SPIKELET NUMBER, ITS CONTROL AND RELATION TO YIELD PER EAR IN WHEAT

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Summary

For 12 cultivars of wheat grown under a 21°C day/16°C night temperature regime, spikelet number was closely related to grain number, but not to grain yield per ear as individual grain weights differed considerably between cultivars. However, when spikelet number was varied by day length or vernalization treatment, grain yield per ear was clearly dependent on spikelet number within each cultivar.

An increase in spikelet number per ear was always associated with longer development. In cultivars with a pronounced response to vernalization (e.g. Late Mexico 120), the length of the period to floral initiation was of prime importance, because during this time potential spikelet sites were established; once floral initiation occurred, development of the inflorescence proceeded rapidly, and few further spikelet primordia were differentiated. In cultivars with no vernalization response (e.g. Triple Dirk), the duration of the period from floral initiation to terminal spikelet formation, during which all the spikelet initials appeared, determined spikelet number. The spikelet number of cultivars with a slight response to cold was associated with the lengths of both these periods.

Spikelet number in Triple Dirk was modified by the number of long-day cycles to which plants were exposed; increase in the number of inductive cycles up to nine reduced the period from floral initiation to the appearance of the terminal spikelet, and also reduced spikelet number per ear from 24 to 17. Exposure to only two long-day cycles resulted in production of double ridges but caused slow inflorescence development thereafter, and there was an appreciable lag before a terminal spikelet appeared. However, development could be accelerated by exposure to further inductive cycles at any time before the spikelet primordia became swollen.

I. Introduction

Farrer (1898) early recognized the need for wheat varieties with rapid development which complete growth during the favourable part of the year. The problem is how to reduce the growing period effectively without loss in yield. It is likely that some phases of development are less closely linked to yield than are others and could therefore be curtailed more readily. Hence, an initial objective is to establish which phases are critical to yield determination, and which are less important.

The central aim of this paper is to examine factors affecting ear size, or more specifically, spikelet number, one of the attributes of yield, particularly to delimit the phases most critical to its expression. It was pointed out 70 years ago that high-yielding wheats should have large ears (Farrer 1898) and recently Donald (1968) has recommended this as a characteristic of a wheat ideotype. The significance of large ears to yield was shown experimentally in a study of spring and winter wheats

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grown under identical conditions (Pinthus 1967). Winter wheats outyielded spring cultivars and the difference in yield was due almost entirely to the number of spikelets produced per ear, as the number of grains per spikelet was relatively constant.

The period of growth during which spikelet number is determined may therefore be regarded as one of the critical phases of the wheat plant. However, there are relatively few studies that have examined the effects of environmental factors on spikelet number per ear and have determined the stages at which the ear is most plastic. It is known that spikelet number may be varied by plant spacing (e.g. Puckridge 1968), by the level of nitrogen nutrition (e.g. Single 1964), by day length [e.g. Wislocka 1959; cf. also Paleg and Aspinall (1966) for barley], and by temperature and light intensity (e.g. Friend 1965).

In the first part of the present study (expt. 1) 12 spring wheat cultivars, grown under conditions of high fertility and at two temperatures, are examined to determine the range of spikelet number between varieties, the degree of dependence of grain yield on spikelet number, and the relationship between the duration of developmental phases and spikelet number. Studies in the second part (expts. 2–6) deal with the effects on spikelet number and on grain yield per ear of altering the duration of the early developmental phases by variations in day length and by vernalization treatments.

II. Materials and Methods

(a) *Experiment 1*

In this experiment, 12 wheat cultivars (Table 1), ranging from very early to late-maturing, were grown during the summer period in glasshouses of CERES, the Canberra phytotron (see Morse and Evans 1962). The natural day length was extended to 16 hr by incandescent lamps and the two regimes of day/night temperature were 21/16°C or 15/10°C; the day temperature applied from 8.30 a.m. to 4.30 p.m. Plants were grown, three per 5-in. pot, in a 1 : 1 mixture of perlite and vermiculite and were supplied with a modified Hoagland's solution in the morning and with water each afternoon.

