PHOTOSYNTHESIS AND RESPIRATION BY THE FLAG LEAF AND COMPONENTS OF THE EAR DURING GRAIN DEVELOPMENT IN WHEAT

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[Manuscript received August 22, 1969]

Summary

Rates of photosynthesis and dark respiration of the ears and flag leaves of three varieties of wheat grown at 21°C under a constant light intensity of 3200 f.c. were measured by infrared gas analysis twice weekly throughout the period of grain development. Measurements were made on both the intact ears and the separated grains and ear structures, in air and in a mixture of nitrogen plus 320 p.p.m. CO₂. Dry weights of the grains, ears, and main stems were also determined.

Photosynthesis by the grains was near maximal at the light intensity measured inside the glumes, and nearly balanced the loss of CO₂ by dark respiration, until the grains ripened. Grain photosynthesis accounted for 33–42% of gross ear photosynthesis. Ear photosynthesis, which was much higher in awned varieties, contributed up to 76% to total grain requirements during early growth, this proportion falling to a minimum of about 26% in Sonora (awned) and 15% in Gabo (unawned) during the period of most rapid grain growth, before rising again as grain growth slowed. Over the whole period of grain development the contribution to grain requirements by ear photosynthesis was 33% in Sonora and 20% in Gabo. The rate of photosynthesis by the flag leaf blades varied apparently in response to changes in the demand for assimilates. In Sonora, requirements by the ear during the period of most rapid grain growth were equivalent to 131 and 43 mg CO₂ per ear per day for growth and respiration of the grain respectively, while net photosynthesis at that time by the ear, flag leaf blade, and stem plus sheaths was 50, 126, and 42 mg CO₂ per day respectively. Photosynthesis by the ear and flag leaf blade alone could meet the needs of the ear at all times, and grain growth did not appear to be limited by the supply of assimilate.

I. INTRODUCTION

The carbohydrate in the grain of temperate cereals is largely derived from photosynthesis during the period of grain development. Carbohydrates stored in the stem prior to anthesis may contribute 5–10% of final grain weight (Wardlaw and Porter 1967), or rather more in plants under stress (Asana and Joseph 1964; Yu et al. 1964), but the major source of assimilate is current photosynthesis by the flag leaf, stem, and ear. The proportion of grain needs met by ear photosynthesis has been the subject of many investigations, reviewed by Thorne (1966). The proportion depends on the variety used, particularly on the presence or absence of awns, since ear photosynthesis tends to be much higher when awns are well developed (e.g. Apel

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1966). It also depends on the environmental conditions (e.g. Buttrose and May 1965), and on the method used to estimate the contribution by the ear (e.g. Kriedemann 1966).

Three methods have been used: shading of the ears or the rest of the plant, interkernel competition, and gas analysis. Shading techniques have been used by many investigators since Boonstra (1929) introduced them, but are subject to a number of serious errors. They can cause early maturation of the ears, and by modifying the environment of the ears can change the rates of translocation to the grain and of grain growth. To some extent these problems can be overcome by more elaborate techniques (Kriedemann 1966) but there remains the problem that translocation of assimilates from the rest of the plant may increase to compensate for the loss of ear photosynthesis, leading to an underestimation of the contribution by the ear.

The interkernel competition method introduced by Buttrose and May (1959) was thought to eliminate the possibility of a compensatory increase in the contribution from the rest of the plant, which was shaded or defoliated; certainly, it yielded much higher estimates of the contribution by the ear. However, Lupton and Ali (1966) found that the estimate obtained depended very much on how many spikelets were left in the ear, more spikelets, up to a point, apparently increasing mobilization to the ear.

Gabrielsen (1942) first used gas analysis to measure ear photosynthesis in wheat. Porter, Pal, and Martin (1950) measured gas exchange by barley ears throughout grain development, and Thorne (1966) concluded that this method probably yielded the most reliable estimates of the contribution by the ear. Enclosure modifies the environment of the ear to some extent, but this effect can be minimized under controlled conditions. Previous estimates by gas analysis of the contribution of the ear (Porter, Pal, and Martin 1950; Thorne 1963, 1965) have not measured grain respiration separately, nor would it be easy to relate this to the ear balance in the field where temperature is continually changing. However, Carr and Wardlaw (1965) have suggested that grain respiration should not be debited against ear photosynthesis in estimating the proportion of grain needs met by ear photosynthesis.

