# THE PATTERN OF GRAIN SET WITHIN EARS OF WHEAT

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[Manuscript received 10 August 1971]

*Abstract*

Experiments involving sterilization, or emasculation and delayed pollination, of the basal florets of central spikelets of wheat ears were carried out in the field, in England and Mexico, and in the Australian phytotron, to investigate how grain set in those florets influences that elsewhere in the ear.

In intact ears of three cultivars of winter wheat, Cappelle-Desprez, Maris Ranger, and Maris Nimrod, only about half of the florets which differentiated in the central spikelets developed green anthers, even fewer reached anthesis, and still fewer set grains. Florets reaching anthesis within 2 days of the earliest florets set grain regardless of their position in the ear, but in later florets those towards the base of the ear were more likely to set grain.

In field experiments with these varieties, and also with the spring cultivar Triple Dirk, sterilization of basal florets of up to eight central spikelets in each ear resulted in more grains being set in the distal florets of those spikelets.

Experiments with Triple Dirk in the phytotron, in which the basal florets were emasculated before anthesis but pollinated at various times thereafter, showed that most ovaries remained viable up to 5 days after anthesis, and that both emasculation and delayed pollination increased grain set above that in intact ears.

## I. Introduction

Grain set in wheat can be reduced by adverse conditions prior to and during anthesis, through effects on floret development and fertilization, and also by interactions between florets at the time of anthesis. Rawson and Evans (1970) found that sterilization of the basal florets of the central spikelets of ears of Triple Dirk wheat 2 days before anthesis led not only to compensatory grain setting in the normally empty distal florets of the same spikelets, but also to additional grain setting at the top and bottom of the ear, resulting in a 20% increase in grain weight per ear. These experiments suggest, therefore, that the development of grains in the earliest florets to reach anthesis inhibited grain set in later ones, and that grain yield under these conditions was limited more by grain set than by the supply of assimilates.

In extending these experiments our objectives were:

(1) to see whether florets which fail to set grain in intact ears are characterized by their position in the ear or by the interval of time between their anthesis and that of the earliest florets;

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(2) to identify the stage at which the earliest florets inhibit grain set in the later ones, by delaying their pollination for varying intervals of time;

(3) to see whether compensatory or increased grain set could be induced under field conditions, or in cultivars which set more grains per spikelet than Triple Dirk sets. The field experiments were done at Obregon, Mexico, with Triple Dirk, and at Cambridge, England, with three cultivars of winter wheat. Triple Dirk was also used in further experiments in the phytotron at Canberra.

## II. Materials and Methods

### (*a*) *Experiments at Cambridge*

Autumn-sown plants of three winter cultivars—Cappelle-Desprez, Maris Ranger, and Maris Nimrod—were dissected at 4-day intervals from inflorescence initiation until 13 days after anthesis in order to follow the course of floret differentiation. For this purpose, detailed measurements of anther and ovary development were confined to the eighth spikelet up from the base of the ear. For each variety the date of anther dehiscence at each floret position was recorded in six intact ears, to determine the relation between time of anthesis and eventual grain set.

Before anthesis, for each variety at least 20 pairs of ears, matched for spikelet number and other characteristics, were selected. One randomly chosen member of each pair was kept as a control, the other having the basal floret of the eight central spikelets sterilized by removal of both anthers and stigma. Four weeks later the number and position of all grains were recorded.

### (*b*) *Experiment at Obregon*

Eight groups of four matched ears on field-grown plants of two cultivars, Triple Dirk and Pitic, were chosen before anthesis. One ear of each group was kept as a control, and in the others the basal florets of either 4, 6, or 8 central spikelets were sterilized. The pattern of grain set within each ear was recorded at maturity. Results with Pitic are not presented since the ears proved to be extremely variable in grain set.