Three plants (one pot) of each cultivar were harvested every few days throughout growth for dissection of the main stem; the apex was measured and examined for stage of development according to the criteria of Friend, Fisher, and Helson (1963). A final harvest of 12 plants of each cultivar was taken at maturity when spikelet and grain numbers and grain weights of the main-stem ear were determined.

(b) *Experiments 2–6*

Triple Dirk wheat was chosen in experiments 2–5 for studies of the effects of day length on spikelet number because of its responsiveness to photoperiod. Seeds were sown, three per 5-in. pot and given the same water and nutrient regime as in experiment 1. The temperature regime was 15/10°C which was preferred to 21/16°C because the slower development allowed more accurate reduction into stages. The plants for day-length studies were grown throughout in "B" cabinets. They remained for 20 days after seedling emergence under short days of 8 hr natural daylight to make them more responsive to subsequent exposure to long days of 16 hr. Plants were usually retained in long days for selected periods before being once more returned to short days where they remained until harvest; this pattern was varied slightly in experiment 4.

Dissections were made on three occasions each week when the length and stage of development of the apex of the main stem was determined.

In experiment 6 the effect of cold treatment of imbibed seeds on subsequent ear growth and on spikelet development was examined for Late Mexico 120 wheat, a cultivar responding to several weeks of vernalization. Seeds were soaked at room temperature for 8 hr and then kept on moist filter paper in Petri dishes at 2–4°C. After 0, 2, 4, 6, 8, 10, and 12 weeks, seeds were planted out as for experiment 1 in the open glasshouse at 21/16°C, under 16-hr days.

Dissections of six plants were made three times weekly when main-stem apices were examined and measured. A final harvest was taken when the plants under each regime were mature.

III. Results

(a) *Varietal Variation in Spikelet Number (Expt. 1)*

(i) *Spikelet Number and Yield*

Spikelet numbers differed greatly between cultivars grown at 21/16°C (Table 1) with Mexico 120 producing 66% more spikelets than Sunset. This difference was also reflected in the number of grains formed per ear (77% more). The Mexican cultivars, especially Pitic and Mexico 120, all had high spikelet and grain numbers. In general, grain number per ear increased with more spikelets. However, single grain weights differed significantly between cultivars but were not always in inverse proportion to the number of grains per ear.

Table 1

MAIN-STEM EAR ATTRIBUTES OF 12 CULTIVARS OF WHEAT GROWN AT TWO TEMPERATURE REGIMES

Results are means for 12 plants of each cultivar

Cultivar	Temperature Regime 21/16°C				Temperature Regime 15/10°C			
	No. of Spikelets per Ear	No. of Grains per Ear	Total Grain Wt. per Ear (mg)	Wt. of 1000 Grains (g)	No. of Spikelets per Ear	No. of Grains per Ear	Total Grain Wt. per Ear (mg)	Wt. of 1000 Grains (g)
Sunset	14·9	26	791	30·1	14·2	37	1763	48·0
Festival	16·0	30	1028	34·7	16·0	44	1874	42·6
Triple Dirk	16·2	30	1359	45·0	15·0	38	2075	54·3
Marquis	17·0	29	1090	37·8	15·8	42	1775	42·1
Bencubbin	17·3	37	1815	48·3	15·8	33	2103	64·7
Gabo	17·8	33	1288	39·6	16·6	34	2035	60·0
Heron	18·3	43	1262	29·0	16·5	41	1782	43·7
Pinnacle	20·0	31	1523	49·1	18·1	37	1778	48·0
Festiguay	20·1	38	1446	38·0	17·8	37	1340	35·7
Nainari	20·1	58	1986	33·8	17·8	46	2441	53·3
Pitic	24·5	66	2102	31·8	18·7	63	2565	40·7
Mexico 120	24·8	46	1571	34·1	18·3	44	1742	39·6

Varietal differences in spikelet number were less marked at 15/10°C and the order of spikelet productivity was slightly changed (Table 1). Pitic, with the highest spikelet number, produced only 32% more spikelets than Sunset.