In the present experiments, therefore, we have followed grain growth in plants held under constant conditions of light and temperature and have measured, at frequent intervals, respiration and photosynthesis of both intact ears and the separated grains and ear structures, under conditions similar to those in which they were developing. Balance sheets of the contribution by ear photosynthesis to the total requirements for grain growth at all stages of ear development in several varieties, both awned and non-awned, were then drawn up.

II. MATERIALS AND METHODS

The wheat varieties used were Gabo, which has only very short awns, an awned form of Gabo developed by Dr. A. T. Pugsley, and two awned Mexican wheats, Sonora 64 and Pitie 62. The plants of Sonora and awned Gabo were grown singly in pots 9 cm in diameter, those of Pitie and awnless Gabo as three per pot of 13 cm diameter. In the first experiment, with Pitie, the plants were grown from germination at 21°C in light of 3200 f.c. intensity from fluorescent and incandescent lamps (8·7 × 10³ µW/cm² of visible radiation) for 12 hr each day. In later experiments, with the other varieties, the plants were grown until ear emergence under 16 hr photoperiods in a glasshouse at 21/16°C. They were then moved to an artificially lit cabinet at 21°C,
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and exposed to light of 3200 f.c. intensity at ear height for 16 hr each day, except for one experiment with Sonora in which the lighting was continuous.

Photosynthesis at 3200 f.c. and dark respiration of the intact ears and of the flag leaves were measured twice weekly, about 1 hr after the beginning of the daily light period, by means of two Grubb Parsons infrared gas analysers, at 21°C and atmospheric CO₂ level. Calibration of the gas analysers was by means of a set of Wösthoff gas mixing pumps, not by the pressure method (Legg and Parkinson 1968). The cross-sectional dimensions of the Perspex assimilation chambers were 15 by 2 cm for flag leaves and 10 by 22 cm for ears, and the flow rate 4 litres/min. With Sonora, three replicates each of three flag leaves or main stem ears were used on each occasion; with Gabo and Pitic only two replicates of three or four plants were used.

When the measurements with intact ears were completed, all grains were removed and placed on moist filter paper, and photosynthesis and respiration of the separated grains and ear structures measured immediately. Removal of grains could be accomplished without obvious damage to the ears early and late in grain filling, but with Sonora and Pitic during the middle of the grain-filling period, grains were difficult to remove and some glumes (both sterile and flowering) were damaged or did not return to the positions they occupied before grain removal. On completion of the gas analysis each day, leaf areas were measured and the grains, ear structures, and main stems were oven-dried and weighed.

Photosynthesis and dark respiration of main stems, both with and without the leaf sheaths, were measured on plants of Sonora. During the measurements the stems, still attached to the plants, were enclosed for their whole length in Perspex tubes and surrounded by other plants to simulate their usual light environment.

Several small photocells were used in attempts to measure the light intensity to which grains are exposed inside the glumes. The most satisfactory was a Mullard germanium photodiode, OAP12, with a sensitive area of 1 mm² and overall dimensions comparable to those of a grain. Grains were removed from various positions in the ear, and a circular hole just large enough to admit the photocell was cut through the base of the sterile glume and lemma. The glumes retained their usual positions and no shading of the ear occurred.

The magnitude of photorespiration was estimated from the difference between the rates of net photosynthesis in air and in a mixture of nitrogen with 320 p.p.m. by volume of CO₂. We have assumed that light has no effect on the turnover of the tricarboxylic acid cycle, as shown by Marsh, Galmiche, and Gibbs (1965), and Anderson and Fuller (1967) and that the enhancement of net photosynthesis in the absence of oxygen is largely due to the inhibition of photorespiration, as suggested by Jolliffe and Tregunna (1968). However, the presence of oxygen may also inhibit cyclic electron flow in photosynthesis (Heber 1969). Photorespiration of the grains could not be measured in CO₂-free air because of their marked reassimilation of respired CO₂ (Kriedemann 1966).

III. Results

Changes with time in photosynthesis and respiration by the ear and its components in Sonora are shown in Figure 1. The detailed data for Gabo and Pitic are not presented, but points of difference from Sonora will be noted.

