THE PATTERN OF GRAIN GROWTH WITHIN THE EAR OF WHEAT

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Summary

In main ears of Triple Dirk wheat plants grown at a temperature of 21/16°C under natural daylight, grains in the second florets of the central spikelets maintained the highest growth rates (1·66 mg/grain/day), those in the first florets of the basal spikelets the lowest rates.

Sterilization of the basal one or two florets of the central spikelets before anthesis led to compensating increases in both grain weight and the numbers of grains set in other parts of the ear, in the two varieties examined. In one variety, Triple Dirk, under high light intensities, sterilization of the first or second florets of the central spikelets led to significant increases of up to 20%, in grain yield per ear, compensating grains being set in distal florets of the central spikelets and additional and heavier grains being formed at the top and bottom of the ear.

Eighty-eight percent of the ^{14}C assimilated by ears 15 days after anthesis was found in the grains at maturity, and was fairly uniformly distributed between spikelets.

^{14}C assimilated by flag leaves, on the other hand, was distributed preferentially to the lower central spikelets, and to the second grains, and partial sterilization of the central spikelets greatly increased the proportion of ^{14}C in the apical and basal spikelets.

We conclude that the setting of grains in upper florets, and grain yield per ear, may be reduced by rapid development of grains from the first flowers to reach anthesis.

I. INTRODUCTION

The basal grains of the central spikelets of mature wheat ears are usually heavier than those of the more distal spikelets and florets, which flower later (Percival 1921). The differences in final grain weight at various positions within the ear could merely reflect the order of floral differentiation and of flowering, the grains of the earliest flowers being heavier by virtue of having a longer period for starch deposition, or they could be due in part to competition for assimilates between grains both between and within spikelets, or to hormonal interactions between them.

The course of grain growth in whole ears has been documented for many varieties (e.g. Stoy 1965), but not apparently for individual grain positions within the ear. Asana and Bagga (1966) present mean data for the two basal grains in the 10 central spikelets of two varieties, and Pál and Tallér (1968) give what are presumably fresh-weight data for individual spikelets.

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Besides presenting data for changes in dry weight at individual grain positions, we also examine the effects of preventing grain formation in the basal florets of the central spikelets, the first to reach anthesis, on both the number and final weight of grains in other positions. The object of these experiments was to obtain evidence on the importance of competition for assimilates between and within spikelets. Comparable treatments have been used in the past mainly to estimate the contribution of ear photosynthesis to grain growth (e.g. Buttrose and May 1959; Buttrose 1962; Lupton and Ali 1966), and to examine the effect of the demand by the ear on the movement of assimilates from the leaves (Wardlaw 1965). In some cases the removal of grains has had no effect on the weight of the remaining grains (e.g. Abolina 1959; Buttrose 1962), suggesting that there was little competition for assimilates between grains. In others (e.g. Bingham 1967), the final weight of the individual grains remaining increased progressively as more grains were removed, but the increases did not entirely compensate for the reduced grain number, particularly under higher light intensities (Stoy 1965).

In many of these experiments the compensatory setting of grains at higher positions within the spikelets was prevented either by the removal of whole spikelets (e.g. Buttrose 1962; Lupton and Ali 1966) or by sterilization of the upper florets within spikelets (e.g. Stoy 1965; Bingham 1967). In our experiments, therefore, the basal one or two florets of the central spikelets were sterilized before anthesis to minimize injury, and to permit compensatory grain setting in distal florets not normally bearing grains.

II. Material and Methods

The variety Triple Dirk was used in most experiments because, in the conditions under which the experiments began, the main ears were particularly uniform and bore 16 spikelets with no more than two grains in each. In one of the later experiments, however, with lower light intensities following anthesis, some of the lower spikelets bore three grains. The variety Late Mexico 120 was also used in one experiment, as a variety with a much higher number of spikelets and grains per spikelet.