(ii) *Spikelet Number and the Duration of Developmental Stages*

In this study, it was hoped to correlate spikelet number with the duration of one or more of the early developmental phases and to this end the lengths of the period from sowing to floral initiation or double ridges (phase I), from double ridges to

TABLE 2

NUMBER OF SPIKELETS, LEAF NUMBER, AND THE DURATION OF DEVELOPMENTAL PHASES OF 12 CULTIVARS OF WHEAT GROWN AT TWO TEMPERATURE REGIMES

Developmental phases I–III are as defined in the text. Results are means for 12 plants of each cultivar

Cultivar	Temperature Regime 21/16°C					Temperature Regime 15/10°C				
	No. of Spikelets	No. of Leaves	Duration of Phase I (days)	Duration of Phase II (days)	Duration of Phase III (days)	No. of Spikelets	No. of Leaves	Duration of Phase I (days)	Duration of Phase II (days)	Duration of Phase III (days)
Sunset	14·9	6·3	13	5	18	14·2	6·0	21	9	36
Festival	16·0	7·3	16	11	15	16·0	6·7	24	15	30
Triple Dirk	16·2	7·3	14	10	17	15·0	7·0	23	14	31
Marquis	17·0	8·6	15	14	14	15·8	7·3	24	15	32
Bencubbin	17·3	7·8	18	14	13	15·8	8·3	28	15	32
Gabo	17·8	8·6	18	14	16	16·6	8·0	25	16	34
Heron	18·3	10·1	26	18	19	16·5	9·3	31	22	22
Pinnacle	20·0	12·2	27	20	17	18·1	9·0	33	24	25
Festiguay	20·1	13·0	27	22	22	17·8	10·0	36	21	32
Nainari	20·1	10·0	25	18	16	17·8	8·0	30	20	31
Pitic	24·5	11·0	22	24	12	18·7	9·3	30	21	31
Mexico 120	24·8	11·1	21	24	15	18·3	9·3	30	21	34

terminal spikelet production (phase II), and from terminal appearance to ear emergence (phase III) were noted for each cultivar (Table 2). Pugsley (1966) has indicated that spikelet number and the final number of foliage leaves on the main stem are related—leaf number being an indication of the length of the vegetative phase of a stem. Therefore leaves were counted in this trial.

Final leaf number was generally related to spikelet number within one temperature regime in the present study, as indeed was the length of the period to floral initiation (phase I). Some cultivars did not entirely fit this pattern. Festiguay, for example, initiated 2 days later and produced three leaves more than Nainari although the two cultivars had the same spikelet number. In spite of these variations, the overall pattern does suggest that the duration of the period from sowing to initiation has some bearing on the number of spikelets produced per ear. However, it is clear that the length of the period to initiation is not the sole determinant of spikelet number, as some cultivars initiated earlier than others, yet produced more spikelets (compare Mexico 120 and Festiguay grown at 21/16°C).

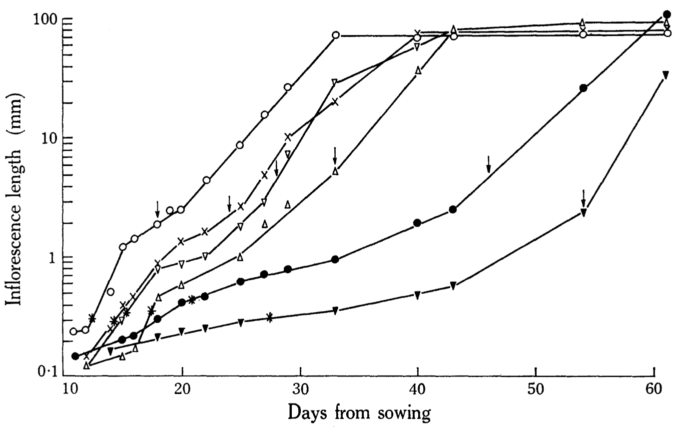

Fig. 1.—Extension growth of the main-stem inflorescence of six wheat cultivars grown at 21/16°C:
○ Sunset
× Triple Dirk
▽ Festival
△ Bencubbin
● Mexico 120
▼ Festiguay
The times of floral initiation (*) and terminal spikelet appearance (↓) are shown.

