PHYSIOLOGY OF CEREAL GRAIN

III. PHOTOSYNTHESIS IN THE WHEAT EAR DURING GRAIN DEVELOPMENT

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Summary

Cereal ears are important as photosynthetic organs in contributing to grain yield and, since ear tissues are the last to yellow, their relative activity may increase during grain development. Glume surface exposed to light has been observed to increase as grains swell, and thus actual photosynthetic capacity of ears may also increase. The contribution of ear photosynthesis to grain growth has now been measured for wheat (*Triticum vulgare* cv. Gabo) over intervals between anthesis and maturity, by a technique involving stem shading and grain removal. In the first 3 weeks after anthesis, when grains grew slowly, florets contributed about $0 \cdot 2$ mg per day to the enclosed grain, representing 50% of grain dry weight increment. During the latter half of grain growth, when grain weight increased more rapidly, florets contributed more than $0 \cdot 6$ mg per day per grain, representing 60% of the weight increment. The technique used is discussed and it is shown that certain precautions must be taken if reliable measurements are to be obtained.

I. INTRODUCTION

Photosynthetic activity of wheat and barley ears is well established as an important contributor to the pool of carbohydrate materials drawn on by developing grains (Asana and Mani 1950; Porter, Pal, and Martin 1950). Quantitative estimates show that ears are capable of contributing up to 50% of wheat grain weight (Asana and Mani 1950), and up to 76% of barley grain weight (Frey-Wyssling and Buttrose 1959). The other important contributors to the general pool are leaf sheaths and peduncle (Archbold 1945).

Asana, Saini, and Ray (1958) observed that yellowing of wheat tissues took place in the order leaves, stem, and ear. The xeromorphic nature of glumes and awns also suggests that ears maintain activity longer than leaf sheaths and stems during general senescence or when plants undergo stresses induced by drought. From these considerations it could be postulated that ears become progressively more important in relation to other organs as contributors to the developing grain. The following observation indicates that actual photosynthesis of ears could increase between anthesis and maturity. During the first two to three weeks of grain development of Gabo wheat, florets are narrow with glumes folded acutely, and the compressed spikelets adpressed to the rachis. As kernels swell with growth the enclosing glumes become noticeably and increasingly distended, and with time spikelets and florets are forced away from a vertical position, and even from each other. It follows that during grain development, of this variety at least, an increasing

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photosynthetic surface becomes exposed to incident light. The present study of the contributory capacity of ear photosynthesis was carried out to determine whether ears retained their activity until maturity and whether this activity increased with time.

Measurements of the contribution of ear photosynthesis to grain growth require a technique in which ear tissues photosynthesize under normal environmental conditions. Such a technique was developed earlier in this Laboratory (Buttrose and May 1959), but it requires floret photosynthesis to be independent of size of the enclosed kernel. It was thus of particular interest to employ this technique and study further its reliability.

TABLE 1

AVERAGE DRY WEIGHTS (MG) PER GRAIN

Time from anthesis (A) to maturity (M) was 60 days; other times in days after anthesis

Treatment No.	Treatment Time	Harvest Time	Control (20 grains)	Shaded (20 grains)	Shaded (8 grains)
1	A	15	5·5	3·2	3·6
2	A	20	8·3	4·6	5·1
3	A	25	10·3	5·3	6·0
4	A	30	14·7	6·7	7·3
5	A	35	16·7	7·5	8·5
6	A	M	42·9	10·3	12·2
7	15	M	41·9	18·8	24·0
8	25	M	42·5	24·7	30·4
9	35	M	42·1	33·9	35·9

II. METHOD

Contributions to grain yield from ear photosynthesis were measured as described in an earlier paper (Buttrose and May 1959). Briefly the technique involves inducing a carbohydrate shortage by stem defoliation and shading, so that grains on an ear are competing for the limited amount of stored material still ascending into the ear. Where grain number is reduced, each grain will grow larger than grains on unreduced ears. If x is the weight contributed to each grain by its associated glumes, w_1 the grain weight on heads with n_1 grains, and w_2 the grain weight on heads with n_2 grains, then

$$n_1(w_1-x) = n_2(w_2-x),$$

as the total material entering the head is independent of grain number under conditions of carbohydrate shortage.

To study ear contribution (x) over the course of grain development, the defoliation and stem-shading treatments were imposed either at anthesis and harvests made at intervals thereafter, or at intervals after anthesis and the grain harvested at maturity. In all there were nine treatment times, as set out in Table 1.

