FIXATION OF $^{14}CO_2$ BY FLOWERING AND NON-FLOWERING GLUMES OF THE WHEAT EAR, AND THE PATTERN OF TRANSPORT OF LABEL TO INDIVIDUAL GRAINS

By P. M. BREMNER* and H. M. RAWSON†

[Manuscript received 20 April 1972]

Abstract

This paper explores the possible role of photosynthesis by individual glumes in influencing the growth rates of individual grains of the wheat ear. Specifically we determined: (1) the photosynthetic capacities of individual glumes (i.e. non-flowering glumes, lemmas, and paleas) of an awned wheat cultivar; (2) the pattern of translocation of ^{14}C-labelled assimilate from individual glumes to individual grains; and (3) the time course of translocation of label from glumes and flag leaf to the grain.

The lemmas were photosynthetically the most active of the glumes; over the greater part of grain filling they accounted for some 15% of whole-plant photosynthesis; non-flowering glumes and paleas accounted for 5–6% and 2–5% respectively. Towards maturity the lemmas decreased in importance in relation to other glumes, particularly paleas. The photosynthetic efficiency (as measured by ^{14}C fixed per unit weight) of glumes was less than half of that of flag and penultimate leaves in the early stages, but declined more slowly with time. The nearest grain was the preferred but not exclusive sink for the ^{14}C-labelled assimilate from any glume. Movement of label was always towards the apex and on the same side of the spikelet as the glume, *if* there was a grain towards the apex on that side; if not, movement across the spikelet, still towards the apex, occurred. This caused an accumulation of label in the distal grains of spikelets. Labelled assimilate from the glumes was detected in the grains within 10 min of the commencement of exposure and the rate of increase in activity was maximal in about 1 hr; corresponding times for flag leaf label were 1 and 2–3 hr.

The distribution of glume assimilate between the grains provided no explanation for differences in their growth rates; there was evidence that the grains themselves exerted a controlling influence.

I. INTRODUCTION

A feature of individual grains within the mature wheat ear is their variation in size. Relative size is largely a function of position, and differences between grains in either or both rate and duration of growth are involved (Rawson and Evans 1970; Rawson and Ruwali 1972; Bremner 1972). Differences in growth rates between grains may be caused by their different capacities for growth (Bremner 1972) or by a pattern of assimilate distribution more favourable to some than others; or by an interaction between the two. The distribution of assimilate between grains might well be influenced by the photosynthetic capacities of the glumes, particularly if subtended grains are the exclusive or preferred sink for the assimilate of their associated glumes.

* Division of Plant Industry, CSIRO, P.O. Box 1600, Canberra City, A.C.T. 2601.
† Division of Land Research, CSIRO, P.O. Box 1666, Canberra City, A.C.T. 2601.

Although photosynthesis by the ear as a whole has been extensively studied, particularly in relation to its contribution to grain filling (see Puckridge 1969), little is known of the importance of the non-flowering glumes, lemmas, and paleas (collectively termed "glumes", and we shall adhere to this usage except where the reference is specific) or of the distribution of their assimilate to the various grains The work reported here was undertaken primarily (1) to estimate the photosynthetic capacities of individual glumes in relation to that of the whole plant, using total fixation of $^{14}CO_2$ and ^{14}C activity per unit weight as measures of photosynthesis; and (2) to determine the destinations of label from the glumes. In addition, we (3) compared the time course of translocation of label to the grains from the glumes with that from the flag leaf.

II. Materials and Methods

(*a*) *Cultural Conditions*

Plants of WW 15, an awned Mexican semi-dwarf wheat cultivar, were grown in winter in a glasshouse of the Canberra phytotron in pots (20 cm deep, 7·5 cm diameter; one plant per pot) containing a mixture of perlite and vermiculite. Nutrient solution was supplied each morning and water each afternoon. The temperature was 21°C from 8.30 a.m. until 4.30 p.m., and 16°C for the remaining 16 hr. Natural light was supplemented with low-intensity incandescent lamps to give a 16-hr day. Tillers were removed periodically, and the experimental material selected from the resulting population of single-culm plants. At anthesis, all leaves except the flag and penultimate ones were removed. At the appropriate times, plants were transferred to an artificially lit cabinet (3200 f.c. at ear level from fluorescent and incandescent lamps) at 21°C, for ^{14}C labelling as described below.