Dark respiration by the intact ear reached a maximum of about 2 mg CO₂/ear/hr 12 days after anthesis, and then declined. In Gabo and Pitic the maximum rates of respiration were lower, about 1.6 and 1.3 mg CO₂/ear/hr respectively, but these were maintained for almost 2 weeks. Dark respiration by the ear structure in all varieties was relatively constant throughout grain development until the ears senesced. For the grains alone, on the other hand, dark respiration followed a course very similar to that of the intact ear.

Early in grain development, with all varieties, the rates of dark respiration of the separated grains plus ear structure were close to those for the intact ears, but from 8 to 30 days after anthesis the respiration rate of the separate components
greatly exceeded that of the intact ears. Carr and Wardlaw (1965) did not encounter this difficulty, and in their material grain respiration represented only about 60% of ear respiration, whereas in Sonora and Gabo it was commonly 80–90%. The high rates of grain respiration measured in these varieties could be sustained for several hours in darkness, and the cause of the higher totals for the separated components is not clear. If the respiration of the grains in situ is taken as the difference between that of the intact ears and that of the structures, it was about 50–57% of ear respiration during rapid grain filling.

Net photosynthesis by the intact ears of all varieties fell slowly over the first 3 weeks from anthesis and then rapidly as the ears matured. Initial rates in the awned ears of Sonora and Pitic were about 3 mg CO₂/ear/hr, whereas they were 1·7 mg CO₂/ear/hr in the awnless Gabo. With awned Gabo the rates were slightly less than those of Sonora ears at the same stage. Net photosynthesis by the ear structures in air was similar to that by the intact ears, the awned structures having a rate about twice that of the awnless Gabo structures. For example, the rates for ear structures 15 days after anthesis were 2·33, 2·09, 1·91, and 1·16 mg CO₂/ear/hr in Sonora, Pitic, awned Gabo, and awnless Gabo respectively. In Sonora and Gabo net photosynthesis by the grains in air was not found at any stage. Nevertheless,
photosynthesis by the grains almost balanced grain respiration until the late stages of grain development, and in all varieties gross photosynthesis (i.e. net photosynthesis + dark respiration) by the grains followed a time course very similar to that of grain respiration. In Pitic there was net photosynthesis by the grains of at least 0.25 mg CO₂/ear/hr until 9 days after anthesis.

Before considering the relation between net photosynthesis of intact ears on the one hand and of grain plus ear structure on the other, we must assess the likely light environment of the grains in the intact ear. This was measured in Sonora and Gabo ears 8 and 19 days after anthesis, and was found to be the equivalent of about 700 f.c. when the ear was at 3200 f.c. The response to light intensity by grain photosynthesis in Sonora and Gabo is shown in Figure 2. The light response curve for the grains, which was similar in the two varieties, differed from that of their leaves in approaching saturation at a much lower intensity. As a result, the photosynthetic rate at 700 f.c., the measured intensity inside the glumes, was 86–94% of the maximum rate.

![Figure 2](image)

Returning to Figure 1 we see that net photosynthesis by the separated grains plus ear structures of Sonora was not greatly different from that of the intact ears between 8 and 12 days after anthesis, after which it tended to be lower. Similar results were obtained with the other varieties. Since the measured rates of grain photosynthesis may have been slightly higher than those of grains in situ, a rate for the components which was higher than that of the intact ears could have been expected. That it was lower may have been due to (1) damage at grain removal; (2) reduced glume photosynthesis in the absence of respiratory CO₂ from the grains—largely discounted above; (3) reduced glume photosynthesis in the absence of the major sink for its products—probably measured too soon after separation of the parts for this to be expressed; and (4) higher respiration rates in the separated components, as noted above. For all varieties, this last effect was sufficient to account for the lower net photosynthesis of the grains plus ear structures compared with the intact ears on most occasions.

The rate of net photosynthesis in the absence of oxygen was approximately doubled for both intact ears and ear structures at all stages of development, in all varieties. The increase in net grain photosynthesis, on the other hand, was only
s slight, averaging 0·16 mg CO₂/ear/hr for Sonora and a similar amount in the other varieties. It is assumed that this represents the upper limit to the additional respiration that may occur in grains in the light.

Changes in the rate of net photosynthesis by the flag leaves of Sonora and awnless Gabo are shown in Figure 3(c), and are discussed later. In both varieties, and also in Pitic, the rate fell from anthesis, then rose to a peak value 15–16 days after anthesis, before falling again, at first slowly and then rapidly as the leaves senesced.