The phase from initiation to the appearance of the terminal spikelet was usually shorter than that from sowing to initiation, but the durations of the phases were often related; cultivars initiating later also took longer to produce a terminal spikelet. In almost every case within one temperature regime, higher spikelet number was found with a longer period from floral initiation to terminal spikelet appearance. When plants were grown at 15/10°C they had fewer spikelets, but the length of phase II, relative to the length of the period from sowing to ear emergence, was reduced. In fact, three of the cultivars for which spikelet number was most affected by the reduction in temperature, completed this phase more rapidly at 15/10°C than at 21/16°C, indicating the importance to spikelet number of the period from initiation to terminal production.

There was no apparent relationship between spikelet number and the time from terminal production to ear emergence.

(iii) *Ear Growth and Development*

Inflorescences of the early emerging cultivars (see Table 2) extended more rapidly at 21/16°C than those of late wheats (Fig. 1). The late cultivars were characterized by a period of slow extension growth after initiation which was followed by a rapid phase commencing shortly before the terminal spikelet was laid down.

The pattern of apex elongation was much the same at 15/10°C and 21/16°C, but the range between slow and fast cultivars was reduced at the lower temperature.

The cultivars in experiment 1 could be subdivided into two groups as regards spikelet production. The first was composed of the early cultivars with a low final spikelet number, the spikelet initials appearing at a constant rate (Fig. 2) in spite of the changes in length growth rate. Late cultivars with higher spikelet numbers made up the second group; these had an initial period during which spikelet primordia appeared relatively slowly, followed by a phase with a rapid rate like that of the early cultivars. The wheats used in this trial were not vernalized and some of the later cultivars show a response to cold. The differences between late and early cultivars may have been at least partially linked with their cold requirement.

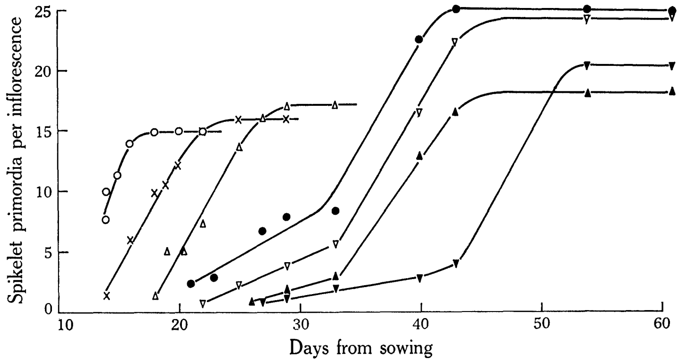

Fig. 2.—Spikelet primordia appearance on the main-stem inflorescence of seven wheat cultivars:
○ Sunset
× Triple Dirk
△ Bencubbin
● Mexico 120
▽ Pitic
▲ Heron
▼ Festiguay

(b) *Control of Spikelet Number by Day Length and Vernalization* (*Expts. 2–6*)

(i) *Modification of Spikelet Number by Photoperiod Control*

Experiment 2 was designed to determine the extent to which spikelet number could be modified by day length in one cultivar, Triple Dirk. Plants were exposed to short days (SD) for 20 days from sowing, then to long days (LD) for 0, 2, 3, 4, 5, 6, 8, 9, 11, 13, 14, 15, 16, 17, or 19 days, after which they were returned to SD. One harvest was taken 56 days from sowing (36 days after completion of the first LD and prior to earing) when eight main-stem apices from each treatment were dissected. In addition, three plants were harvested daily from the 19 LD treatment to determine the date of floral initiation for that treatment.

The number of LD to which the plants were exposed affected both the number of spikelets and the size and stage of development of the inflorescence (Fig. 3). Exposure to 9 LD or more reduced spikelet and leaf number to a minimum. With fewer than 9 LD, spikelet number progressively increased from 17 to a maximum of 24 per ear when plants were retained under SD throughout, though the effect on leaf number of the main stem was small. Floral initiation of plants remaining in LD occurred 9 days after the first LD and as no further reduction in spikelet number resulted from more than 9 LD cycles, it is likely that the terminal spikelet had been committed by this time.

Experiment 3 examined the effects of day length on the durations of the pre- and post-inflorescence initiation phases and on the rate of spikelet production. Plants were exposed to 0, 1, 2, 5, 8, or 12 LD after the initial period of 20 SD. Six plants per treatment were dissected at 2- and 3-day intervals and a final harvest was made shortly after the terminal spikelet had differentiated in each treatment.