(*b*) *^{14}C Labelling*

A closed-circuit system was used for labelling; it consisted of a CO_2 generator, a peristaltic pump, a Perspex plant chamber, and a gas flow G.M. tube connected to a ratemeter and recorder. $^{14}CO_2$ was generated by the addition of 50% HCl to $Na_2{}^{14}CO_3$ (52 mCi/mmole); Table 1 provides the details of exposure. ^{14}C activity of the various plant parts was determined by liquid scintillation counting after wet digestion (Shimshi 1969).

Table 1

Details of ^{14}C-labelling in the various experiments

Expt.	Part labelled	No. labelled	Amount of ^{14}C per part (μCi)	Chamber details	Exposure period (min)	^{14}C uptake (%)
1	Whole plants	4	30·5	20 by 20 by 80 cm 1 air change/2 min	6	40–50
2	Glumes	6	20·3	2 by 15·5 by 30 cm 6 air changes/min	20	10
3*a*	Ears	15	16·3	2, 2 by 15·5 by 30 cm, connected in parallel; 6 air changes/min	5	75
3*b*	Flag leaves	24	6·3	2, 2 by 15·5 by 30 cm, connected in parallel; 6 air changes/min	5	90

(*c*) ^{14}C *Fixation by the Glumes, Stem, and Leaves* (*Expt. 1*)

Labelling was done at 5, 15, and 25 days after anthesis (Table 1). After exposure, plants were immediately divided into ears, flag leaf laminae, penultimate leaf laminae, and stem (with leaf sheaths). The ears were instantly frozen in liquid nitrogen, then freeze-dried and spikelets *1*, *3*, *6*, *9*, *12*, and *15* (counting from the apex) dissected into non-flowering glumes *a* and *b*, lemmas *a*, *b*, and *c*, paleas *a*, *b*, and *c*, grains *a*, *b*, and *c*, and remaining florets, which were nearly always sterile (see Fig. 1). Individual parts were weighed and their activity determined. The remainder of the ear and other plant parts were oven-dried, ground, and two 10-mg subsamples taken from each for determination of activity.

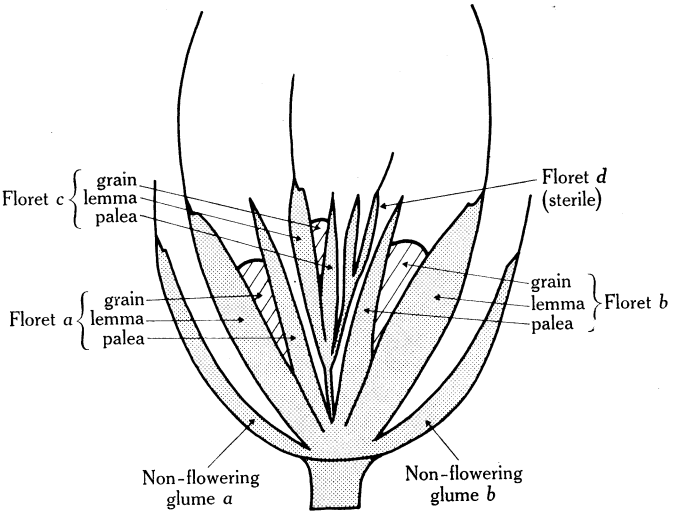

Fig. 1.—Diagrammatic representation of the spikelet.

(*d*) *Translocation of* ^{14}C *from Individual Glumes to Individual Grains* (*Expt. 2*)

At 5, 15, and 25 days after anthesis, either non-flowering glume *a* or *b*, or lemma *a*, *b*, or *c* of spikelet *9* from the apex was exposed to $^{14}CO_2$ (Table 1). The exposure was achieved by enveloping the de-awned ear in aluminium foil with the appropriate glume protruding through a V-shaped slot. Six ears fed simultaneously comprised six replicates. After exposure, the plants were kept at 20°C for 24 hr in the dark to prevent external movement of ^{14}C by reassimilation of respired $^{14}CO_2$. Spikelets *7*, *8*, *9*, *10*, and *11* were then dissected into their component parts, and in two replicates these were autoradiographed. The autoradiographs showed no movement of ^{14}C out of spikelet *9* (cf. Buttrose and May 1959), so in the remaining four replicates activity was determined only in this spikelet.

