PHYSIOLOGY OF CEREAL GRAIN

I. THE SOURCE OF CARBON FOR THE DEVELOPING BARLEY KERNEL *

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Summary

Organic substrate for development of the barley kernel rises mainly from current assimilation of carbon dioxide. This paper describes a study of the relative importance of the several potential sources of substrate using ear shading, carbon-14 as tracer, and kernel-competition techniques. The application of the ear-shading technique to awnless, single-awned, and triple-awned varieties of barley led to significant reductions in yield of 9, 23, and 18 per cent. respectively, although the differences between the reductions themselves were not significant. Carbon-14 was supplied either to attached ears as ^14CO$_2$ or to detached ears through the peduncle as ^14C-sucrose. Whichever source of carbon-14 was supplied, radioactivity was incorporated in the kernel from anthesis through to maturity, and its subsequent distribution in the kernel was similar. Translocation following ^14CO$_2$ feeding was also examined, and it is concluded that little movement occurred except at an early stage of ear development. Competition between kernels was not evident, although it was induced when carbohydrate supply was artificially depleted. A scheme to accommodate the results is discussed, and a new method for calculating the maximum contribution of photosynthesis within the ear to kernel yield is presented.

I. INTRODUCTION

Archbold (1945) reviewed the endeavours of researchers over a half-century to define and evaluate the several sources of the carbohydrates that form the substrate for kernel development in the cereal ear. The conclusions reached were that material for endosperm development arose mainly from current carbon dioxide fixation in the upper leaf sheaths, the stem, and the ear itself, and that the contribution from sugar previously stored in the stem was small. More recently Porter, Pal, and Martin (1950) made the first direct measurement of assimilation and respiration of barley ears attached to the plant, and their results confirmed earlier estimates, involving shading techniques, that ear assimilation contributes about 30 per cent. of the final ear dry weight. For wheat, the ear's contribution has been calculated from ear-shading experiments to fall within the range 11-46 per cent. depending on season and variety (Asana and Mani 1950, 1955).

A feature of research in this field has been the wide range of the estimates of contributions from the several sources. This variability may stem not only from differences of environment and variety, but also from differences of technique. It has been generally recognized that the shading technique is open to serious

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criticism. Watson and Norman (1939) called attention to the alterations of temperature, rate of respiration, and rate of senescence which might be induced by shading. Again, Archbold and Datta (1944) concluded that secondary effects of shading were also at play affecting kernel yield by mechanisms other than the prevention of photosynthesis. One further criticism of the ear-shading technique, or any technique which removes one source of substrate, may be raised. This is to question the assumption, implicit in these techniques, that the various plant organs always contribute the same amount of carbon substrate to kernel development. It could equally be assumed that in the normal plant these organs do not contribute a maximum and that when one contributor is removed contributions from the remainder compensate at least in part for the deficiency.

In this work three approaches have been made to study further the role of photosynthesis in the ear, especially with a view to circumventing the difficulties inherent in shading techniques. Firstly, it is argued that ear shading in different varieties, similar except for their ear’s photosynthetic surface area, should lead to reductions in yield in proportion to this area, providing that the only effect of ear shading is to prevent photosynthesis. This argument is supported by the observation of Vervelde (1953) that carbon dioxide assimilation in ears of barley, wheat, and rye respectively contributes to kernel development in this order of importance, which follows the order of the relative photosynthetic area of their ears. Secondly, radioactive carbon is used to examine, without shading, the ear’s contribution to kernel yield and to follow the subsequent fate of the ear assimilate. Little previous work of this nature has been reported although some measurements of translocation of assimilate from leaves to the ears have been made (Fujiwara and Suzuki 1957; Kravecova 1957). These studies have indicated that only the uppermost leaves contribute to any marked extent. Thirdly, the proposition that plant organs may not normally contribute to their full potential is examined through a study of interkernel competition. Appleman and Eaton (1921) have noted that a change in kernel number per ear in maize had little effect on seed weight, and Donald (1954) found only relatively small effects in rye. However, information on this aspect of cereal physiology is scarce.