### (*c*) *Experiments at Canberra*

Plants of Triple Dirk were grown in a phytotron glasshouse at 21/16°C under a day length of 16 hr, with nutrient solution and water supplied daily. Three days before anthesis the basal florets of the eight central spikelets of groups of 11–18 main-shoot ears were emasculated by removing the anthers, leaving the stigmas intact. The emasculated florets were covered individually with transparent conical hoods of adhesive tape to prevent fertilization until they were pollinated by hand at anthesis of the earliest florets or at intervals up to 10 days later. Patterns of grain set were recorded 4 weeks after anthesis. In the first experiment only main-shoot ears with 16 spikelets were used, and only ears with 15 spikelets in the second experiment. Groups of comparable ears reaching anthesis at the same time provided unemasculated controls. Incident radiation during the grain filling period averaged 622 cal $cm^{-2}$ $day^{-1}$ in the first experiment, and 395 cal $cm^{-2}$ $day^{-1}$ in the second.

## III. Results

### (*a*) *Floret Development and Grain Set*

Plants of Cappelle-Desprez, Maris Nimrod, and Maris Ranger all reached the double ridges stage of inflorescence development by April 24, 1970, and had initiated their terminal spikelet, and anther primordia on the most advanced spikelet, by

May 7. The number of florets initiated and the number with anther primordia, continued to increase throughout the next 3 weeks. By June 1, 9 days before anthesis began in all three cultivars, 7–8 florets had been initiated on the eighth spikelet up from the base of the ear (see Table 1). In the following 9 days peduncle growth was rapid, no more florets differentiated, and the uppermost ones showed signs of regression, becoming opaque and losing turgidity. However, nearly all those with green anthers before rapid peduncle elongation set in appeared to be viable. Most of these anthers dehisced in Maris Ranger and Maris Nimrod, whereas in Cappelle-Desprez those in the uppermost florets failed to do so (Table 1). In Maris Ranger failure in the uppermost florets became evident within 5 days of the beginning of anthesis, the ovaries failing to elongate and becoming shrunken; no further failure occurred after that stage. Fewer florets failed in Maris Nimrod and they did so rather later, between 5 and 9 days after anthesis.

Despite these differences between the three cultivars, it is clear that the failure of well-developed florets to set grain occurred mainly at anthesis and during the following week.

TABLE 1

DEVELOPMENT OF FLORETS WITHIN THE EIGHTH SPIKELET FROM THE BASE OF EARS OF THREE WHEAT CULTIVARS AT VARIOUS STAGES

| Days before (−) or after (+) anthesis began | Stage of floret development | No. of florets | | |
|---|---|---|---|---|
| | | Cappelle-Desprez | Maris Ranger | Maris Nimrod |
| (a) −9 | anther primordia | 7·5 | 7·8 | 7·8 |
| (b) −1 | green anthers | 4·3 | 4·8 | 4·8 |
| (c) Anthesis | dehiscent anthers | 3·5 | 4·5 | 4·5 |
| (d) +5 | viable ovaries | 3·5 | 3·5 | 4·5 |
| (e) +9 | viable ovaries | 3·5 | 3·3 | 4·0 |
| (f) +13 | viable ovaries | 3·5 | 3·3 | 4·0 |

### (*b*) *Pattern of Anthesis and Grain Set*

Probably because of hot, dry weather at the time, anthesis within each ear was almost completed within an interval of 5 days. Average profiles of time of anthesis in Cappelle-Desprez and Maris Ranger ears are shown in Figure 1, in which the hatched areas indicate those positions where more than half of the anthesing florets failed to set grain. In Cappelle-Desprez virtually all florets anthesing within 2 days of the earliest set grain. Of those reaching anthesis on the third day many in the upper part of the ear failed to set grain, while of florets anthesing even later, only those at the base of the ear set grain. The pattern was similar in Maris Ranger and Nimrod except that third florets of the uppermost spikelets which reached anthesis on the second day failed to set grain, whereas florets in basal spikelets which reached anthesis up to 3 days later often set grain. Clearly, position of the floret within the ear is of more importance than time of anthesis in determining whether grains will set, late florets of lower spikelets having some advantage over earlier florets of upper