The plants were grown in pots containing a mixture of perlite and vermiculite, and given water and a nutrient solution daily. From germination until maturity they remained in a glasshouse controlled at 21°C for 8 hr (day) and at 16°C for 16 hr, under natural daylight extended to a photoperiod of 16 hr by light of 50 f.c. intensity from incandescent lamps.

During anthesis, two groups of five main ears of Triple Dirk were examined each morning to obtain the average time of anthesis for each floret position. Eighty-one ears which began anthesis on the same day were used to follow the course of grain growth, groups of nine ears, selected at random from the block, being harvested twice weekly beginning 5 days after anthesis. The ears were oven-dried and all individual grains weighed, a Cahn electrobalance being used for the early stages of grain growth.

(*a*) *Floret Sterilization*

At ear emergence, about 4 days before anthesis, groups of ears taken at random were either left intact or sterilized according to a fixed pattern by removing both the anthers and the stigma with forceps. Preliminary experiments showed that removal of the anthers alone, or pricking the ovaries with a needle, was not sufficiently reliable. After the sterilization treatments the ears were left until maturity, when they were dried and all grains weighed individually.

In two experiments using Triple Dirk ears with 16 spikelets, sterilization was confined to the central 8 spikelets, either the first (basal) floret, or the second, or both being sterilized. In the first experiment, for which there were 12–15 ears in each treatment, the light intensity was high from ear emergence to maturity (711 cal cm^{-2} day^{-1} on average). For the second experiment,

in autumn, there were 18 main stem ears in each treatment group, and the mean light intensity was much lower, 424 cal cm^{-2} day^{-1}.

For the experiment with Late Mexico 120 wheat, grown at the same time as the first experiment with Triple Dirk, groups of 16 ears with at least 24 spikelets were either left intact or had the first or first and second florets of the middle 12 spikelets sterilized, the top six spikelets and the lowermost six or more being left intact.

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

Plants in the second sterilization experiment with Triple Dirk were allowed to assimilate $^{14}CO_2$ 15 days after anthesis, at mid-grain filling. Either the ears or the flag leaf blades were exposed to $^{14}CO_2$ under light of 3200 f.c. intensity from fluorescent and incandescent lamps. $^{14}CO_2$ was generated by the addition of 50% lactic acid to $BaCO_3$ (1 mCi/m-mole), used at the rate of 2 mg per plant. There were three replicates of three main ears in each treatment group, one replicate of each treatment being included in each exposure to $^{14}CO_2$. The grains from these ears were harvested at maturity, dried, individually weighed, and grouped into lots of three grains from each floret position within each replicate. The lots of three grains were then ground and their relative specific activity determined by the powder counting method of O'Brien and Wardlaw (1961).

Additional control and treated ears were harvested 1 hr after beginning their exposure to $^{14}CO_2$ to determine the initial pattern and amount of $^{14}CO_2$ assimilation. The ears were divided into three parts (top four, middle eight, and bottom four spikelets), dried, ground, and their ^{14}C activity determined, that in the grains and that in the ear structures being determined separately.

III. Results

(*a*) *The Course of Grain Growth*

Detailed data for the time of anthesis at each floret position are not presented. In Triple Dirk the basal floret of the central spikelet (8) was the first to reach anthesis. The basal floret of the top spikelet reached anthesis 1 day later, that of the basal spikelet 3 days later, with those between being intermediate. Four florets reached anthesis in each of the eight central spikelets (although only two or three set grains), there being a 4-day interval between anthesis of the first and the fourth florets in each spikelet, with more distal florets reaching anthesis progressively later. Sterilization of the basal florets of the central spikelets did not affect the time to anthesis of the other florets.

Figure 1 shows the changes in dry weights of the grains from the first and second florets of each spikelet in ears of Triple Dirk until 29 days after anthesis. A final harvest, taken at maturity is included. The grains of the central spikelets were the heaviest at the first harvest, and remained so throughout. The grains from the second florets were initially lighter than those from the basal florets, and remained so in the three apical spikelets. In the lower spikelets, however, the first and second grains were about equal in weight 15–18 days after anthesis, and thereafter the second grains were heavier.