II. MATERIALS AND METHODS

(a) Barley Varieties

In the ear-shading experiment three six-row varieties were selected for uniformity of vegetative characters and growing period; their major difference lay in the extent of awn development. One variety was awnless (*Hordeum vulgare* var. Arlington Awnless), the second had one awn per floret (*H. vulgare* var. Mars), and the third had three awns per floret (*H. vulgare* var. Long-awned Outer Glume). Assimilatory activities of normal ears from these varieties are different, and they have been estimated by measuring rates of carbon dioxide uptake under comparable conditions to lie in the proportion 3 : 7 : 10 respectively (Buttrose 1956).

In all other experiments a two-row barley (*H. distichum* var. Prior) was used. It is a single-awned local selection widely grown in South Australia.
(b) Culture Techniques

A sand-culture technique was used in much of this work. Enamel pots were filled with well-washed river sand (16.9 kg), and water added to bring to 65 per cent. of field capacity. Water additions were regulated by periodic weighings, and inorganic nutrients were added at weekly intervals between 2 and 10 weeks after planting.

In the remainder of the work plants were grown in “John Innes” potting compost in earthenware pots. Water additions were frequent so as to maintain the soil at field capacity.

(c) Ear-shading Technique

Opaque shades comprising two paper cylinders, one inside the other, were modelled on those described by Archbold (1942). Ventilation holes were provided in such a way that direct pathways for light entry were avoided, and the amount of light which penetrated to the inside, where the ear was housed, was very small. Individual ears were tagged at anthesis but shades were not fitted until 4 days later, otherwise pollination of the later-flowering spikelets may have been impaired.

(d) Feeding Radioactive Sucrose (\(^{14}\)C-sucrose)

An ear with a portion of stem was removed, and the stem recut twice beneath water to leave 3 cm below the basal floret. The attached part of the stem was placed in a small tube containing 3 per cent. \(^{14}\)C-sucrose (1.5 \(\mu\)c in 1.5 ml). Feeding took place in a glass-house for 5 hr. Then the ear was transferred, after rinsing its stem, to distilled water and kernels were sampled at intervals over a period of 9 days.

(e) Feeding Radioactive Carbon Dioxide (\(^{14}\)CO\(_2\))

(i) To Whole of Attached Ears.—A 1-cm strip of thin rubber sheeting was wrapped and fixed, under slight tension, round 3 cm of peduncle immediately below the ear. After this preparation, the ear, still attached to the potted plant, was introduced into the apparatus illustrated in Figure 1. The bound portion of the stem was inserted through a slit into a hole in a rubber stopper which, in turn, was secured in the mouth of a glass tube (12 by 1 in.). The outside of the stopper was heavily greased to make an air seal. The glass aspirator (A) contained water covered by a layer (0.5 cm) of paraffin oil (D). The rubber stopper in the mouth of this aspirator positioned a glass tube (B), which contained lactic acid (80 per cent.), so that its lower opening was inside a second tube (C) containing \(^{14}\)C-barium carbonate (5 \(\mu\)c in 8.9 mg). Air (6 l.) was drawn through carbon dioxide-absorption towers (E) by draining the aspirator, and a negative pressure was established inside the aspirator sufficient to accommodate the \(^{14}\)CO\(_2\) released when lactic acid was added to the barium carbonate. The concentration of carbon dioxide was 0.076 per cent. (v/v). When the gases inside the aspirator had equilibrated they were drawn over the ear by regulating a vacuum pump at one end of the gas line and the rate of water replacement to the aspirator from the reservoir (F) at the other. By suitable adjustment a steady flow rate (1.5 l./hr) was maintained at a slight negative pressure (1 cm of water, manometer G). It follows that feeding occupied 4 hr.
After treatment the ear was removed from the apparatus and the whole plant placed beneath a wire-netting cage on an open site. Kernels were harvested at intervals in the period to ear maturity.

