

# STUDIES OF GRAIN PRODUCTION IN *SORGHUM VULGARE*

## I. THE CONTRIBUTION OF PRE-FLOWERING PHOTOSYNTHESIS TO GRAIN YIELD

By K. S. FISCHER\* and G. L. WILSON\*

[*Manuscript received February 25, 1970*]

### *Abstract*

Sorghum plants were allowed to assimilate known relative amounts of  $^{14}\text{C}$  in the two periods: (i) from full expansion of the third uppermost leaf to anthesis; and (ii) from anthesis to grain maturity. By comparing relative  $^{14}\text{C}$  activity in the mature grain, the relative partitioning of photosynthate between grain production and other uses in the two periods was calculated.

Plant and grain dry weight data from another experiment showed the amounts of net photosynthesis in the two periods.

It was then possible to calculate the maximum amount of the material assimilated in the pre-anthesis period that could have gone to grain production, and thus the percentage of grain material derived from this earlier period. The estimate was 12%.

### I. INTRODUCTION

The role of photosynthate produced before anthesis in the filling of the sorghum grain has not been recorded, but in most cereals it contributes only a small portion of the yield (Thorne 1965). In wheat it provides a maximum of 10% of the grain (Archbold and Mukerjee 1942; Archbold 1945; Stoy 1963; Wardlaw and Porter 1967), in barley 20% of the total ear weight (Archbold 1945; Porter, Pal, and Martin 1950), and in rice a maximum of 30% of grain yield (Takeda and Maruta 1955). In maize it provides negligible amounts (Kiesselbach 1948; Allison and Watson 1966), although it may act as a source if photosynthesis by the leaves is restricted (van Eijnatten 1963).

The present work was done to determine the contribution of pre-anthesis photosynthate to the filling of the grain in sorghum. This cannot be satisfactorily estimated from dry weight changes unless respiratory losses and the redistribution pattern are known. These can be determined by use of photosynthate labelled with  $^{14}\text{C}$ . In the course of other studies of grain filling activities in sorghum, some dry weight data, and methods for using  $^{14}\text{C}$  were made available. By deriving additional information from labelling with  $^{14}\text{C}$  during a pre-anthesis and the whole post-anthesis period, it was possible to estimate the importance of the two periods in grain yield.

### II. MATERIALS AND METHODS

Data were obtained from two populations. Studies with use of  $^{14}\text{CO}_2$  were carried out on plants grown in a glasshouse. Dry weight data were taken from plants in the field.

\* Agriculture Department, University of Queensland, St. Lucia, Qld. 4067.

Consideration was given only to the pre-anthesis period following full expansion of the third uppermost leaf, during which there appears to be minimum production of new structures and thus a likely period of carbohydrate accumulation. The important assumption is therefore made that earlier storage does not contribute to grain material.

(a) *Dry Weight Studies*

Plants were grown in the field, widely spaced in a 1 metre square pattern.

A sample of five plants from each of four blocks was harvested weekly and dried in a forced draught oven at 80°C, and the weights of stem, leaf, and grain recorded.

(b) *Radioactive Carbon Dioxide Studies*

Plants were grown in 5-gal drums, widely spaced in an evaporatively cooled glasshouse. Sufficient seed was sown to permit selection of a single uniform plant per container.

Thirty plants selected for uniformity of size were enclosed individually in Polythene bags and arranged in three rows of 10 plants.

Three treatments were applied, one to each row. These comprised exposure to a set amount of  $^{14}\text{CO}_2$  every second day during one of the following periods:

- (i) from full expansion of the third uppermost leaf to anthesis;
- (ii) from anthesis to grain maturity;
- (iii) for the total of these two periods.

The 10 plants in the row were replicates. Full randomization was impracticable because of the complexity of the air circulating system which would have been required.

The replicate plants in each treatment were connected in parallel and formed, with an air pump, a closed system. A set amount of  $^{14}\text{CO}_2$  was injected into the system, the air monitored with an infrared gas analyser, and the  $\text{CO}_2$  concentration maintained at 300 p.p.m. (v/v) over the treatment period by manually admitting  $^{12}\text{CO}_2$  when required. After each hourly treatment with  $^{14}\text{CO}_2$  the closed circulatory system was opened and connected to an external air supply which not only provided a continuous flow of air of ambient temperature and  $\text{CO}_2$  concentration, but also flushed away from the plants and the glasshouse any respiratory  $^{14}\text{C}$  released in the Polythene enclosures.

