shade 2
Total dry matter	1/2A	63·3	—	—	15·9	4·9	
	1/2A+1	79·2a*	68·2b	—	15·8	—	2·7
	1/2A+2	95·0a′	—	81·9b	—	—	—
	Maturity	127·2a	117·5b	116·4b			
Grain dry matter	1/2A	5·5	—		4·9	2·6	
	1/2A+1	10·4a	8·1b		15·3		8·6
	1/2A+2	25·7a′	—	19·0b′	—	—	—
	Maturity	59·2a	56·6b	54·2b			
Stem plus leaf dry matter	1/2A	43·4	—		6·7	−0·5	
	1·2A+1	50·1a	42·9b		−2·3		−7·9
	1/2A+2	47·8a	—	42·2b	—	—	—
	Maturity†	—	—	—			
Root dry matter	1/2A	14·4	—	—	2·9	1·5	
	1/2A+1	17·3a	15·9a	—	1·4	—	−2·0
	1/2A+2	18·7a	—	13·9b	—	—	—
	Maturity	16·4a	14·6a	13·3a			

* Symbols as in Table 1.

† Not recorded.

However, when the supply of assimilates was reduced by shading during these stages, differences in the final distribution of dry weights appeared. During the first shading period net photosynthesis was only 4·9 g (compared with 15·9 g in control plants) and 52·7% was allocated to the grain (compared with 30·6% in the control). Root and inflorescence weights increased, but stem plus leaf weights decreased (Table 2). Thus loss of current assimilate was partially compensated for by an increase in favour of the grain. Shading for the second week resulted in a net gain in photosynthesis of 2·7 g (compared with 15·8 in control plants) but grain increased 8·6 g, i.e. more than twice the total plant gain. There was a combined loss of 11·3 g from the stem plus leaf and roots.

Discussion

Grain sorghum displayed plasticity in both grain number and grain size when the supply of assimilates was increased between 10 and 15 days after floral initiation, although the effect on grain number was much larger. An increase in the amount of assimilate during either the week prior to or the week after anthesis only affected grain size. Grain number was regulated in such a way that grain size varied only marginally, but individual grains were capable of storing extra material. Goldsworthy and Tayler (1970) found that plants grown at 246,000 plants ha^{-1} until initiation and then thinned to 24,600 plants ha^{-1} had the same number of grains at maturity as plants established at 24,600 plants ha^{-1}. In experiment 1, exposure 1 week after floral initiation increased grain number by 240% in plants originally in the high density population (645,800 plants ha^{-1}) and 83% in those from the medium density population (143,500 plants ha^{-1}), but the treatment increased grain size by only 28·0 and 16·6% respectively. No record was made of the precise stage of development reached by the plants when exposure commenced, but the panicles were *c.* 1·5 cm long and appeared complete with respect to development of their branches.

A description of the morphology and development of the sorghum panicle for cvv. RS671 and Redlan is given by Lommasson *et al.* (1972). Enlargement and elongation of the apex as a whole resulting from the presence of higher order branch primordia occurred between 5 and 10 days, and spikelet primordia were developing 10 days after elongation of the apex. By day 21 development of the spikelet, which is basipetal, had occurred. As might be expected, the exposure treatment reported here did not affect the number of either primary or secondary branches. At maturity, differences in grain numbers were due to more grains on the secondary branches in the lower section of the inflorescence. It is not known whether the exposure treatment increased the number of spikelets which developed or the number which survived.

It would appear unlikely that the difference in grain size between pre- and post-anthesis exposure (1000 grain weights of 33·4 and 30·2 g respectively) was caused by a greater supply of grain-filling assimilates (because of the longer duration of exposure in the former treatment). In both treatments, stem plus leaf weights were significantly greater than those of the controls, which indicated that there was a supply of assimilates in excess of grain requirement. Moreover, Fischer and Wilson (1975) found that the removal of 45% of spikelets at post-anthesis in the same stands (medium population, trial 2) resulted in an excess of assimilates and a 1000 grain weight at maturity of 30·0 g compared with a value here of 30·2 g for the post-anthesis exposure.

The pre-anthesis treatment applied in this work appears to have enlarged the potential storage capacity of individual grains leading to production of larger grains. It is not known to what extent the exposure treatment affected plants other than by increasing photosynthesis. Recent literature suggests that cytokinins are important regulators of kernel size. Manipulations which altered the number of grains in barley also altered the concentration of this hormone in the developing grain (Michael and Seiler-Kelbitch 1972). In sorghum, Fischer and Wilson (1975) reported differences in grain size due to interspikelet competition at anthesis which could not be explained by the supply of assimilates. Exposure of lower leaves to higher radiation could increase the supply of assimilates to the roots, and this may have affected their production of growth regulators.

The reduction in grain yield caused by shading (experiment 2) both at anthesis and during grain development corresponds to the reduction in net photosynthesis caused by the treatments. The experiment was unable to demonstrate changes in the potential grain size. There were probably insufficient assimilates in both the control and treated plants to fill the grains to their maximum potential. However, a similar treatment (shading during early grain development) reduced the number of endosperm cells produced in wheat (Wardlaw 1970) and rice (Wang and Yan 1965), and this significantly reduced the final grain weights because of the restricted capacity for storage.

Nevertheless, the experiment did demonstrate that in the early stages of grain development the supply of assimilates exceeds the demand by the developing grain, but in the later stage almost all of the current assimilate goes to the grain. If the plant is deprived of assimilates during either of these periods, material moves from other plant parts to the grain in order to compensate for the reduction of current assimilate. In the early shading treatment this material was probably produced prior to anthesis. If this is in fact the case it would seem that there is a source of assimilates for grain filling which is not fully utilized by the normal plant. Fischer and Wilson (1971*a*) could account for only 12% of the grain yield from assimilates produced prior to anthesis.

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References

Fischer, R. A., and Kohn, C. D. (1966). *Aust. J. Agric. Res.* **17**, 281–95.
Fischer, K. S., and Wilson, G. L. (1971*a*). *Aust. J. Agric. Res.* **22**, 33–7.
Fischer, K. S., and Wilson, G. L. (1971*b*). *Aust. J. Agric. Res.* **22**, 39–47.
Fischer, K. S., and Wilson, G. L. (1975). *Aust. J. Agric. Res.* **26**, 11–23.
Goldsworthy, P. R., and Tayler, R. S. (1970). *J. Agric. Sci.* **74**, 1–10.
Lommasson, R. C., Lee, K. W., and Eastin, J. D. (1972). The physiology of yield and management of sorghum in relation to genetic improvement. Univ. Nebr., Annu. Rep. No. 5, pp. 32–9.
Michael, G., and Sieler-Kelbitch, H. (1972). *Crop Sci.* **12**, 162–5.
Rawson, H. M., and Evans, L. T. (1970). *Aust. J. Biol. Sci.* **23**, 753–64.
Wallpole, P. R., and Morgan, D. G. (1970). *Ann. Bot.* (*Lond.*) **34**, 309–18.
Wang, T. D., and Yan, R. H. (1965). *Acta Physiol. Sin.* **1**, 9–13.
Wardlaw, I. F. (1970). *Aust. J. Biol. Sci.* **23**, 765–74.
Welbank, P. J., Witts, K. J., and Thorne, G. N. (1968). *Ann. Bot.* (*Lond.*) **32**, 79–95.

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