(ii) To Half of Attached Ears.—To observe translocation within the ear either the top or bottom half of the ear was supplied with $^{14}$CO$_2$. Where the top half was exposed to $^{14}$CO$_2$, three florets on either side at the centre of a two-row ear were removed and the exposed rachis denuded of hairs and sterile spikelets. A narrow strip of rubber sheeting was bound round this part of the rachis and the top half of the ear inserted into the assimilation apparatus. Where the bottom half was fed $^{14}$CO$_2$, the whole ear was inserted into the assimilation apparatus, and light was excluded from the top half of the ear with an aluminium shade. Again six central florets were removed.

(f) Autoradiography

Samples were stored in ethanol after harvest, and the ethanol was changed several times to remove soluble substances. Kernel sections were cut either transversely, midway between base and apex, or longitudinally, through the kernel “cheeks”. The sections were washed with three changes of ethanol (80 per cent.), dried, and transferred to the photographic emulsion, close contact being maintained between section and emulsion. Two types of film were employed: 3 by 3 in. lantern-slide plates (Kodak Ltd.), and “Kodirex” X-ray film. When plates were used they were exposed for 28 days in the dark, developed in “D72” (Kodak...
developer) for 3 min at 23°C, fixed in acid fixer for 15 min, and washed. When X-ray film was used it was exposed for 7 days, developed for 2 min at 23°C with X-ray developer, and fixed. Plant material other than sections was examined for radioactivity in a similar way.

(g) Reducing Kernel Numbers and Substrate Supply

Treatments were carried out on ears (two-row) initially reduced to 18 florets, the number in excess being removed from the apex. Where a further six florets were removed those taken were 1, 4, and 7 on each side (counting from the base). Where 12 florets were removed those in positions 3, 6, and 9 were also taken. In another treatment kernel development was prevented in 12 florets without removing their glumes or awns by incising the outer glume and removing the ovule. Finally, defoliation and stem shading were superimposed on a reduction in kernel number. This was achieved by cutting the leaf blade at the junction with the leaf sheath, and loosely wrapping the stem with several layers of brown paper. The shades were extended where necessary to cover later stem growth. Treatments were imposed between 3 and 5 days after anthesis.

III. Results

(a) Effects of Ear Shading on Kernel Development

Four seeds of awnless, single-awned, and triple-awned barley were planted in each of 15 pots of sand; 2 weeks later plants were thinned to six per pot (two per variety). In each pot all the ears on three plants, one of each variety, were shaded; the other three plants remained untreated. Ears were harvested when the peduncle was dry, threshed, and the kernels oven dried at 105°C.

The results (means of 15 plants) for the shaded and unshaded treatments are shown in Table 1. The mean yield per kernel for each variety was reduced by shading. However, the differences between the reductions themselves were not significant at the 5 per cent. level. The data collected in these experiments were very variable. Analysis of this variation showed it to be independent of treatment and pot, and suggested that the occurrence was at random. In this connexion great variation was also noted during growth; some plants within each variety were apparently quite healthy, while others in the same pot were not. It is concluded that the varieties used were unsuited to the environment imposed upon them since the Prior variety, grown under exactly the same conditions, did not show this variation.

(b) The Fate of Radioactive Carbon (carbon-14) Supplied to the Ear either as Carbon Dioxide or Sucrose

Results from these experiments are illustrated by autoradiographs (Plate 1). The images here are faint, but the original negatives show good resolution. The close correspondence between photographs of sections and their autoradiographs permits results to be presented in the latter form. Sections of kernels from untreated plants did not produce any reaction on the photographic plates.
(i) \(^{14}\text{CO}_2\).—Prior variety barley plants grown in potting compost were used. Ears were treated on one of the following occasions: at 3-day intervals to 18 days, then at 27, 36, and 45 days after anthesis. After treatment the ear was removed from the assimilation apparatus and the intact plant transferred to the open. Two kernels were taken as samples at 1, 3, 9, 15, 21, 30, and 39 days after treatment, freed of glumes, and stored in absolute ethanol. The distribution of carbon-14 within the kernel is illustrated in selected autoradiographs (Plate 1, Figs. 1 and 2).