(*e*) *Time Courses of Translocation of* ^{14}C *from the Glumes and Flag Leaf to the Grain* (*Expts. 3a and 3b*)

(i) *Translocation of Ear Assimilate* (*Expt. 3a*).—Seven days after anthesis, 15 ears were exposed to $^{14}CO_2$ (Table 1), and sequential harvests of individual spikelets made at 10, 20, 30, 40, 50, 60, 70, 80, 100, and 140 min, and 3, 6, 12, and 24 hr from the commencement of exposure. The harvesting procedure was as follows: the plants were divided into five groups of three plants, and a group provided the material for three successive harvests; on each occasion, either spikelet *7*, *8*, or *9* (a different one from each plant) was taken, and after the third harvest the group was discarded and another used. The activities of grains *a*, *b*, and *c* were determined.

(ii) *Translocation of Flag Leaf Assimilate* (*Expt. 3b*).—Equal areas of the flag leaves of 24 plants were exposed to ^{14}C (Table 1) at 7 days after anthesis. Of these, 12 were chosen at

random for a series of sequential spikelet harvests as above, except that those at 3, 6, and 24 hr were omitted. Of the remaining 12 plants, six were subjected to an ear-shading treatment to eliminate ear photosynthesis and increase the demands made on shoot assimilate by the developing grain. Spikelet harvests, as outlined above, were made from these and six control plants at 3, 6, 24, and 48 hr, and the values for control plants were fitted into the sequential harvesting pattern of the first 12 plants, to complete the series. In addition, whole plants were harvested at 48 hr and the activities of their various parts determined.

III. Results

(*a*) $^{14}CO_2$ *Fixation by the Glumes* (*Expt. 1*)

Total fixation declined sharply between 15 and 25 days after anthesis (Table 2). Generally the importance of the leaves in relation to that of the remainder decreased with time. The large difference in total activity between the flag and penultimate leaves was due wholly to a difference in their size; their specific activities were always the same (41,000, 42,000, 20,000 counts per minute per milligram at 5, 15, and 25 days respectively).

Table 2

Total activity per plant and activity of the various plant parts (Expt. 1)

Activity of plant parts is expressed as a percentage of total plant activity; measurement after exposure for 5 min to $^{14}CO_2$ and immediate freezing. Results given are means of four replicates

Days from anthesis	Activity (% of total)				Total activity per plant (millions of counts/min)
	Ear	Flag leaf	Penultimate leaf	Stem and leaf sheath	
5	21·5±0·72	40·6±2·34	22·7±2·10	15·2±0·58	17·8±0·73
15	21·8±1·60	38·1±1·57	21·4±2·01	18·8±2·64	19·7±0·72
25	24·4±2·95	34·7±2·67	19·7±2·15	21·1±1·03	11·4±0·69

In Table 3, we present (*a*) mean values for glumes, lemmas, and paleas in three grain spikelets, for comparison of florets within spikelets, and (*b*) means of glumes, lemmas, and paleas of florets *a* and *b* for all spikelets, this to provide a basis for comparing spikelets according to their position. Values for 5 days after anthesis are absent due to a procedural mishap, and we have omitted those for the grains, which were only lightly labelled.

At 15 days, the specific activity of the glumes was usually less than half that of the leaves, but at 25 days it was rather more than half. The exception (data not presented) was the few distal sterile florets we assayed: their specific activity was 25% greater than that of the leaves—perhaps because of their relative immaturity. This apart, the lemmas had the greatest specific activity at 15 days and the paleas at 25 days; the paleas were, in fact, the only parts which increased in total and specific activity with time.

Total activity was less in floret *c* than others, because it was smaller. Total and specific activities decreased towards the bottom of the ear on both occasions, and at the top on the second occasion, towards maturity Had values for floret *c* been included in Table 3(*b*), the well-defined profile of total activity shown by Rawson and Evans (1970) would have been observed, with spikelets *6*, *9*, *12*, and *15* predominating.