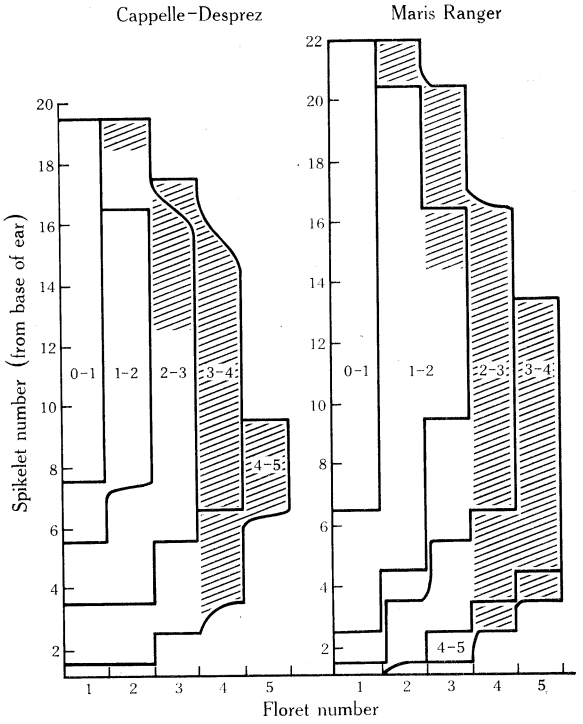


Fig. 1.—Profiles of time of anthesis and of grain setting within ears of Cappelle-Desprez and Maris Ranger wheat. The numbers indicate average days to anthesis of a particular floret after that in the earliest floret. The hatched areas indicate positions where more than half of the anthesing florets in six ears failed to set grains.

TABLE 2

EFFECT OF STERILIZATION OF THE BASAL FLORETS OF THE CENTRAL SPIKELETS ON THE NUMBER OF GRAINS SET IN EARS OF FOUR WHEAT CULTIVARS GROWN IN THE FIELD

| Cultivar | No. of florets sterilized | No. of grains per ear | | Grains per ear in third (III) or fourth (IV) florets | | |
|---|---|---|---|---|---|---|
| | | Control | Treated | Control | | Treated |
| Cappelle-Desprez | 8 | 41·9 | 39·0 | 1·0 | (IV) | 3·6 |
| Maris Ranger | 8 | 42·7 | 41·3 | 0·2 | (IV) | 2·7 |
| Maris Nimrod | 8 | 52·8 | 48·7 | 5·9 | (IV) | 8·4 |
| Triple Dirk | 4 | 35·5 | 34·5 | 2·6 | (III) | 4·4 |
| | 6 | | 33·7 | | | 6·3 |
| | 8 | | 32·6 | | | 6·5 |

spikelets in this respect. In one ear of Maris Ranger, for example, several florets anthesing on the first day in upper spikelets failed to set grain, whereas a basal floret anthesing 8 days later succeeded.

### (*c*) *Floret Sterilization Experiments in the Field*

The results of the floret sterilization experiments in the field at Cambridge and Obregon are summarized in Table 2. In no case was there an increase in the total number of grains set following sterilization, such as was found in the earlier phytotron experiments, but in all cases there was compensatory grain setting, particularly in the distal florets of the same spikelets. This was so even in Maris Nimrod which already had many grains in fourth florets of control ears, but the compensation was more pronounced in the varieties setting fewer grains. Clearly, many of the upper florets which fail to set grain in the field are quite capable of doing so when grain set is prevented in the basal florets.

### (*d*) *Effects of Delayed Pollination*

In preliminary experiments with Triple Dirk grown in a phytotron glasshouse it was found that a high proportion of the basal florets emasculated before anthesis were apparently fertilized in the first few days after anthesis unless they were covered at the time of emasculation with individual hoods. When this was done it was found that most ovaries remained viable and able to be fertilized up to 5 days after anthesis, as previously found by Hoshikawa (1961) and Imrie (1966), and that they continued to expand throughout that interval.