Wheat (*Triticum vulgare* cv. Gabo) seeds were planted on April 6, 1961, in 6-in. earthenware pots containing compost, 10 seeds per pot, and the seedlings were thinned to six per pot at 2 weeks. Tillers were removed as they appeared, so that at maturity each pot contained six mother shoots. Twenty pots were allotted at random to each of the nine treatment times, there being in all 180 pots. At anthesis each ear was tagged, and at the appropriate time three treatments were imposed on each pot, one treatment per pair of randomly selected ears, as follows:

    (*a*) spikelets reduced to 10 per ear (five each side), the basal pair and excessive pairs at the apical end being cut off;

    (*b*) as for (*a*), but stem defoliated and shaded with a triple thickness of brown paper;

    (*c*) spikelets reduced to four, such that the second and fourth lowest on each side of the ear remained, and the stem defoliated and shaded.

Only the two basal florets were left on each spikelet, those in excess being cut off. In all cases only eight grains, corresponding to those developing in treatment (*c*), were harvested, oven dried, and weighed.

III. Results

Grain dry weights are presented in Table 1. More than half the dry weight increase took place after 35 days, but no harvests were made between this time and maturity. Maximum dry weight was attained at 60 days, judging by the loss of green in the ear, and by the form of the growth curve constructed from the available data. From the results it is seen that stem defoliation and shading greatly reduced grain weight in all cases, and that the reduction was invariably greatest where 20 grains (10 spikelets) rather than 8 (4 spikelets) developed. A statistical analysis of the data showed that, considering each harvest separately, these two populations with shaded stems in treatments 1–4 were not significantly different. By considering the populations of the treatments together, however, they were found to be significantly different at the 1% level. It therefore appeared possible to employ the equation

$$20(w_1 - x) = 8(w_2 - x)$$

to assess ear contribution, w representing weight gains between treatment and harvest times. However, a private communication had been received, indicating that the operation of spikelet removal had a consistent deleterious effect on growth of the residual grains. These results are now published (Lupton 1961). To test whether this was so under the experimental conditions employed here, a concurrent experiment was carried out as follows. Wheat was grown in 36 pots in exactly the same manner as for the main experiment. At anthesis the following three treatments were imposed: (1) control; (2) the basal pair of spikelets and the requisite number from the apical end were cut off to leave eight spikelets (four per side); (3) in addition to spikelets removed in the second treatment, the upper three pairs remaining were cut off to leave one pair. Florets in excess of the basal

two in each spikelet were cut off. There were three harvests, at 15 and 30 days after anthesis and at maturity, 12 pots being allotted to each harvest. Only four grains were harvested from each ear, corresponding to those of treatment (3), oven dried, and weighed. Results are summarized in Table 2. There was no significant difference between treatments at any harvest, nor between populations derived from all three harvests, and it is concluded that in the present experiments ear surgery had no effect on grain growth. Lupton's data also indicate that varieties may vary in response to this apparent injury, and possibly Gabo is a fortunate choice.

TABLE 2

DRY WEIGHTS (MG) PER GRAIN FROM WHEAT EARS CARRYING DIFFERING NUMBERS OF GRAINS

Harvest Time	Control (36 grains)	16 Grains	4 Grains
15 days	4·9	4·6	4·6
30 days	13·3	13·8	12·8
Maturity	41·8	42·8	41·0

From these considerations it appeared that the equation presented above was valid as a basis for the calculation of the following:

(i) average daily contribution by spikelet photosynthesis to grain weight;

(ii) average daily contribution from non-ear sources to grain weight;

(iii) percentage contribution by spikelet photosynthesis to grain weight from treatment to harvest.

TABLE 3

AVERAGE DAILY INCREASES IN CONTROL GRAIN DRY WEIGHT, AND AMOUNTS AND PROPORTIONS CONTRIBUTED BY EAR AND NON-EAR ORGANS, OVER VARIOUS PERIODS

Treatment numbers as in Table 1

Treatment No.	1	2	3	4	5	6	7	8	9
Daily weight increase (mg)	0·37	0·42	0·41	0·49	0·47	0·71	0·81	0·92	1·02
Ear contribution (mg)	0·20	0·21	0·19	0·21	0·19	0·15	0·22	0·30	0·64
Non-ear contribution (mg)	0·17	0·21	0·22	0·28	0·28	0·56	0·59	0·62	0·38
Percentage ear contribution	54	50	47	42	41	21	27	33	63