When \(^{14}\text{CO}_2\) was supplied at 3, 6, and 9 days, radioactivity became concentrated in the peripheral tissues, especially in the furrow of the kernel. As the kernels matured radioactivity persisted in these tissues, i.e. the pericarp. Traces of radioactivity were detected 1 day after feeding in the small endosperm of kernels treated at 3 days, and

![Table 1](image)

**Table 1**

**Mean dry weight per kernel (mg) from shaded and unshaded treatments for the three barley varieties (15 replicates)**

<table>
<thead>
<tr>
<th>Variety</th>
<th>Treatment</th>
<th>Difference</th>
<th>Level of Significance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unshaded</td>
<td>Shaded</td>
<td></td>
</tr>
<tr>
<td>Awnless</td>
<td>27.9</td>
<td>25.4</td>
<td>2.5</td>
</tr>
<tr>
<td>Single-awned</td>
<td>23.6</td>
<td>18.0</td>
<td>5.6</td>
</tr>
<tr>
<td>Triple-awned</td>
<td>42.7</td>
<td>34.8</td>
<td>7.9</td>
</tr>
</tbody>
</table>

traces were still present at maturity. Feeding between 12 and 18 days led to a greater accumulation of carbon-14 in the endosperm than the pericarp, and distribution was uniform throughout the former tissue. At 27 days the response was similar although, at this stage and increasingly through to 45 days, relatively less radioactivity was evident in the centre of the endosperm. However, the lowered activity of this zone was not as marked as in the corresponding tissue supplied with \(^{14}\text{C}-\text{sucrose}\).

(ii) \(^{14}\text{C}-\text{sucrose}\).—Ears were taken for sucrose feeding at the same times after anthesis as for \(^{14}\text{CO}_2\) feeding. Two kernel samples were taken immediately after the radioactive sucrose was replaced with water, then at 1, 2, 4, 6, and 9 days. After removal of the glumes, kernels were stored in absolute ethanol. The distribution of carbon-14 within the kernel is illustrated in Plate 1, Figures 3 and 4. Between anthesis and 9 days radioactivity was concentrated towards the periphery in the regions corresponding to the pericarp. From 12–27 days concentration was mainly in the endosperm and uniformly spread while from 36–45 days greatest concentration had again reverted to the periphery. The amount of carbon-14 supplied as sucrose that was fixed in ethanol-insoluble forms reached a maximum within 24 hr of feeding, although little fixation occurred during the actual feeding, as shown by the “zero” samples. This result allows of two interpretations: accumulation of sucrose into the endosperm may be rapid, but its conversion into insoluble compounds slow;
accumulation of sucrose into the stem and rachis may be rapid, but its entry into the kernel slow.

Soon after feeding either $^{14}$CO$_2$ or $^{14}$C-sucrose the distribution of radioactivity was very similar in both cases; the subsequent differences are attributed to the continued growth of kernels on the ears of intact plants in contrast to the cessation of growth in excised ears. In this connexion where $^{14}$CO$_2$ was fed at 18 days, or earlier, carbon-14 was present in highest concentrations no later than 1 day after treatment, and thereafter the concentration of radioactivity, as judged from the autoradiographs of whole kernels, decreased. No decrease was observed following $^{14}$C-sucrose feeding. The decrease in the first instance could be due to loss by respiration or translocation of resolubilized materials, or dilution in the expanding cells or to all three.

(iii) Distribution of Carbon-14 between Different Chemical Fractions.—The fractions examined were: those soluble in 80 per cent. ethanol—mainly sugars; those insoluble in ethanol but soluble in 33 per cent. chloral hydrate—mainly starch; those insoluble in either of these solvents. Radioactivity was detected in all three fractions from kernels of ears supplied $^{14}$CO$_2$ 18 days after anthesis. No change in either “starch” or “residue” components was apparent between 1 and 27 days after treatment. This supports a previous notion that the decrease in concentration of radioactivity noted in autoradiographs of kernels of ears subsequent to feeding is due to dilution by non-radioactive materials. However, radioactivity in the ethanol-soluble fraction decreased with time and at maturity was negligible. The fate of this carbon-14 remains uncertain; losses by translocation are unlikely (see Sections III (d) and III (e)), but it could have been respired or transformed into insoluble forms. The present evidence allows no choice between the alternatives; nevertheless, these losses are small compared with the radioactivity permanently retained within the starch and residue components.