The results of two experiments in which pollination of the basal florets of the eight central spikelets was delayed for various intervals are given in Table 3. Because damage to florets can occur at emasculation and at the positioning and removal of the hoods, the appropriate controls were thought to be emasculated ears pollinated at the time of first anthesis, rather than intact ears. However, comparison of the ears pollinated on the day of first anthesis with the non-emasculated ears in experiment B reveals that two more grains per ear were set in the emasculated and hand-pollinated ears, mainly in the basal spikelets. This difference does not quite reach significance at $P = 0{\cdot}05$, but given the many chances of injury to the emasculated, hooded florets, it suggests that floret development or grain set in these regions was to some extent inhibited by the presence of anthers in the basal florets during the 3 days before anthesis.

In both experiments, the number of sterile basal florets in the central spikelets remained low in ears pollinated up to 6 days after anthesis, indicating that their ovaries remained viable through that period. Further delay in pollination resulted in failure of grain set. In the non-pollinated ears the hoods were removed 11 days after anthesis and failure of grain set was virtually complete.

Few third floret grains were set in intact ears under the conditions of these experiments, but with delay in pollination their number rose in parallel with the failure of grain set in the basal florets, in both experiments. This suggests that in Triple Dirk the ovaries of the basal florets in some way inhibit ovary development in the third florets of those spikelets so long as they are viable. As they begin to fail 5–6 days after anthesis, grains in the third florets can set.

TABLE 3

EFFECT OF DELAYED POLLINATION OF THE BASAL FLORETS OF THE EIGHT CENTRAL SPIKELETS ON THE PATTERN OF GRAIN SET IN MAIN-STEM EARS OF TRIPLE DIRK WHEAT GROWN AT 21/16°C UNDER 16-HR PHOTOPERIODS

| | | | | | | |
|---|---|---|---|---|---|---|
| | | Experiment A (ears with 16 spikelets) | | | | |
| Days after anthesis at pollination | | | 0 | 3 | 6 | not pollinated |
| No. of replicates | | | 15 | 14 | 14 | 11 |
| No. of grains per ear | | | 29·4±0·87 | 31·1±0·82 | 30·6±0·99 | 29·7±0·76 |
| No. of grains per top 4 spikelets | | | 4·7±0·22 | 5·6±0·31 | 5·7±0·19 | 5·7±0·27 |
| No. of grains per mid 8 spikelets | | | 15·4±0·36 | 16·3±0·44 | 13·9±0·51 | 12·8±0·35 |
| No. of grains per lowest spikelets | | | 9·2±0·61 | 9·2±0·54 | 11·0±0·53 | 11·2±0·69 |
| No. third floret grains per ear | | | 1·4±0·46 | 3·4±0·77 | 6·4±0·69 | 6·9±0·61 |
| No. of sterile basal florets in central 8 spikelets | | | 0·6±0·25 | 1·7±0·37 | 6·5±0·29 | 8·0±0·00 |
| | | Experiment B (ears with 15 spikelets) | | | | |
| Days after anthesis at pollination | ears not emasculated | 0 | 2 | 4 | 6 | not pollinated |
| No. of replicates | 10 | 16 | 14 | 18 | 15 | 18 |
| No. of grains per ear | 23·6±0·85 | 25·6±0·82 | 26·7±0·77 | 27·6±0·73 | 25·8±0·72 | 26·8±0·68 |
| No. of grains per top 4 spikelets | 4·3±0·56 | 4·8±0·36 | 5·1±0·25 | 6·2±0·25 | 6·1±0·24 | 6·6±0·22 |
| No. of grains per mid 8 spikelets | 15·3±0·30 | 15·3±0·29 | 15·9±0·27 | 15·7±0·57 | 14·1±0·48 | 12·9±0·37 |
| No. of grains per lowest spikelets | 4·0±0·42 | 5·5±0·34 | 5·7±0·41 | 5·7±0·24 | 5·4±0·34 | 7·2±0·30 |
| No. of third floret grains per ear | 0·5±0·17 | 1·8±0·42 | 1·6±0·47 | 1·9±0·49 | 3·1±0·49 | 6·7±0·46 |
| No. of sterile basal florets in central 8 spikelets | 0·6±0·27 | 1·9±0·33 | 0·9±0·23 | 1·6±0·42 | 4·3±0·39 | 7·9±0·06 |
| Grain weight per ear 30 days after anthesis (mg) | 620±55·6 | 797±42·7 | 806±58·7 | 782±31·9 | 782±28·5 | 795±40·3 |