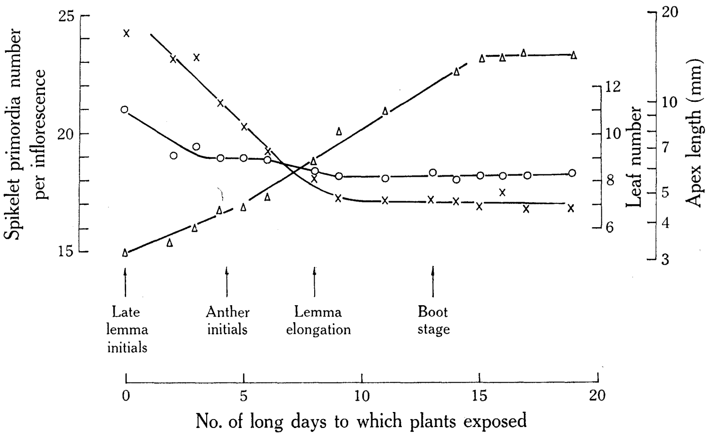

Fig. 3.—Number of spikelet primordia (×) and the length (△) and stage of development of the main-stem inflorescence of Triple Dirk wheat grown at 15/10°C and exposed from seedling emergence to 20 short days, then to various numbers of long days followed by short days and harvested when 56 days old. Foliage leaf number of the main stem is shown (○).

Plants exposed to 1 LD became floral at approximately the same time as those retained in SD throughout, but exposure to 2 LD resulted in much earlier appearance of double ridges (Fig. 4). If plants were exposed to more than 2 LD, inflorescence initiation was hastened further by only 1 or 2 days, but the terminal spikelet was produced more rapidly and at a lower spikelet number.

The time of initiation was difficult to ascertain exactly because advanced double ridges were not apparent on the 2, 5, and 8 LD apices for some time after double ridges first appeared. The period during which the ridges were indistinct was longer for plants given fewer LD (see the dotted lines on Fig. 4). If initiation is taken as the time of first appearance of double ridges, then for the 12, 8, 5, 2, 1, and 0 LD treatments, floral initiation occurred approximately 9, 10, 10, 11, 25, and 29 days after the first LD, and the period from initiation to terminal formation for each of these treatments was 17, 21, 23, 28, 17, and 28 days respectively. The conclusion from these results is that 2 or more LD cause initiation at more or less the same time and that the major effect of additional LD is on the duration of the period from initiation to appearance of the terminal spikelet.

Discrepancies in final spikelet number between equivalent treatments in experiments 2 and 3 were probably due to differences in total radiation (cf. Friend 1965); experiment 2 was completed in late summer and experiment 3 in early winter.

It is not clear from experiments 2 and 3 how long after initiation day length could influence final spikelet number; experiment 4a, commenced in June (winter), was designed to examine this. After the initial period of 20 SD, plants were exposed to 2 LD then returned to 2, 5, 8, 10, 15, 20, 30, or 50 SD, and finally moved back to LD where they remained until harvested. One harvest was taken at ear emergence when the spikelet numbers of 18 plants were determined. In essence, these treatments were designed to give an initial stimulus to flowering and additional boosts at different times thereafter.

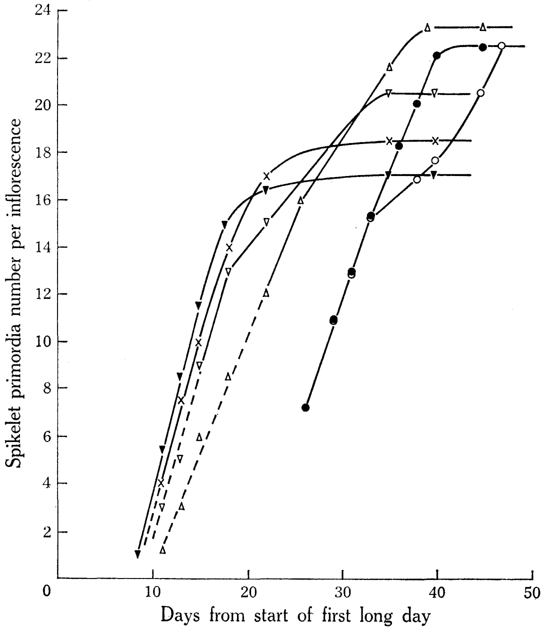

Fig. 4.—Spikelet primordia appearance on the main-stem inflorescence of Triple Dirk wheat grown at 15/10°C and exposed from seedling emergence to 20 short days, then to 0 (○), 1 (●), 2 (△), 5 (▽), 8 (×), or 12 (▼) long days, followed by short days. The period during which double ridges were indistinct is shown as a dotted line.