The course of growth in dry weight of the first and second grains of three central and three more basal spikelets, together with the mean daily radiation totals for the intervals between harvests, indicated that from 8 days after anthesis the increase in dry weight per grain was approximately linear, deviations being largely associated with changing daylight conditions. The computed average growth rate of individual grains over the interval between 8 and 29 days after anthesis is given in Table 1. Growth rates at all positions did not differ greatly, but were significantly higher in the

central spikelets than in the upper and lower ones, and higher for second grains than for the first.

The higher growth rate, and final weight, of the second grains could be due to competition between the first and third grains, since their vascular systems may be more closely connected. However, the second grain grew faster than the first even when no third grain was present, as in the lower spikelets.

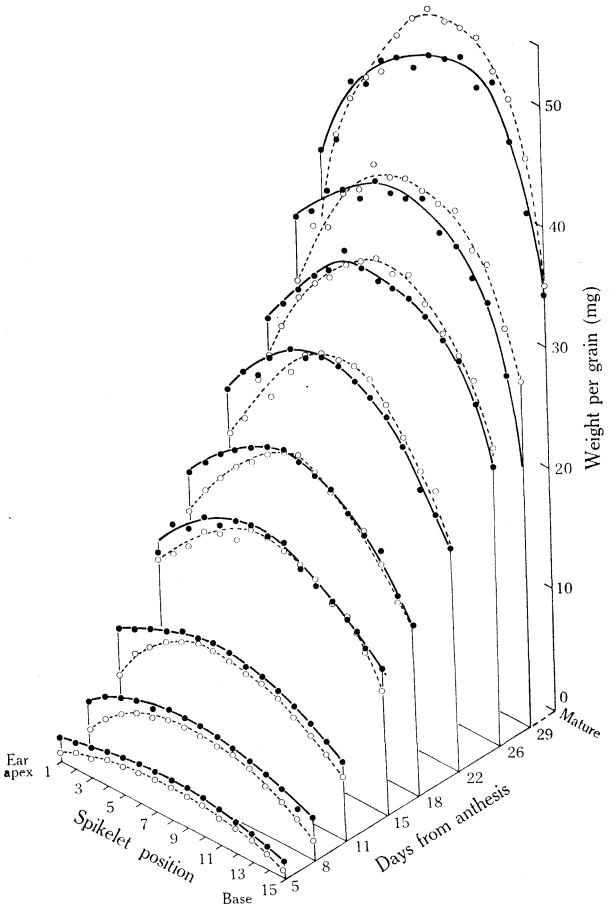

Fig. 1.—Diagrammatic representation of the changes with time from anthesis in the dry weights of the first (●) and second (○) grains in each spikelet of ears of Triple Dirk wheat.

(*b*) *Effects of Floret Sterilization on Final Grain Weights*

(i) *Summer Experiment with Triple Dirk Wheat*

Sterilization prior to anthesis of the first or second floret of the central spikelets, whose grains are normally the most advanced in development, did not cause any reduction in total grain weight per ear (Table 2). In fact, grain yield was increased by about 20% ($P<0{\cdot}01$) for both treatments in which only one grain was removed from each spikelet. The increase was due both to greater number and weight of grains.