![Diagram](https://via.placeholder.com/150)

**Fig. 3.**—Changes during grain development of Sonora (□), awnless Gabo (○), and awned Gabo (△) wheat in: (a) the estimated contribution by ear photosynthesis to the total requirements of the grain; (b) the requirements of the grain for assimilates, in addition to those supplied by the ear, expressed in relation to net photosynthesis by the flag leaf blade; (c) the rate of net photosynthesis by the flag leaf blades. The vertical line indicates the value of the square root of error mean square; the error terms for harvest times were homogeneous.

Net photosynthesis by the stem and leaf sheaths, in a light environment matching that of the growing plants, was substantial. In Sonora 12–15 days after anthesis, for example, net photosynthesis by each ear, flag leaf blade, and stem plus leaf sheaths was 49·7, 126·2, and 41·7 mg CO₂/day respectively.

The course of grain growth and changes in the dry weight of the main stem and ear structure of Sonora are given in Figure 4. High rates of grain growth were achieved, the highest (12–15 days after anthesis) being 97·7 and 81·7 mg/ear/day in awnless Gabo and Sonora respectively, and 74·0 mg/ear/day in Pitic which was exposed to only 12 hr light each day. These rates are higher than those usually obtained under favourable conditions in the field, although still higher rates have been recorded by Asana and Bagga (1966), Asana and Joseph (1964), and Birecka and Dakic-Wlodkowska (1966). The ear structures and stems fell in weight during the period of fastest grain growth, and rose by about 130 mg each during maturation.
Plants of Sonora were also grown under continuous light of 3200 f.c. intensity in an attempt to maximize the rate of grain growth. However, although spikelet number per ear was the same (17.5) in the two lots of plants, far fewer grains per ear were set in continuous light than in 16-hr days (29.5, cf. 47.6). Initial grain growth was faster in continuous light, but the maximum rate (68.1 mg/ear/day) was lower, and grain growth ceased sooner. However, the maximum growth rate per grain was somewhat higher in continuous light (2.05, cf. 1.78 mg/grain/day), as was the final weight per grain (43.7, cf. 35.9 mg).

IV. DISCUSSION

From the results presented above for Sonora, and from the data obtained with Pitic and the awned and awnless forms of Gabo, balance sheets of the total requirements of the grain and of the potential contributions by photosynthesis of the ear and the flag leaf were drawn up for each 3- or 4-day interval during grain development. Daily grain requirements per ear were estimated as the sum of:

1. the increase in grain dry weight, converted to the equivalent amount of CO₂ by the usual factor of 1.6 (Nomoto and Saeki 1969),
2. dark respiration of the grains, assuming a constant rate throughout the day, and
3. additional photorespiration of the grains, from the difference in rates of net photosynthesis in air and in the absence of oxygen.

Item (2) may have been overestimated since dark respiration of the separated ears and grains tended to be higher than that of intact ears. The major requirement of the grain at all stages was carbohydrate for storage rather than for respiration. During the period of most rapid grain growth storage accounted for 78–82% of the total grain needs, but at the beginning and end of grain growth it was only 65–66%, respiration losses representing about half as much as storage. The additional photorespiration represented only 1–3% of the total grain needs.
The probable contribution to grain needs by ear photosynthesis was estimated by subtracting the dark respiration of the ear structure over 24 hr from the gross photosynthesis by the intact ear. Respiration loss by the ear accounted for about 28–31% of gross ear photosynthesis in Sonora, and a higher proportion (36–50%) in the awnless Gabo ears. The ear contribution could also be estimated from the rate of gross photosynthesis in the absence of oxygen by subtracting terms for both dark respiration of the ear structure and the additional photorespiration indicated by the increase in net photosynthesis in the absence of oxygen. However, because the absolute increases in net photosynthesis of the intact ear and of the ear structure were of similar magnitude, this had little effect on the estimated ear contribution. It is shown elsewhere (Rawson and Evans 1970) that most of the CO₂ assimilated by the ear is found in the grain at ripeness.

The proportion of grain needs which could be contributed by ear photosynthesis at various stages in Sonora and Gabo is indicated in Figure 3(a). It was higher throughout grain development in the awned Sonora than in the awnless Gabo. It was also consistently higher in the awned Pitic than in Gabo. It was lower in Pitic than in Sonora mainly because of the reduced ear photosynthesis and greater respiration losses of the ear structure in 12-hr days compared with the 16-hr days in which Sonora was examined. In awned Gabo the proportion was somewhat higher than in Sonora. Since grain and spikelet numbers were very similar in the two forms of Gabo, the difference between them presumably reflects the substantial contribution by awns to ear photosynthesis.