(c) Competition between Kernels for Substrate from Outside the Ear

Prior variety barley was sown at 10 seeds per pot in sand culture and later thinned to six per pot. The following six treatments were represented in every pot by assigning, at random, each treatment to one of the six plants: (1) 18 florets per head; (2) 12 florets per head; (3) 6 florets per head; (4) 6 florets per head plus 12 empty florets; (5) 18 florets per head, stems defoliated and shaded; (6) 6 florets per head, stems defoliated and shaded. All ears on any one plant were treated. There were harvests at 15, 25, 35, and 45 days after anthesis, three pots being used for each harvest. Only six kernels (corresponding ones in all cases) were taken from each head at harvest, the glumes were removed, and the kernels of each plant combined and oven dried.

The progressive change of kernel weight when ears carried different numbers of kernels (treatments (1), (2), and (3) above) is illustrated in Figure 2. The three values were almost identical at harvests up to 25 days, thereafter variability increased although differences were not significant at the 5 per cent. level. The average final weight of kernels from these treatments was 44·5 mg per kernel. It is concluded that in plants grown under these conditions there is no competition between kernels for substrates.
The situation appears very different when the additional treatments of stem defoliation and shading are applied. The weight of kernels from ears bearing 18 florets was significantly less than corresponding unshaded ones at all harvests \((P < 0.05)\). That from ears bearing six florets was also less than corresponding unshaded ones at 15, 25, and 45 days \((P < 0.05)\) although at 35 days the difference did not quite attain the 5 per cent. level of significance. Furthermore, differences between these last two treatments themselves were highly significant at 25, 35, and 45 days; at maturity kernels from the 18-kernel ear weighed 19.9 mg, those from the six-kernel ear were 31.8 mg. Therefore, it is further concluded that where substrate supply is greatly curtailed competition between kernels arises, and moreover, the competition is evident throughout growth.

\[(d) \text{ Translocation between Kernels of Substrate Assimilated within the Ear}\]

Ears of Prior variety were used 24 days after anthesis, when either the top or bottom portions were supplied \(^{14}\text{CO}_2\) for 4 hr. After treatment, ears were removed from the assimilation apparatus and the whole plant allowed to mature in the open. The bottom portion of one ear, whose top portion was fed \(^{14}\text{CO}_2\), was subsequently de-awned and shaded. At maturity two kernels (the apical and basal) were taken from both portions of treated ears and autoradiographs were made of their transverse sections. The findings are set out in Table 2.
Thus there seems little doubt that the carbon-14 assimilated by the upper half of the ear was not translocated to kernels in the lower half, even when these kernels were shaded and hence entirely dependent on substrate from elsewhere for their subsequent maturation. However, there is some doubt as to whether carbon-14 assimilated by the lower half of the ear (treatment (3)) was translocated upwards, despite the fact that traces of radioactivity were recorded. This result may have been due to dark fixation of $^{14}CO_2$ in situ, since, unlike the other treatments, both halves of the ear were here exposed to $^{14}CO_2$ (see Section III (e)(ii)). The rachii and awns showed responses similar to those of the kernels. Awns from the top half of the ear (treatment (3)) appeared to accumulate concentrations of radioactivity comparable to the kernels. This supports the notion that carbon-14 arises in this instance from dark fixation, and not translocation, otherwise kernels, which act as sinks for substrates, should accumulate more than awns.