In the central spikelets sterilization of a basal floret (first or second) led in almost every case to the setting of a grain in the third floret, although there was only one third floret grain in 13 control ears. Moreover, sterilization of either the first or second florets of the central spikelets also caused additional grains to be set in the top four

TABLE 1

COMPUTED AVERAGE INCREASE IN DRY WEIGHT BETWEEN 8 AND 29 DAYS AFTER ANTHESIS FOR GRAINS OCCUPYING VARIOUS POSITIONS WITHIN THE EAR OF TRIPLE DIRK WHEAT

Nine replicates per treatment. The average L.S.D. at 5% between average increases in dry weight of grains in the first and second florets is 0·09

Spikelets	Dry Weight Increase (mg/grain/day)		
	Floret No. 1	Floret No. 2	Floret No. 3
3–5	1·49	1·50	
6–8	1·58	1·66	1·42
9–11	1·56	1·65	1·66
12–14	1·36	1·50	

and bottom four spikelets. These additional grains were also set when two florets were sterilized in each of the central spikelets, but in that treatment the setting of grains in the more distal florets did not completely compensate for the absence of grains in sterilized florets, and grain yield per ear was less than in the control ears. Table 2 also shows that the average weights of the heaviest grain and the heaviest

TABLE 2

EFFECTS OF STERILIZATION OF THE FIRST, SECOND, OR BOTH THE FIRST AND SECOND FLORETS OF THE CENTRAL EIGHT SPIKELETS OF EARS OF TRIPLE DIRK WHEAT DEVELOPING DURING SUMMER

Mean values ± S.E.

	Florets Sterilized			
	None	First	Second	First and Second
Grain weight per ear (mg)	1326·2 ± 45·5	1604·1 ± 53·2	1588·3 ± 43·0	1263·5 ± 95·4
Grain number per ear	25·4 ± 0·47	28·4 ± 0·91	27·1 ± 0·90	23·2 ± 1·29
Av. heaviest grain (mg)	60·6 ± 1·37	70·7 ± 0·81	69·9 ± 0·67	65·8 ± 1·83
Av. heaviest spikelet (mg)	121·0 ± 4·5	128·2 ± 13·6	147·9 ± 5·6	141·7 ± 8·2
Average weight per grain (mg) in the eight central spikelets				
Floret 1	54·9 ± 0·51	—	64·0 ± 0·55	—
Floret 2	56·0 ± 0·59	64·8 ± 0·96	—	—
Floret 3	—	54·0 ± 0·59	56·5 ± 0·78	57·5 ± 1·39
Floret 4	—	—	—	50·0 ± 1·62

spikelet in each ear were increased by the sterilization treatments. Mean weight per grain in the second florets of the central spikelets was considerably increased when the first florets were sterilized, and that of the first grains when the second florets were sterilized, even though the compensating grains were almost as heavy as the

ones they replaced. The grains set in the third and fourth florets of the central spikelets were heavier than the first and second grains in the top and bottom spikelets although they derived from flowers which reached anthesis later. Once again, the differences in final weight per grain cannot be wholly ascribed to differences in time of anthesis.

Figure 2(*a*) presents the profile of grain weight per spikelet for the various treatment groups. This indicates the pronounced increases in grain weight in the upper and lower spikelets caused by sterilization of the lower florets of the central spikelets, despite the fact that there was almost full compensation within the central spikelets when only one floret was sterilized. Compensation was incomplete in the uppermost sterilized spikelet, but some overcompensation occurred in the lower ones.

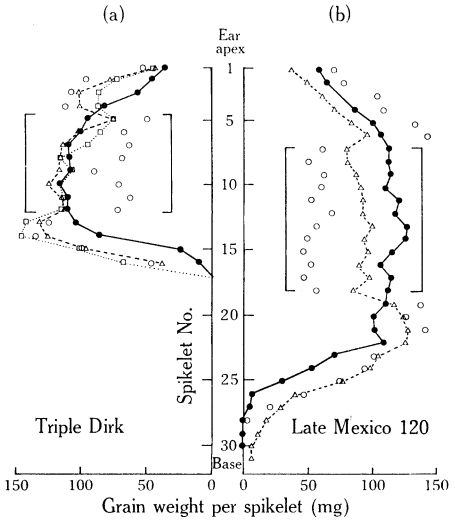

Fig. 2.—Ear profiles showing grain weight per spikelet in ears of wheat left intact (●) or with the first (△), second (□), or first and second (○) florets of the central spikelets sterilized. The area within square brackets indicates the zone of sterilization. (*a*) Triple Dirk (eight spikelets sterilized); (*b*) Late Mexico 120 (12 spikelets sterilized).