In all varieties the proportion of grain needs contributed by ear photosynthesis was highest during early grain development, fell to a minimum during the peak period of grain growth, rose again as grain growth slowed, and finally fell as the ear dried off. For the whole period of grain development, the estimated contribution to total grain requirements by ear photosynthesis was 32-8% in Sonora, 28.3% in Pitic, and 20.4% in Gabo.

Gross photosynthesis by the grains was a substantial proportion of that by the intact ears, 34% in Sonora, 31% in awned Gabo, and 42% in unawned Gabo ears 12 days after anthesis. These proportions can be compared with Gabrielsen’s (1942) finding that 25% of ear chlorophyll was found in the grains at a similar stage. Both Gabrielsen and Kriedemann (1966) have suggested that the immature wheat grain is incapable of net photosynthesis in air, but in at least one variety, Pitic, there was net photosynthesis by the grains until 9 days after anthesis. This finding is in agreement with the work by Carr and Wardlaw (1965) and Polimbetova and Kamonov (1967) who found that excised grains could assimilate externally supplied ¹⁴CO₂ in the light. If the grains reassimilate most of their respired CO₂, as the close similarity of net photosynthesis by intact ears and by ear structures indicates, glume and awn photosynthesis will not take place in an atmosphere highly enriched in CO₂ derived from grain respiration, as has been suggested.

The net requirement by the ears of Sonora and Gabo for photosynthesize from elsewhere in the plant, expressed in terms of net photosynthesis by the flag leaf blade, is given in Figure 3(b). This rises as the rate of grain growth rises (Fig. 4), to reach a peak about 15 days after anthesis, but it is evident that in Sonora and awned Gabo, as also in Pitic, photosynthesis by the ear and the flag leaf blade alone
was almost sufficient to meet all ear requirements. Photosynthesis by the stems, leaf sheaths, and lower leaf blades provided ample spare capacity, and under these conditions grain yields were unlikely to have been limited by the supply of photosynthetic. In awnless Gabo, with less ear photosynthesis, assimilate from the rest of the plant, or from stored reserves, was required during rapid grain growth.

Changes in the rate of flag leaf photosynthesis [Fig. 3(c)] are of interest in relation to the changes in demand by the ear. In Sonora the rate fell throughout the first 12 days after anthesis, but rose somewhat at the period of peak demand. In Gabo, there was a similar initial fall followed by a more marked rise, perhaps reflecting the greater demand in this variety [Fig. 3(b)]. Pronounced and reversible changes in photosynthetic rate of flag leaves of wheat under constant conditions, in response to changes in demand, have been established by King, Wardlaw, and Evans (1967), and it seems likely that the changes in Figure 3(c) reflect changing demands for photosynthesis by the ear. Similar changes in the rate of flag leaf photosynthesis are evident in the results of Birecka and Dakic-Wlodkowska (1966) and Lupton (1968), the rise in flag leaf photosynthesis 12 days after anthesis in the Polish varieties occurring in spite of a pronounced fall in the chlorophyll content of the leaves. Rawson and Hofstra (1969) also found a rise in the photosynthetic rate of the leaf below the flag leaf 10 days after anthesis in Sunset wheat.

In Gabo, the peak photosynthetic rate in the flag leaves appeared to be reached a day or two after the peak demand. Jenner (1968) found that detached ears of Gabo wheat held in darkness produced almost as much starch in 24 hr as did ears provided with sucrose, implying that reserves of carbohydrate in the ear are sufficient to maintain grain starch synthesis for at least a day. Carbohydrate in reserve or in transit in the stem and leaf sheaths and blades could further increase the lag between peak grain requirements and photosynthetic response by the leaves. The timing of such rises in leaf photosynthesis in intact wheat plants suggests that they are likely to be a response to increased demand for assimilates rather than to reduced competition for cytokinins from the roots, an alternative suggested by the work of Wareing, Khalifa, and Treharne (1968).

V. Acknowledgments

We thank Dr. I. F. Wardlaw for discussion of the results, and the Wheat Industry Research Council for support.

VI. References


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