Final spikelet number was affected by LD introduced at up to 30 days after the first two inductive cycles, the effect being greatest when the additional LD were given between the eighth and the fifteenth day (Table 3). The effect after 20 SD or more, when double ridges became clearly defined in the 2 LD treatment of experiment 3, was small, indicating that by this stage the terminal spikelet was already committed. This is not in accordance with the suggestion of Nicholls and May (1963) for barley that the terminal spikelet is determined at the stage of anther initials. These results suggest much earlier commitment.

Experiment 4b, begun in December, replicated experiment 4a but six plants from each treatment were dissected every 2 days to examine the pattern of spikelet production. Spikelet numbers were higher than in the previous study, presumably due to greater daily radiation, but otherwise the results followed the same pattern. Additional LD had little effect on the rate at which spikelet primordia appeared (Fig. 5), but accelerated formation of the terminal spikelet.

In experiment 5, plants of Triple Dirk wheat sown in April, after an initial period of 20 SD were exposed to 2, 5, 8, or 12 LD, thus fixing their spikelet number per ear at 23, 22, 19, and 17 respectively. One harvest was taken at maturity when

TABLE 3

THE EFFECT ON SPIKELET NUMBER PER EAR OF EXPOSING PLANTS (CV. TRIPLE DIRK) FROM SOWING TO 20 SHORT DAYS, THEN 2 LONG DAYS FOLLOWED BY A VARYING NUMBER OF SHORT DAYS AND RETURN TO LONG DAYS

Values are means of 18 plants

No. of Short Days	No. of Spikelets per Ear ($\pm$ S.E.)	Effect/Day of Short Days on Spikelet No.	No. of Short Days	No. of Spikelets per Ear ($\pm$ S.E.)	Effect/Day of Short Days on Spikelet No.
					0·30
0	16·00 $\pm$ 0·017		15	19·98 $\pm$ 0·763	
		0·08			0·25
2	16·17 $\pm$ 0·013		20	21·22 $\pm$ 0·017	
		0·22			0·06
5	16·83 $\pm$ 0·013		25	21·50 $\pm$ 0·018	
		0·26			0·10
8	17·61 $\pm$ 0·015		30	22·00 $\pm$ 0·015	
		0·44			0
10	18·50 $\pm$ 0·017		50	22·00 $\pm$ 0·018	

the main ears of nine plants from each treatment were examined. Spikelet number, grain number, and grain weight were determined for these ears.

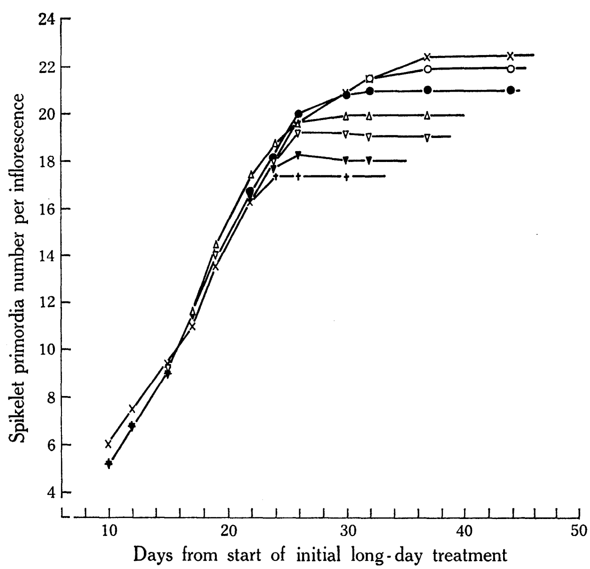

Fig. 5.—Spikelet primordia appearance on the main-stem inflorescence of Triple Dirk wheat grown at 15/10°C and exposed from seedling emergence to 20 short days, then to 2 long days followed by 2 (+), 5 (▼), 8 (▽), 10 (△), 15 (●), 30 (○), or 50 (×) short days and finally to long days.