TABLE 3

ACTIVITY AND SPECIFIC ACTIVITY OF THE VARIOUS PARTS OF THE FLORAL STRUCTURE (EXPT. 1)

Activity expressed as thousands of counts per minute and specific activity as thousands of counts per minute per milligram. Activities measured after exposure for 5 min to $^{14}CO_2$ and immediate freezing. Values given are means of four replicates

Plant part	15 days after anthesis		25 days after anthesis	
	Activity	Specific activity	Activity	Specific activity
(*a*) Means of spikelets 6, 9, 12, and 15				
Non-flowering glumes	51·7	12·2	47·0	8·6
Floret *a*				
Lemma	60·3	15·5	43·0	10·8
Palea	11·3	12·4	15·8	17·1
Floret *b*				
Lemma	63·9	16·9	45·3	10·0
Palea	6·9	7·4	11·8	11·8
Floret *c*				
Lemma	39·7	17·8	30·5	10·9
Palea	5·7	6·8	10·6	14·7
(*b*) Means of non-flowering glumes, lemmas, and paleas of florets *a* and *b*				
Spikelet 1	41·5	20·4	23·6	14·4
3	39·6	14·3	34·6	19·3
6	40·8	14·5	36·5	14·4
9	48·8	14·7	33·9	11·1
12	41·2	11·8	33·6	11·2
15	26·0	10·4	24·2	9·8

In order to put glume photosynthesis into better perspective in relation to both the ear and the whole plant, we have proceeded as follows:

(1) assumed a 17-spikelet ear in which the uppermost three and lowermost two spikelets contained two grains each, and the remainder three (in fact a fair description of the material we worked with); and

(2) assumed that appropriate values for spikelets in which activity was not determined are those of the nearest recorded spikelet towards the apex—i.e. the values obtained for spikelet *1* were also used for *2*, those for *3* were used for *4* and *5*, and so on.

This gives the following estimates of photosynthesis in the non-flowering glumes, lemmas, and paleas:

Days from anthesis	Plant part	Photosynthesis in plant part as % of photosynthesis in:	
		Ear	Whole plant
15	Non-flowering glumes	21·3	4·6
	Lemmas	68·7	15·0
	Paleas	10·0	2·2
25	Non-flowering glumes	24·7	6·0
	Lemmas	55·5	13·5
	Paleas	19·8	4·8

(*b*) *Translocation of Label from Glumes to Grains (Expt. 2)*

In presenting the results of this study we have averaged the three occasions—5, 15, and 25 days after anthesis—as differences between them were small.

On average, 63% of the activity remaining in the spikelet 24 hr after labelling was located in parts other than that originally labelled. The proportion exported tended to decrease with increasing proximity of the labelled structure to the spikelet apex, perhaps because of the smaller number of sinks available. The pattern of export is readily apparent from Table 4. First, with one exception (lemma *b*/grain *c*), the nearest

TABLE 4

DISTRIBUTION OF ^{14}C FIXED BY INDIVIDUAL NON-FLOWERING GLUMES AND LEMMAS OF SPIKELET 9, 24 HR (IN THE DARK) AFTER FIXATION (EXPT. 2)

Values given are the means of four replicates for each of days 5, 15, and 25 days after anthesis (i.e. with the exception noted below, each value is the mean of 12 determinations); those in bold type represent parts originally labelled and the grains they supply. L, lemmas; P, paleas; G, grains

Part originally labelled	% total spikelet activity in: Non-flowering glumes		Floret *a*			Floret *b*			Floret *c*			Florets *d* and *e* (sterile)
	a	*b*	L	P	G	L	P	G	L	P	G	
Glume *a*	**29·6**	2·0	2·9	2·5	**30·3**	3·5	3·8	3·9	3·1	3·7	**11·2**	4·1
Glume *b*	1·1	**36·4**	1·0	1·2	1·9	4·4	1·7	**35·1**	1·9	1·3	**12·9**	1·2
Lemma *a*	1·1	0·8	**35·0**	1·2	**36·4**	1·3	0·4	5·0	1·5	0·6	**13·2**	3·5
Lemma *b**	1·1	4·6	1·2	0·8	2·8	**40·9**	1·4	**14·7**	3·5	1·3	**27·4**	2·4
Lemma c	2·1	1·7	2·4	2·1	3·5	2·3	1·4	4·3	**43·5**	3·4	**24·3**	8·5