### Table 2

<table>
<thead>
<tr>
<th>Treatment No.</th>
<th>Treatment of Ears</th>
<th>Location of Kernels</th>
<th>Radioactivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Top half fed $^{14}CO_2$</td>
<td>Top half Bot. half</td>
<td>Present Absent</td>
</tr>
<tr>
<td>II</td>
<td>Top half fed $^{14}CO_2$; bottom half subsequently de-awned and shaded</td>
<td>Top half Bot. half</td>
<td>Present Absent</td>
</tr>
<tr>
<td>III</td>
<td>Bottom half fed $^{14}CO_2$</td>
<td>Top half Bot. half</td>
<td>Traces Present</td>
</tr>
</tbody>
</table>

(e) **Translocation of Substrate Assimilated within the Ear to other Sites**

Autoradiographs were made of the flag leaf, the flag leaf sheath, and portions of the stem from shoots whose ears were supplied with $^{14}CO_2$ at 3, 15, or 27 days after anthesis. These revealed that carbon-14, assimilated by the ear at 3 days, was subsequently distributed throughout the internode between the flag leaf and the ear. However, there was no trace of activity in the stem below this node, in the flag leaf sheath, or in the flag leaf. No trace of radioactivity was found outside the ear when $^{14}CO_2$ was supplied at either 15 or 27 days after anthesis.

### IV. DISCUSSION

Application of the ear-shading technique to awnless, single-awned, and triple-awned varieties of barley led to reductions in yield per kernel of 9, 23, and 18 per cent., respectively. The contribution of photosynthesis in the ear itself to grain yield may depend on the assimilatory activity of the ear. If so, these activities should
approach the proportions by which ear shading reduced yield, i.e. 3 : 8 : 6. Previous estimates have given the relative assimilatory activities of ears of these three varieties as 3 : 7 : 10 (Buttrose 1956). Attention has already been drawn to the fact that the reductions in yield by shading were not significantly different from each other, and since the two relationships are so close it is difficult to decide whether there is a real difference between them or not. Results presented here throw no further light on this matter, but lend some support to the proposition (see below) that discrepancies between shading estimates arise because of compensatory mechanisms in the plant. Thus, under some circumstances or with some varieties certain sources of carbon substrate may replace others rendered ineffective (e.g. by shading). It is to be noted that in such circumstances the two above relationships need not be the same to conform with the proposition that ear shading reduces yield only by preventing photosynthesis.

Despite the uncertainties in interpreting shading experiments, it has been concluded that carbon dioxide fixed in the ear makes a substantial contribution to yield. This work, using carbon-14 to trace ear assimilate, lends strong support to this conclusion. Radioactivity supplied as $^{14}\text{CO}_2$ to the ear was permanently incorporated into kernels throughout development. It seems equally clear that carbon substrate translocated from other organs also makes a major contribution, since $^{14}\text{C}$-sucrose supplied through the stem was always as readily, and as permanently, incorporated into the kernel. Whatever the source, the starch and other alcohol-insoluble carbon fractions remained apparently unchanged between 24 hr after carbon-14 was supplied and maturity. Again, the source was without influence on the site of incorporation within the kernel. However, the stage of kernel development influenced the site: early, accumulation was greatest at the periphery of the kernel; throughout the greater part of development, accumulation was greatest in the endosperm and uniformly distributed therein; near maturity, accumulation was again greatest at the periphery. These changes probably reflect alterations in synthetic activities during kernel development.

When carbohydrate supply was greatly reduced by defoliation and stem shading, competition between kernels occurred for storage products of the stem. Under normal conditions competition was not observed, hence substrate was not limiting. It is admitted that in this experiment the maximum kernel number was 18 per ear, whereas a normal ear carried about 23 kernels. However, it was found that final weight per kernel (where there were 18 per ear) was not significantly different from that of kernels where there were 28 per ear (unpublished data). It is of interest that Archbold (1945) has also suggested that there is an excess of carbohydrates in the barley plant, sugar accumulating as an inevitable consequence of assimilatory products exceeding growth and respiratory requirements.