In both experiments, delayed pollination of the basal florets of the central spikelets resulted in increased setting of grains in spikelets above and below the emasculated zone. Consequently, grain number per ear was higher than in the ears pollinated at the beginning of anthesis. This was not reflected in increased grain weight per ear in experiment B, but grain weight in the emasculated ears was 26–30% higher ($P < 0{\cdot}02$) than that in intact ears with the same spikelet number and reaching anthesis on the same day.

## IV. Discussion

Ways of increasing the storage capacity of cereal ears, and insight into their mechanisms, would be valuable in the analysis of the processes limiting grain yield, and in defining objectives for increasing potential yields in new cultivars. Earlier experiments with Triple Dirk wheat grown in the phytotron (Rawson and Evans 1970) showed that increased grain set following sterilization of basal florets in the central spikelets could result in a 20% increase in grain yield per ear. Under these conditions, then, the capacity for storage rather than that for photosynthesis or translocation was apparently limiting grain yield.

Even greater increases in grain yield per ear were found in the experiments reported here with Triple Dirk grown in the phytotron (Table 3). But in comparable experiments in the field, with Triple Dirk and other cultivars, no increases in grain setting over that in intact ears was found, although there was considerable compensatory grain setting in the distal florets (Table 2). Nevertheless, there are clearly many florets which reach anthesis and are competent to set grains but fail to do so, as was also suggested by the developmental data in Table 1. Konovalov (1966) mentions that partial sterilization of wheat ears in the field led to some compensatory grain setting in more distal florets, but in his experiments no increases in grain yield per ear were obtained. Details of his sterilization treatments are not given, but in some experiments at least the central spikelets were the ones left intact, in which case increase in yield would not be expected.

As to the mechanisms involved in the inhibition of grain setting in the more distal florets and spikelets, other experiments suggest that they are more likely to be correlative and hormonal in nature rather than due to competition for assimilates. Detailed measurements of the carbon balance sheet of wheat ears at anthesis suggested that the ears are largely self-supporting at that stage (Evans and Rawson 1970). Grain set can be reduced by low light intensities at anthesis (e.g. Wardlaw 1970) but this need not be due to reduced assimilate supply. Rawson (unpublished data) found shading of ears to reduce grain set substantially, whereas complete inhibition of ear photosynthesis by treatment with DCMU had no effect on set, suggesting that photomorphogenic reactions are involved, but intensified competition between florets for assimilates may have contributed.

The delayed pollination experiments give some insight into the sources and timing of the inhibitory effects. These appear to be twofold. First, the presence of well-developed anthers in basal florets of central spikelets prior to anthesis may inhibit grain set in spikelets at the top and base of the ear, presumably through effects on floret development. Secondly, the presence of viable ovaries in basal florets appears to prevent distal ovaries in the same spikelets from setting grain. Only when the

basal ovaries lost viability about 5 days after anthesis could grain set occur in the third florets, although they had reached anthesis, and their ovaries had presumably been fertilized, 2–3 days earlier (cf. Hoshikawa 1960).

Virtually nothing is known of the patterns of growth substance production and movement within cereal inflorescences, but these results suggest they must be examined before we can begin to understand the pattern of grain set and how it can be influenced.

## V. Acknowledgments

We are grateful to Mrs. Kati Bretz for technical assistance with these experiments, and to Dr. I. F. Wardlaw for discussion of the results.

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