(ii) *Autumn Experiment with Triple Dirk Wheat*

The results of this experiment are given in Table 3. Under the much lower light intensities during ear development in this experiment, individual grain weight and grain yield per ear were greater than for summer-grown plants. Third grains were set in many lower spikelets of the control ears, thus reducing the scope for compensatory grain setting in the partially sterilized ears. Even so, compensation was substantial, and grain number and weight per ear were only slightly reduced by sterilization of the first florets. As may be seen from Table 3, grain weight in the four top and four basal spikelets of the treated ears was greater than in the control ears, as in the summer experiment, but compensation in the central spikelets was not as complete. Grains in the second florets of the central spikelets were again heavier than those in the first florets. Grains in the third florets can be as heavy as those in the first floret, as shown in the treatment in which the two lowest florets were sterilized.

(iii) *Partial Sterilization of Ears of Late Mexico 120 Wheat*

The control ears of Late Mexico 120 wheat differed from those of Triple Dirk in having far more spikelets (24 or more) and more grains per spikelet, nearly all the

central spikelets having three grains, and some four. Nevertheless, sterilization of the basal floret of the 12 central spikelets resulted in almost complete compensation

TABLE 3

EFFECTS OF STERILIZATION OF THE FIRST OR BOTH THE FIRST AND SECOND FLORETS OF THE CENTRAL EIGHT SPIKELETS OF EARS OF TRIPLE DIRK WHEAT DEVELOPING IN AUTUMN

Eighteen replicates per treatment; mean values ± S.E.

	Florets Sterilized		
	None	First	First and Second
Grain weight per ear (mg)	1920 ± 37·2	1831 ± 39·8	1686 ± 65·7
Grain number per ear	33·0 ± 0·71	31·8 ± 0·64	29·7 ± 0·88
Grain weight (mg)			
Spikelets 1–4	254·6 ± 9·6	306·8 ± 16·3	362·3 ± 8·2
Spikelets 5–8	489·3 ± 8·3	432·5 ± 13·3	286·7 ± 12·4
Spikelets 9–12	657·0 ± 19·6	540·5 ± 13·6	417·7 ± 17·9
Spikelets 13–16	519·1 ± 33·0	555·2 ± 29·3	608·3 ± 32·4
Average weight per grain (mg) in eight central spikelets			
Floret 1	60·6 ± 0·37	—	—
Floret 2	63·6 ± 0·49	66·2 ± 0·43	—
Floret 3	55·0 ± 0·71	56·0 ± 0·54	62·1 ± 0·56
Floret 4	—	—	46·8 ± 0·79

in grain number and weight per ear (Table 4). The third and fourth grains in the central spikelets of control ears were much lighter than the basal grains, and their

TABLE 4

EFFECTS OF STERILIZATION OF THE FIRST OR BOTH THE FIRST AND SECOND FLORETS OF THE CENTRAL 12 SPIKELETS OF EARS OF LATE MEXICO 120 WHEAT DEVELOPING IN SUMMER

Sixteen replicates per treatment; mean values ± S.E.

	Florets Sterilized		
	None	First	First and Second
Grain weight per ear (mg)	2437 ± 97·4	2356 ± 178·4	2122 ± 144·4
Grain number per ear			
Spikelets 1–6	12·3	10·8	12·7
Spikelets 7–18	32·3	26·4	13·1
Spikelets 19–28	13·8	20·9	15·3
Total	58·4 ± 3·07	58·1 ± 2·70	41·1 ± 2·78
Average weight per grain (mg) in 12 central spikelets			
Floret 1	46·6 ± 0·27	—	—
Floret 2	47·0 ± 0·53	48·9 ± 0·64	—
Floret 3	37·5 ± 0·62	40·0 ± 0·75	51·4 ± 0·40
Floret 4	18·7 ± 1·76	21·6 ± 0·90	35·2 ± 0·50

weight increased with increasing sterilization of the lower florets. However, the number of grains set in the fourth florets of the central spikelets did not increase

noticeably, even when the two lowest florets were sterilized, and no fifth floret grains formed, with the result that compensation in the central spikelets was incomplete [Figure 2(*b*)].