* Values here are for 5 and 15 days only; at 25 days, 95% of the activity remained in glume *b* in each replicate.

grain is the most potent sink for any structure (*a* structure → *a* grain). Second, the next most potent sink is the next grain towards the apex on the same side of the spikelet (*a* structure → *a* and *c* grains, but not grain *b*); or if there is no grain towards the apex on the same side, the next grain on the opposite side (*b* structure → *b* and *c* grains). Apparently only in this latter event does assimilate cross the spikelet. Third, movement in the direction base to apex is the rule; movement down the spikelet was never observed. In consequence of these restrictions, in a three-grain spikelet grains *a* and *b* have only three sources of assimilate within the ear (associated non-flowering glume, subtending lemma, and palea; we are assuming here that assimilate from the palea would be distributed on the same basis as that from the lemma). On the other hand, grain *c* has eight—both non-flowering glumes and all the lemmas and paleas. This leads to an accumulation of ear assimilate in the distal grains of spikelets (cf. Evans *et al.* 1972).

In connection with the anomaly of lemma *b*/grain *c*, these data are based on 5 and 15 days after anthesis only: at 25 days, 95% of the ^{14}C fixed by lemma *b* remained within it 24 hr later in all four replicates Presumably we damaged the vascular connections. This raises the question whether the apparent greater affinity of lemma *b* with grain *c* than with *b* at 5 and 15 days after anthesis is an artefact, a result of partial damage during shade application. We have some evidence that this is so and will return to this point.

(c) *Time Course of Translocation of Label from the Glumes and Flag Leaf to the Ear (Expts. 3a and 3b)*

The logarithm of the increase in grain activity with time after first exposure of either ears or flag leaves to $^{14}CO_2$ is well described by the modified Mischerlich curves of Figure 2:

$$y = ct + a\{1 - \exp[k(t - t_0)]\},$$

where y is estimated log ^{14}C activity, t, t_0, time, and a, c, and k constants. In both cases, the equation accounted for more than 95% of the change with time.

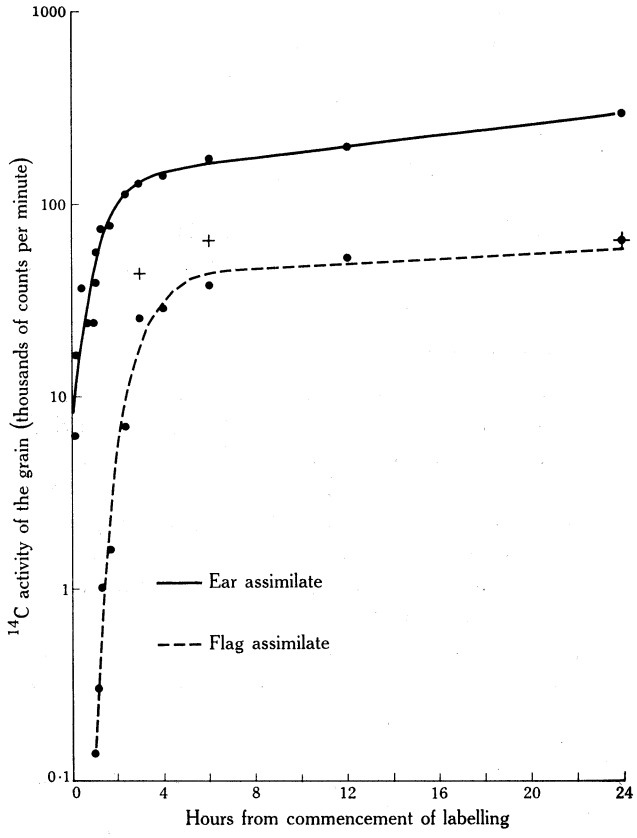

Fig. 2.—Change with time in the ^{14}C activity of the grain; means of grains *a*, *b*, and *c* (expt. 3*a*). + Values obtained when ears were shaded (expt. 3*b*).