*Harvesting and Counting*

Heads were harvested at maturity of grain and dried for 48 hr at 80°C. The grain was separated, weighed, and ground with a mortar and pestle to pass through a 0.2 mm sieve.

Radioactivity was measured by means of a nuclear Chicago Mark I liquid scintillation counter. A 50 mg sample of ground material was suspended in the scintillation medium (2,5-diphenyloxazole in toluene, 5 g/l) by the use of Cab-o-sil, and counted over a period of 10 min, or until 10,000 counts were accumulated. Each sample was recounted once, and two replicates were counted on each sample.

## III. RESULTS

From probable photosynthetic rates, it can be calculated that virtually all of the  $^{14}\text{C}$  applied on any one occasion would be assimilated well within the 1 hr of exposure. Thus plants would take up similar amounts of  $^{14}\text{C}$  during each such application and the relative inputs of  $^{14}\text{C}$  into the plant would be proportional to the number of applications.

TABLE 1

THE GROWTH PERIODS DURING WHICH SORGHUM PLANTS WERE EXPOSED TO  $^{14}\text{C}$ , THE RELATIVE AMOUNTS OF  $^{14}\text{C}$  ASSIMILATED DURING THESE PERIODS, THE SPECIFIC ACTIVITY OF THE GRAIN AT MATURITY, AND THE RELATIVE  $^{14}\text{C}$  CONTENT OF THE GRAIN

Period of Exposure to $^{14}\text{C}$	Relative Inputs of $^{14}\text{C}$	Specific Activity of grain (c.p.m./50 mg)	Relative $^{14}\text{C}$ Content of Grain
Full expansion of third uppermost leaf to anthesis (12 days)	6	2,400	1
Anthesis to grain maturity (36 days)	18	27,600	11.5
Full expansion of third uppermost leaf to grain maturity (48 days)	24	31,100	

The relative amounts of  $^{14}\text{C}$  assimilated by the plants in the growth periods are shown in Table 1, together with the specific activity of the grain at maturity. The close agreement of the  $^{14}\text{C}$  counts for plants treated during the whole period with the sum of counts for plants treated in the separate periods suggests that the failure to randomize replicate plants had no harmful consequences.

TABLE 2

PLANT AND GRAIN DRY MATTER WEIGHTS FOR SORGHUM AT THREE GROWTH STAGES

Weeks from Anthesis	Plant		Grain
	Dry Weight (g)	Increment (g)	Dry Weight (g)
-2	45		
0 (anthesis)	94	49	0
+5 (grain maturity)	200	106	103

The ratio of  $^{14}\text{C}$  inputs in the two periods was 3 : 1 (18 to six doses). However, the ratio of  $^{14}\text{C}$  counts in the grain was 11.5 : 1. Thus the partitioning of photosynthate into the grain material was 3.8 times as great in the post-anthesis period.

Dry weights during a comparable period in the field experiment are shown in Table 2. Note that in the  $^{14}\text{C}$  experiment the commencement of the pre-anthesis

treatment was anthesis minus 12 days. In the field experiment, the closest observation was for anthesis minus 14 days. One cannot expect different distribution patterns between these two similar periods.

Remembering the assumption that material from an earlier period than those shown does not go to grain, the maximum amount of material available from the pre-anthesis period is 49 g. The highest proportion of this which could have been used is 0.26 (the partitioning ratio of 1 : 3.8), viz. 12.9 g, or 12% of the grain weight.