In the spikelets below the partially sterilized zone more grains were formed, individual grain weight increased considerably over the controls, and the lowermost spikelets which are usually sterile bore some grains. At the top of the ear, however, sterilization of the first floret of the central spikelets resulted in a decrease in grain number and grain weight, although weight per grain increased considerably when two florets were sterilized.

(*c*) *The Pattern of* ^{14}C *Labelling*

$^{14}CO_2$ was assimilated by the ears fairly uniformly throughout their length. With ears harvested immediately after exposure to $^{14}CO_2$ total activity was similar regardless of treatment, and in control ears 24% of the activity was found in the top four spikelets, 57% in the central eight spikelets, and 19% in the basal four spikelets of which two were poorly developed. Partial sterilization of the central spikelets only slightly reduced their proportion of the $^{14}CO_2$ assimilated, to 54%. About 20% of the ^{14}C in the ears at the initial harvest was lost by maturity, in all treatments.

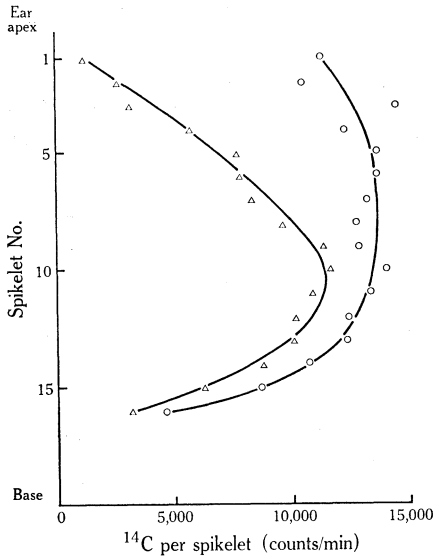

Fig. 3.—Profiles of ^{14}C activity in the grains of mature ears of Triple Dirk wheat when either the ear (○) or the flag leaf (△) assimilated $^{14}CO_2$ 15 days after anthesis. In both cases the $^{14}CO_2$ was derived from $BaCO_3$ (1 mCi/m-mole) used at the rate of 2 mg per plant. The two profiles should not be taken as indicating the relative contributions of ear and flag leaf assimilates to grain filling.

Of the ^{14}C present at maturity, only 11·8–13·6% was present in the ear structures, the remainder being in the grains. The proportions of activity in the various zones of the ear at maturity were similar to those at the initial harvest, and in the control ears there was no evidence of movement of ^{14}C assimilates from one part of the ear to another. Some movement may have occurred away from the partially sterilized central spikelets, since the proportion of ^{14}C in those spikelets at maturity fell to 50% when the two basal florets were sterilized, and the proportion in the top four spikelets

rose to 29·6%. Buttrose and May (1959) also obtained some evidence of very slight movement of ^{14}C assimilated by the basal half of the ear to the top half, when the latter was shaded.

The profile of ^{14}C activity in the grains of the various spikelets is shown in Figure 3.

$^{14}CO_2$ assimilated by the ears was fairly uniformly distributed on a per spikelet basis, except that the less developed spikelets at the base of the ear had a lower activity. Of the activity within each spikelet more was found in the more distal grains, as indicated for the central spikelets in Table 5. However, the highest activity per grain (11,282 counts/min) was found in the basal grain of the uppermost spikelets, in which only one grain was present. Similarly, the relative specific activity was progressively higher in spikelets nearer the top of the ear.