The values obtained are set out in Table 3. Daily weight increments are in all cases the average gain over the period from treatment to harvest. The results indicate, as would be expected from a normal growth curve, that average daily increments in grain weight are low (approx. 0·4 mg) for a considerable period at the beginning but rise markedly (to at least 1 mg) after 35 days. The calculated contribution made by the ear to this increment remains constant at about 0·2 mg per day, where the treatment (stem defoliation and shading) was

commenced at anthesis, while contributions by non-ear organs increase in actual amount and thus relative importance. When stem defoliation and shading treatments were imposed progressively later during the course of grain development, calcuated daily ear contribution to grain growth rose progressively. For instance, ear contribution estimates never rose higher than $0\cdot21$ mg per day, when treatment began at anthesis, but when treatment began at 35 days the value rose to $0\cdot64$ mg per day. This suggested that early treatment affected subsequent activity of the ear. In an effort to explain this effect, a study was made of the appearance of ears on control and treated plants during grain development. Until about 20 days after anthesis kernels grew relatively little in size and florets retained their narrow shape and proximity to the rachis. Thereafter kernel volume increased more rapidly, and by the 30th day was such that the glumes became noticeably distended. With further swelling of the grain ear morphology underwent changes as described in Section I. However, when stems were defoliated and shaded at anthesis, kernel growth was so curtailed that there was hardly any displacement of glumes during development, and thus little change in the photosynthetic area exposed to light. No measurement was attempted of the actual increase in area exposed for photosynthesis on control plants, but the increase was judged to be two- to threefold.

Following these observations, the data in Table 3 were interpreted as follows. At anthesis the photosynthetic organs on a floret were capable of contributing $0\cdot2$ mg to a grain per day. If stem shading was imposed at anthesis or not later than 15 days (Table 3, treatment 7), grain growth was so curtailed that floret shape and surface area remained unchanged until maturity, and ear contribution remained constant. If plants received treatment first at 25 days after anthesis, kernels were able to swell to such an extent that a slightly greater glume area was exposed. This change resulted in a contribution over the period to maturity of $0\cdot3$ mg per day per kernel. Finally, if plants were treated first at 35 days after anthesis, kernels were able to expand still further exposing additional photosynthetic surface, such that each floret could contribute at an average rate of $0\cdot64$ mg per day to its kernel.

IV. Discussion

The foregoing results indicate that ear photosynthesis can contribute at a high rate to grains in the latter half of their growth, when vegetative organs could be senescent. Furthermore they indicate that the ear of Gabo wheat increases during kernel growth in its capacity to contribute products of photosynthesis to the kernel. It is most reasonable to infer that the increase is due to the observed rise in photosynthetic surface area, rather than to a more intense photosynthetic activity, or to a diversion of photosynthetic products from some other sink into kernels (see Buttrose and May 1959). If floret photosynthesis can in fact depend on kernel size in wheat, it will be recognized that the extent of dependence would vary widely with differing ear types. Factors such as row number in barley, awnedness, and spacing of spikelets on the rachis would all have influence.

Considering the total contribution of ear photosynthesis to grain yield, the technique as originally proposed (Buttrose and May 1959) gives a value of 21%

from the present data (Table 3, treatment 6). This is based on a daily floret con- tribution of about $0 \cdot 2$ mg, which would, had no other measurements been made, have been assumed to remain constant from anthesis to maturity. Actually this low contribution rate was operative only early, when it represented some 50% of grain dry weight increment, while towards maturity it rose to $0 \cdot 64$ mg per day (Table 3, treatment 9) which represented some 60%. The inference is that about one-half of grain dry weight on control plants could have been contributed by ears. The technique as originally proposed can therefore give underestimations of total ear contributory capacity, and it is clear that it should receive further consideration.

Previously this technique combining stem shading and floret removal to measure ear contribution has yielded a value of 76% for a two-rowed barley (Frey- Wyssling and Buttrose 1959) and up to 50% for six wheat varieties (Lupton 1961). Compared with the value of 21% (Table 3, treatment 6) these values are high, and it is concluded that the technique may underestimate ear capacity only in cer- tain cases. An example of a faulty measure is found, on the one hand, in the present experiment. On the other hand it is conceivable that with certain vari- eties no additional photosynthetic area is exposed as kernels swell, so that stem shading, while reducing kernel growth, would not result in reduced average floret photosynthesis. Further it is conceivable that if only a mild stem shading had been imposed on Gabo plants, such that final grain weight (and thus swelling) was only slightly reduced, florets would have increased in photosynthetic activity similarly to those of control plants. In both these cases it is proposed that measures of maximum ear contribution would be reliable.