The picture is one of diverging curves displaced in time. However, it is probably proper to place more emphasis on the displacement than on the divergence. The ear labelling resulted in more $^{14}CO_2$ fixation than the flag leaf labelling (about 13 and 8 million counts per minute per plant respectively) and this might well account for the divergence.

Appreciable activity was found in the grains 10 min after first exposure of the ears to $^{14}CO_2$: the level was much higher than could be accounted for by grain photosynthesis, which, in experiment 1, we found to be negligible. The rate of increase in label

in the grains was maximal in about 1 hr, and began to decline in 2 hr, when the grains contained some 40% of the activity present at 24 hr. Slow movement continued up to and obviously beyond 24 hr. Label from the flag was not detected until 1 hr after feeding, and then only at a low level of activity. Maximum rate of entry of ^{14}C into the grain—which was about 25% that of glume label—occurred at 2–3 hr. At 3 hr, the grains contained 30% of the activity present at 24 hr. A slow increase was observed between 24 and 48 hr (cf. Carr and Wardlaw 1965)—the 24 hr value was 80% of that at 48 hr; the 48-hr point, although not shown in Figure 2, was included in the curve fitting.

Movement of label from the flag leaf was apparently faster when the ears were shaded (crosses at 3, 6, and 24 hr in Fig. 2). And ear shading had the following effect on distribution of ^{14}C after 48 hr:

	% of total counts/min in		
	Ear	Flag leaf	Remainder
Control plants	32·8	53·7	13·5
Ears shaded	41·2	53·4	5·4

Thus, in control plants, current assimilation was in excess of the needs of grain filling and the surplus was used or stored in the stems (cf. Asana, Parvatikar, and Saxena 1969; Bremner 1972).

IV. Discussion

Our values for the contributions to total photosynthesis of the various plant parts (Table 2) are in reasonable agreement with the consensus of other work (see Puckridge 1969). We would draw attention to the importance of the stem (including leaf sheaths) and ear, and the increase in this with time; their combined contribution was just over a third of the total at 5 days after anthesis, and just under half at 25 days. It is possible that the relative importance of the stem and ears would be even greater under many field conditions, where the normal occurrence of high temperatures and drought can cause rapid leaf senescence. The increase in importance of the stems and ears was associated with a lesser decline in photosynthetic efficiency (as measured by specific activity, weight basis) than occurred in the leaves, which, however, always had the higher specific activity. The lesser decline in glume photosynthesis was probably due, at least in part, to an improving light environment as the lemmas and the paleas were pushed apart by the developing grains. The paleas, in particular, benefit from this, because the lemmas largely envelope them in the early stages; between 15 and 25 days after anthesis, their carbon-fixing capacity increased by over 60% (Table 3) and their contribution to ear photosynthesis doubled.

Our results show that the distribution between grains of assimilate fixed in the ear (Table 4) is not a causal agent in their differing growth rates. The most rapidly growing grains are the second ones (*b*) of central spikelets, but these were not especially favoured as regards the supply of ear assimilate, having only three sources, similar in carbon-fixing capacity to the three supplying grain *a*, which grows more slowly. By contrast, the distal grain (*c* here) had available to it eight sources of ear assimilate, yet it grows still more slowly. Indeed we may infer from experiment 3*b* and a number of others done in similar conditions (e.g. Rawson and Evans 1970; Bremner 1972) that grain growth was not

limited by the availability of assimilate from any source, but by the capacity of the grains to utilize assimilate.

In an attempt to quantify the distribution effects we observed, we have in Table 5 used the results of experiments 1 and 2 to compute values for the relative distribution of glume assimilate between grains in spikelet *9* at 15 days after anthesis. These we compare with the values obtained in experiment 3*a* at 24 hr after ears were exposed to $^{14}CO_2$. Both the predicted and observed values show the expected accumulation in

TABLE 5

PREDICTED (FROM EXPTS. 1 AND 2)* AND OBSERVED (FROM EXPT. 3*a*) RELATIVE ACTIVITIES OF GRAINS *a*, *b*, AND *c* OF SPIKELET *9*, 24 HR AFTER LABELLING