An increase in spikelet number per ear was accompanied by an increase in grain yield per ear of over 30% (Table 4). This was due entirely to more grains being filled; individual grain weight remained relatively constant. One surprising finding, not found in a later summer trial, was that flag leaf size decreased with increase in spikelet number. However, in spite of its reduced size, the flag leaf could support a larger ear with more grains.

TABLE 4

EAR ATTRIBUTES OF WHEAT (CV. TRIPLE DIRK) AS AFFECTED BY CYCLES OF 2, 5, 8, OR 12 LONG DAYS

Long days commenced 20 days after sowing

No. of Long Days	No. of Spikelets per Ear (± S.E.)	No. of Grains per Ear (± S.E.)	Av. Weight of Each Grain (mg)	Total Grain Wt. per Ear (mg)	Flag Leaf Area (cm^2)
2	$23 \cdot 4 \pm 0 \cdot 53$	$37 \pm 1 \cdot 41$	55	2035	48
5	$22 \cdot 3 \pm 0 \cdot 94$	$38 \pm 0 \cdot 74$	50	1852	61
8	$19 \cdot 0 \pm 0 \cdot 46$	$31 \pm 1 \cdot 44$	56	1725	86
12	$16 \cdot 8 \pm 0 \cdot 49$	$28 \pm 1 \cdot 00$	53	1495	91

(ii) *Modification of Spikelet Number by Vernalization*

In experiment 1, plants grown at 15/10°C had fewer spikelets than those of the same cultivar grown at 21/16°C. Initiation occurred at a lower leaf number at the lower temperature although, because of slower leaf production, this was at a later point in time. Presumably plants became competent to flower at a lower leaf number at 15/10°C because vernalization proceeds slowly at 10°C (Gott 1961); several of the cultivars in this study have some response to cold.

Late Mexico 120, a cultivar with a major response to cold, was chosen for a study of the effects of vernalization on spikelet number and on grain yield. The effects were marked; 12 weeks cold reduced spikelet number on the main ear from 31 to 16 (Fig. 6) and grain yield from 3364 mg/ear to 1667 mg/ear, a reduction of 50% for both attributes. Grain production per ear was similarly related to spikelet number in plants from the intermediate treatments and, as shown for Triple Dirk, spikelet number was the main determinant of grain production as grain size did not differ significantly between ears (47·0 mg/grain for unvernalized plants and 48·8 mg/grain for plants vernalized for 12 weeks). Far fewer ears were produced on vernalized plants, the range being from between 8 and 12 for the unvernalized plants to 2–3 ears for plants vernalized for 12 weeks, so that total plant yields were much reduced by cold treatment.

As would be expected from the work of Gott (1961), the duration of the vernalization treatment affected the time of floral initiation; plants not exposed to cold produced double ridges some 40 days after sowing, while those vernalized for 12 weeks became floral only 12 days after they were planted out. At the time of floral initiation, the number of leaf primordia (potential spikelet sites) accumulated on the apex differed greatly between treatments (see arrows on Fig. 6) and this accounted largely for the difference in final spikelet number; almost all these leaf primordia eventually carried an axillary spikelet. The final spikelet number of plants vernalized for 0, 2, and 4 weeks was 12 greater than the number of unexpanded leaf primordia accumulated at floral initiation, while the final spikelet number of plants exposed to 6, 8, 10, or 12 weeks cold was 8 greater than the number of leaf primordia. The