Further investigations will be necessary to determine how extensively floret photosynthesis and grain swelling are related. However, existing data may be examined to learn whether this relationship could have been operative in the experiments concerned. From Lupton's (1961) data a value for percentage ear contribution was calculated as:

$$\frac{\text{weight from ear photosynthesis}}{\text{average of grain weights from 10- and 30-grain ears, stems unshaded}} \times 100.$$

The degree to which kernels were capable of swelling was calculated as:

$$\frac{\text{average grain weight of 10- and 30-grain ears, stems shaded}}{\text{average grain weight of 10- and 30-grain ears, stems unshaded}} \times 100.$$

The two sets of values so obtained, together with corresponding values for Prior barley (Frey-Wyssling and Buttrose 1959) and for Gabo wheat of the present experiment, are compared in Figure 1. There is a general tendency for high measures of ear contribution to be associated with a high degree of grain swelling. The values from Lupton's data may be considered together, and are found to be significantly correlated. It should be stressed that six different varieties are compared here, but it is clear that there is a common influence which controls the relationship examined. This influence might normally have been taken as inherent activity of ear photosynthesis, for, if non-ear organs are eliminated, grain size should depend on ear activity. However, the alternative possibility,

that ear photosynthetic activity depends on grain size, must now be advanced. Only further experiments can determine which alternative applies, but it may be remarked that swelling-induced alterations to ear morphology would have to differ very considerably between the six varieties if the second alternative was to apply. It is felt that the relationship derived from Lupton's data reflects inherent photosynthetic differences, so that relative activities of ears as measured are meaningful.

The influence of grain size on ear photosynthesis of Gabo, postulated above (see Section III), may be illustrated by considering the regression line together with the dotted lines in Figure 1. Thus until grains could grow to some 50% of control grain weight (considered at maturity) a steady low (21%) value for ear contribution was measured. If, for instance, stem shading was reduced so that
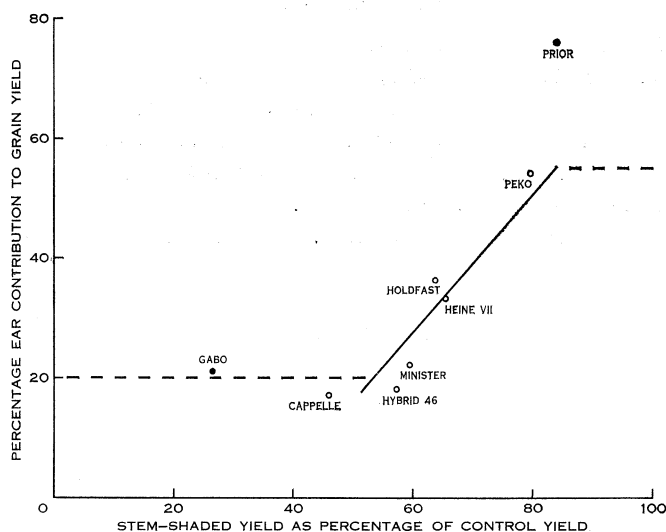

Fig. 1.—Relationship between calculated ear contribution to grain yield and extent to which grains on stem-shaded plants could grow, for Prior barley and seven wheat varieties. The regression line is fitted to values (open circles) obtained from Lupton's data. The regression coefficient b ($= 1 \cdot 15$) is significant at $P < 0 \cdot 05$. Dotted lines explained in text.

grains could grow larger, increasing photosynthetic area would result in increased measures of ear contribution, until values of 50–60% were obtained. As it is considered unlikely that ear photosynthesis could account for much more of the grain dry weight, it is postulated that with further reduction in shading no increase in the measure would be expected. From these considerations it appears that maximum measures would be obtained when kernels could grow to about 75% of control kernel weight.

It will be apparent that the measurement of ear photosynthesis as a factor in grain yield is still beset with difficulties. Ear-shading techniques measure non-ear contributory capacity rather than ear capacity. Direct measurements of photosynthesis, or the use of isotope methods, involve the enclosure of organs in

artificial environments in which their behaviour may be abnormal. The competition technique used above is still recommended as the most reliable method for measuring maximum ear capacity. For those who compare different varieties, as plant breeders may wish to do, it must be realized that ear photosynthesis may possibly increase during the period anthesis to maturity. To allow this to proceed on both treated and control plants, it is suggested that shading be only severe enough to give approximately a 20–30% reduction in grain weight.

V. ACKNOWLEDGMENT

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