The results for $^{14}CO_2$ assimilated by ears which were partially sterilized are not presented, because the profiles of ^{14}C activity per spikelet were similar to that presented for intact ears in Figure 3, except that there was rather more activity in the top four spikelets.

TABLE 5

^{14}C ACTIVITY AT MATURITY IN GRAINS OF THE CENTRAL SPIKELETS OF TRIPLE DIRK WHEAT WHEN $^{14}CO_2$ WAS ASSIMILATED BY EITHER THE EAR OR THE FLAG LEAF BLADE 15 DAYS AFTER ANTHESIS

Nine replicates per treatment; mean values ± S.E.

$^{14}CO_2$ Assimilated by	^{14}C Activity (counts/min/grain)		
	Floret No. 1	Floret No. 2	Floret No. 3
Flag leaf	3748 ± 201	4408 ± 130	3422 ± 223
Ear	4396 ± 191	5546 ± 300	6756 ± 419

$^{14}CO_2$ assimilated by flag leaf blades was distributed very differently from that assimilated by the ear, in that spikelets in the upper half of the ear received progressively less the nearer they were to the top of the ear (Fig. 3) and had lower relative specific activities. Flag leaf assimilates also differed from ear assimilates in their partitioning within the spikelet, second grains receiving the most, but with the distribution between grains being much more uniform than was the case for ear assimilates (Table 5). The two profiles in Figure 3 should not be taken as indicating the relative contributions of ear and flag leaf assimilates to grain filling because, although the same total activity per plant was assimilated, the rate of assimilation by the ears was much slower.

Partial sterilization of the central spikelets caused considerable changes in the distribution of flag leaf assimilates within the ear, as may be seen from Figure 4. ^{14}C activity in the top four and bottom four spikelets increased, both in absolute terms and as a proportion of total grain activity (Table 6). Activity in the central spikelets was greatly reduced when the two basal florets were sterilized, but not when only

the first floret was sterilized. With this latter treatment the total ^{14}C activity found in the grain was much higher than that for the control ears.

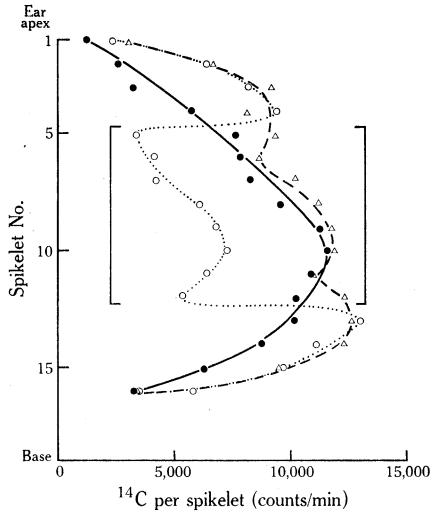

Fig. 4.—Profiles of ^{14}C activity assimilated by flag leaves 14 days after anthesis and translocated to ears of Triple Dirk wheat, as influenced by partial sterilization of the central spikelets: ● intact ears; △ first florets of eight central spikelets sterilized; ○ first and second florets of eight central spikelets sterilized. Square brackets indicate the zone of sterilization.

IV. Discussion

The earlier anthesis of the florets in the central spikelets may have given their grains an initial advantage which was subsequently accentuated by their slightly higher growth rates compared with those of grains in more apical and basal spikelets.

Table 6

Effect of sterilization of the first or both the first and second florets of the eight central spikelets of main ears of Triple Dirk wheat on the percentage distribution within the ear of ^{14}C assimilated by the flag leaf 15 days after anthesis

Spikelets	Percentage Total Ear ^{14}C in Grains of Spikelets when:		
	No Florets Sterilized	First Floret Sterilized	First and Second Florets Sterilized
1–4	10·8	17·9	24·1
5–12	65·2	57·1	39·9
13–16	24·0	25·0	36·0
Total counts/min/ear*	118,469	151,484	109,778

* Standard error ±7392 counts/min.