Plant part	Relative photosynthesis	Amount of relative photosynthesis in grains		
		a	*b*	*c*
Glume *a*	30	9	—	4
Glume *b*	30	—	13	9
Lemma *a*	100	36	—	13
Lemma *b*	95	—	14	26
Lemma *c*	64	—	—	16
Total		45	27	68
Relative total		100	60	151
Observed relative values (expt. 3*a*)		100	120	170

* These activities were calculated as follows: the relative photosynthesis (lemma *a* = 100) of each main source of assimilate in spikelet *9* at 15 days after anthesis (established in expt. 1) was multiplied by the appropriate factor representing the fraction exported to each grain (expt. 2; Table 4); the contributions to each grain were then summed and converted to the scale grain *a* = 100.

the distal grain, but there is a large discrepancy in the two values for grain *b*; since the data of experiment 3*a* represent a continued trend of previous harvests, we must accept them as being nearer the truth. This confirms the suspicion that manipulation of lemma *b* during shading may have damaged its vascular connections with the remainder of the spikelet.

The accumulation of assimilate in the distal grain perhaps indicates an unimportant role for assimilate supply as a factor limiting grain set (cf. Rawson and Evans 1970).

It follows that the fast growth rate of grain *b* must be associated with a greater utilization of shoot assimilate—much the larger source for grain filling—by this grain. The 24-hr harvest of the shaded ear treatment of experiment 3*b* (in which flag leaves were fed) gave relative activities for *a*, *b*, and *c* of 100, 117 and 87 respectively. Rawson and Evans' (1970) labelling studies and Bremner's (1972) grain growth studies also show that grain *b* gets more shoot assimilate than others.

Finally, our results (Table 4) perhaps indicate more discrete vascular connections between sources within the ear and the grains than the anatomical studies of Zee and O'Brien (1971) suggest. For example, their Figure 1 shows vascular strands linking glume *a* glume *b* and lemma *a* with a plexus of vascular tissue in the rachis, with which the vascular elements of the rachis also merge, and from which vascular strands pass to the

grains. Their diagram—which they admit to be a simplification—would not lead one to suppose that the distribution of assimilate from glume *a* or lemma *a* would be confined to one side of the spikelet; or that material from glume *b* should not fairly readily find its way into grain *a*.

V. Acknowledgments

We are grateful to Mesdames Marilynne Ashby and Rita Berra for technical assistance, and to Mr. W. Muller for curve fitting.

VI. References

Asana, R. D., Parvatikar, S. R., and Saxena, N. P. (1969).—Studies in the physiological analysis of yield. IX. Effect of light intensity on the development of the wheat grain. *Physiologia Pl.* **22**, 915–24.

Bremner, P. M. (1972).—The accumulation of dry matter and nitrogen by grains in different positions of the wheat ear as influenced by shading and defoliation. *Aust. J. biol. Sci.* **25**, 657–68.

Buttrose, M. S., and May, L. H. (1959).—Physiology of cereal grain. I. The source of carbon for the developing barley kernel. *Aust. J. biol. Sci.* **12**, 40–52.

Carr, D. J., and Wardlaw, I. F. (1965).—The supply of photosynthetic assimilates to the grain from the flag leaf and ear of wheat. *Aust. J. biol. Sci.* **18**, 711–19.

Evans, L. T., Bingham, J., Jackson, P., and Sutherland, J. (1972).—Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. *Ann. appl. Biol.* **70**, 67–76.

Puckridge, D. W. (1969).—Photosynthesis of wheat under field conditions. II. Effect of defoliation on the carbon dioxide uptake of the community. *Aust. J. agric. Res.* **20**, 623–34.

Rawson, H. M., and Evans, L. T. (1970).—The pattern of grain growth within the ear of wheat. *Aust. J. biol. Sci.* **23**, 753–64.

Rawson, H. M., and Ruwali, K. N. (1972).—Ear branching as a means of increasing grain uniformity in wheat. *Aust. J. agric. Res.* **23**, 551–9.

Shimshi, D. (1969).—A rapid field method for measuring photosynthesis with labelled carbon dioxide. *J. exp. Bot.* **20**, 381–401.

Zee, S. Y., and O'Brien, T. P. (1971).—Vascular transfer cells in the wheat spikelet. *Aust. J. biol. Sci.* **24**, 35–49.