#### IV. DISCUSSION

Conventional methods of assessing the importance of assimilate produced prior to anthesis have depended on changes in dry weight or in carbohydrate concentration, and cannot differentiate between changes due to translocation of material to the grain and those resulting from respiration. The use of  $^{14}\text{C}$  would appear to avoid such difficulties of interpretation. If equipment were available for maintaining set levels of  $^{14}\text{CO}_2$  in the atmosphere during each occasion of exposure, then photosynthate would be uniformly labelled with  $^{14}\text{C}$ , and comparisons of  $^{14}\text{C}$  activity in the grain would allow a direct comparison of contributions from photosynthesis in the two periods (or indeed, in any shorter subdivisions of development). The simple arrangement used here was developed for other work, for which it was adequate, but led to the need for the use of dry weight data from another experiment. Rather extensive experimental work has shown sufficiently uniform plant dry weight and grain growth patterns to justify the essential conclusion, viz. that the pre-anthesis contribution is small — 12% of the total grain.

Although the conditions of growth prior to anthesis do not greatly influence the yield of grain through assimilate supply, they may affect the grain yield potential. In Australian wheats, Davidson (1965) found that yield was correlated with leaf area index before ear emergence. He and other workers (Womack and Thurman 1962) suggested that conditions of growth prior to anthesis influence the yield not only by the number of grains but also by determining the ultimate magnitude of the organs involved in the storage of grain dry matter. Moreover the supply of assimilate in the immediate period after anthesis, during which there is rapid grain growth in the histological sense rather than in terms of dry matter accumulation, may influence the ultimate storage capacity of the grain (Bingham 1967).

#### V. ACKNOWLEDGMENTS

This work was carried out during the tenure by one of us (K.S.F.) of an Australian Wool Board Scholarship. Dr. J. N. Mansbridge, Department of Biochemistry, University of Queensland, made available his equipment for carbon-14 counting.

#### VI. REFERENCES

- ALLISON, J. C. S., and WATSON, D. J. (1966).—The production and distribution of dry matter in maize after flowering. *Ann. Bot.* **30**, 365–81.
- ARCHBOLD, H. K. (1945).—Some factors concerned in the process of starch storage in the barley grain. *Nature, Lond.* **156**, 70–3.

- ARCHBOLD, H. K., and MUKERJEE, B. N. (1942).—Physiological studies in plant nutrition. XII. Carbohydrate changes in the several organs of the barley plant during growth, with special reference to the development and ripening of the ear. *Ann. Bot.* **6**, 1–42.
- BINGHAM, J. (1967).—Investigations on the physiology of yield in winter wheat, by comparison of varieties and by artificial variations in grain number per ear. *J. agric. Sci., Camb.* **68**, 411–22.
- DAVIDSON, J. L. (1965).—Some effects of leaf area control on the yield of wheat. *Aust. J. agric. Res.* **16**, 721–31.
- VAN EIJNATTEN, C. L. M. (1963).—A study of the development of two varieties of maize at Ibadan, Nigeria. *J. agric. Sci., Camb.* **61**, 65–72.
- KIESSELBACH, T. A. (1948).—Endosperm type as a physiological factor in corn yields. *J. Am. Soc. Agron.* **40**, 216–36.
- PORTER, H. K., PAL, N., and MARTIN, R. V. (1950).—Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. *Ann. Bot.* **14**, 55–63.
- STOY, V. (1963).—The translocation of <sup>14</sup>C-labelled photosynthetic products from the leaf to the ear in wheat. *Physiologia Pl.* **16**, 851–66.
- TAKEDA, T., and MARUTA, H. (1955).—Studies on carbon dioxide in crop plants. 4. Roles played by the various parts of the photosynthetic organs of rice plant in producing grain during the ripening period. *Proc. Crop Sci. Soc. Japan* **24**, 181–4.
- THORNE, G. N. (1965).—Physiological aspects of grain yield in cereals. In “The Growth of Cereals and Grasses”. (Ed. F. L. Milthorpe and J. D. Ivins.) Proc. Univ. Nottingham 12th Easter School in Agric. Sci., p. 88. (Butterworths Sci. Publs: London.)
- WARDLAW, I. F., and PORTER, H. K. (1967).—The redistribution of stem sugars in wheat during grain development. *Aust. J. biol. Sci.* **20**, 309–18.
- WOMACK, D., and THURMAN, R. L. (1962).—Effect of leaf removal on the grain yield of wheat and oats. *Crop Sci.* **2**, 423–6.