The above results confirm the now commonly held view that several different sources in the plant contribute to kernel development. As a speculation it is now proposed that these several sources comprise a general pool from which the kernel derives its substrate, and moreover, a deficiency in one source may be offset by an added contribution from another. A tentative scheme which accommodates these suggestions is presented in Figure 3. If there is a general surplus of carbohydrates
(scheme B) the ear could contribute, in the normal plant, as much as 50 per cent. of its kernels' dry weight, but ear shading might assess this contribution at only 33 per cent. because of induced contributions from other sources. If there is not a surplus of carbohydrates (scheme A) shading techniques might give an accurate assessment. There is, however, no a priori reason for assuming that the conditions of scheme A always apply; in other words, that all potential sources always make their

![Fig. 3.-Two schemes showing: 1, actual contributions by plant parts to kernel development; 2, potential contributions; 3, contributions assessed by ear shading. Scheme A, classical interpretation—plant parts always contribute to a maximum; scheme B, proposed interpretation—some parts not always contributing to their maximum potential.](image)

maximum contribution or that their contribution is constant. Notwithstanding these considerations the ear is represented (scheme B) as contributing its maximum to kernel development. This conclusion follows the findings that exposure of ears to $^{14}CO_2$ between 15 and 27 days after anthesis (the period of rapid kernel development) gave no evidence of translocation to organs outside the ear, and that only in the early stages of kernel development was some ear assimilate translocated down the uppermost internode. Furthermore, the evidence suggests that even translocation between kernels within an ear did not occur.

Where there is competition for substrate between kernels an assessment of the maximum contribution of photosynthetic products of the ear to kernel yield can be made. Thus in the competition experiment described it may be assumed that the
contribution of each floret remains constant. If each floret contributes \( x \) to its kernel weight then the total contribution from the ear to kernel yield per head will be \( nx \), where \( n \) is the number of kernels per head. When the final weight per kernel is \( w \), the yield per head is \( nw \), and the non-ear contribution \( n(w-x) \). In competitive conditions it may now be assumed that the same amount of material enters the ear from other plant parts, irrespective of the number of kernels per head. Thus the following equation,

\[
n_1(w_1-x) = n_2(w_2-x),
\]

can be derived for two ears showing competition for substrate, bearing \( n_1 \) and \( n_2 \) kernels, and each kernel weighing \( w_1 \) and \( w_2 \) respectively. A solution for \( x \) allows the calculation of percentage contribution by ears in the normal plant as \( x/w_0 \times 100 \), where \( w_0 \) is the weight of kernels which develop on control plants.

The application of this method to the inter-kernel competition experiment, where defoliation and stem shading were imposed on plants with either six or 18 kernels per head, gives the following results:

<table>
<thead>
<tr>
<th>No. of Days</th>
<th>Ear Contribution (%)</th>
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<tbody>
<tr>
<td>15</td>
<td>63</td>
</tr>
<tr>
<td>25</td>
<td>43</td>
</tr>
<tr>
<td>35</td>
<td>64</td>
</tr>
<tr>
<td>45</td>
<td>31</td>
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No claim is made that these results represent accurate estimates; the experiment was designed to study inter-kernel competition. But the approach has much to commend it. It is a maximum contribution that is measured rather than a minimum. Furthermore, the estimate \( x \) is obtained from two treatments identical with respect to shading and hence it is independent of secondary effects of shading. Its further application may contribute to a better understanding of the problem—how much carbon substrate for kernel development arises from the several potential sources of the normal plant?

V. Acknowledgment

The barley varieties used in this work were supplied by Dr. K. W. Finlay, Plant Breeding Section, Waite Agricultural Research Institute. The authors wish to express their gratitude for his assistance.

VI. References


 Autoradiographs of sections of kernels

Figs. 1 and 2.—Autoradiographs from heads treated with $^{14}$CO$_2$ at 15 and 27 days after anthesis. Days after treatment when samples taken indicated for each group.

Figs. 3 and 4.—Autoradiographs from heads treated with $^{14}$C-sucrose at 15 and 27 days after anthesis. Days after treatment when samples taken indicated for each group.

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