However, even the third grains of the central spikelets had higher growth rates than grains from florets nearer the tip or base of the ear which reached anthesis at the same time, and the final weights of grains in the third and fourth florets of partly sterilized

central spikelets also exceeded those of grains from other florets which reached anthesis at the same time. Thus, although ultimate grain size bears no simple relation to time of anthesis of the floret, the earlier development of the central spikelets presumably confers some advantage on their grains.

The results in Figure 3 suggest that although all except the most basal spikelets assimilate comparable amounts of CO_2, the lower central spikelets have a very great advantage in the import of flag leaf assimilates, and that the supply becomes progressively more limiting as the terminal spikelet is approached. The central spikelets apparently have a similar advantage in relation to the supply of nitrogen (McNeal and Davis 1954). Partial sterilization of the central spikelets increased the amount of ^{14}C-labelled flag leaf assimilates reaching the spikelets above and below them, and also increased both the number and size of grains in those spikelets in ears of both Triple Dirk and Late Mexico 120 wheat. This suggests that the early-differentiating central spikelets are able to compete more effectively than the distal spikelets for assimilates imported from the flag leaf.

The two varieties differed considerably on the situation *within* spikelets. In Triple Dirk no more than two grains per spikelet occurred in ears which developed under high-intensity light, although up to four flowers reached anthesis. Sterilization of the first or second floret in the central spikelets resulted in grains developing in virtually all third florets, while sterilization of both first and second florets resulted in grains in nearly all fourth florets. Thus, the distal florets of Triple Dirk are competent to set grains. Since we found no evidence of young grains in the third and fourth florets failing during the development of intact ears of Triple Dirk, they presumably failed at grain set or soon after. As competition for available assimilates was probably minimal at that time, a hormonal interaction between florets may have been involved. Ears of Late Mexico 120 wheat set up to four grains in each spikelet, but these showed a marked gradient in weight, the more distal grains being much smaller. Partial sterilization of the central spikelets caused no compensatory increase in grain set in the more distal florets, but some increase in the weight of the distal grains. Thus, there was no evidence that grain setting in the upper florets was inhibited by grain setting in the lower ones. This could possibly be due to the apparently slower initial development of grains in ears of Late Mexico 120 (Rawson and Evans, unpublished data). Slower initial growth of early setting grains could also account for the setting of third grains in the ears of Triple Dirk which developed under the much lower light intensities prevailing in the second experiment, and for the increased grain set in ears of Sonora 64 grown in 16-hr days compared with those grown in continuous high-intensity light (Evans and Rawson 1970).

In the experiment with Triple Dirk under high light intensities, sterilization of either the first or second florets of the central spikelets led to a higher grain set and a highly significant increase in grain yield per ear. Under the lower light intensity of the second experiment there was no comparable increase in grain yield, although there was a large increase in the amount of labelled flag leaf assimilate translocated to ears in which the first florets were sterilized. Nor was any increase found in the already high grain yield of ears of Late Mexico 120.

For the summer experiment with Triple Dirk, the 20% increase in grain yield following partial sterilization of the ears suggests that yield was not limited by the

supply of assimilates. Similarly, however, one can also conclude that grain yield was not limited by storage capacity, since heavier spikelets and grains were also obtained with partial sterilization, and because grain size was greater in ears which developed in autumn. Bingham (1967) also found a progressive increase in mean weight per grain with progressive reduction in grain number per ear, even though the increase in grain weight at each stage did not fully compensate for the reduced grain number. Thus, neither storage capacity alone, nor supply of assimilates alone, limited grain yield in the first experiment with Triple Dirk. Either some other process, such as the translocation of assimilates to and within the ears, was limiting, or there were complex feed-back effects between the supply of and demand for assimilates.

V. Acknowledgments

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