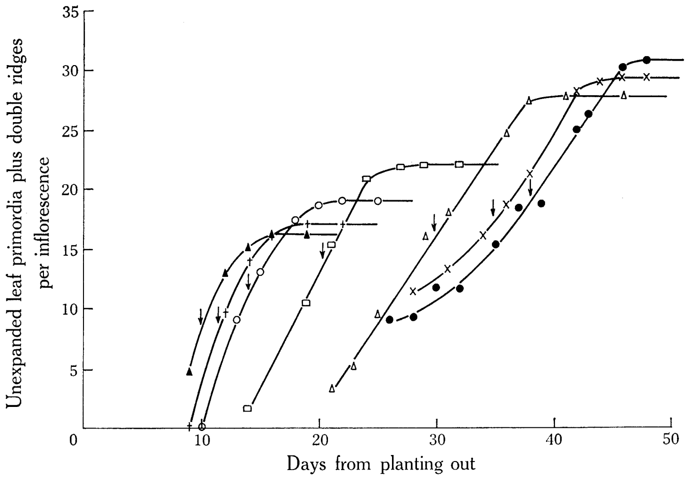

Fig. 6.—Spikelet primordia appearance on the main-stem inflorescence of Late Mexico 120 wheat grown at 21/16°C after imbibed seeds had been exposed to cold for 0 (●), 2 (×), 4 (△), 6 (□), 8 (○), 10 (+), or 12 (▲) weeks before planting. The numbers of unexpanded leaf primordia present at floral initiation are indicated by arrows.

differing number, between treatments, of spikelets without apparent sites at floral initiation was associated with the duration of the period from initiation to terminal spikelet appearance which was between 10 and 12 days for the treatments lasting 0,

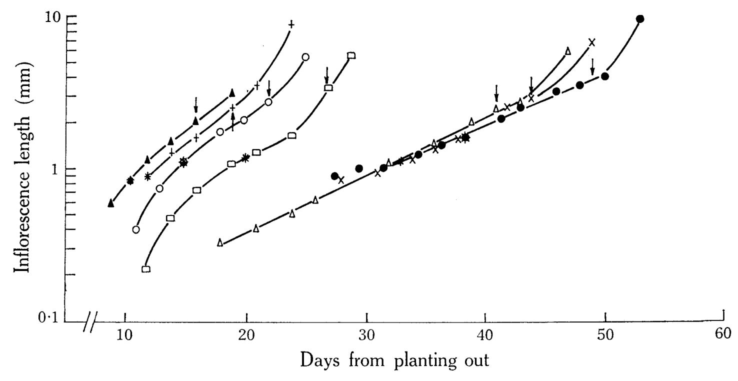

Fig. 7.—Extension growth of the main-stem inflorescence of Late Mexico 120 wheat grown at 21/16°C after imbibed seeds had been exposed to cold for 0 (●), 2 (×), 4 (△), 6 (□), 8 (○), 10 (+), or 12 (▲) weeks before planting. The times of floral initiation (*) and terminal spikelet appearance (↓) are shown.

2, and 4 weeks (these formed 12 spikelets more than the number of sites at initiation) and was approximately 7 days for other regimes (these produced 8 spikelets lacking sites at initiation). Clearly therefore, the spikelet number of cultivars responding to cold treatment is related particularly to the duration of the period prior to floral initiation when leaf primordia (potential spikelet sites) are laid down, and only partially to the length of the phase from initiation to appearance of the terminal spikelet.

Apex extension growth of plants vernalized for 0, 2, and 4 weeks followed a similar pattern although spikelet number was affected differently (Fig. 7), indicating that apex extension and spikelet number are controlled by a different mechanism. Plants subjected to 6 or more weeks cold treatment had apex growth curves similar to those of cultivars such as Sunset and Triple Dirk with no vernalization response (Fig. 1).

IV. Discussion

(a) *Relation between Spikelet Number and Grain Yield per Ear*

Pinthus (1967) showed for a range of winter and spring wheats that grain number was closely correlated with spikelet number per ear, but that weight of grain was not necessarily proportionate. Similarly, in the first part of the present study, grain number was related to spikelet number per ear for several cultivars grown at 21/16°C. Again, the relation between spikelet number and grain weight per ear was less close, as mean weight per grain differed between varieties. Spikelet number and grain yield per ear were not clearly related when plants were grown at 15/10°C, but at this regime there was little difference between varieties in spikelet number. However, when spikelet number was varied in one variety (Triple Dirk), by photoperiod manipulation, grain yield was closely related to spikelet number as both grain number per spikelet and individual grain weight were relatively constant regardless of spikelet number. The trial, in which spikelet number was varied between 31 and 16 and grain weight per ear between 3364 mg and 1667 mg in Late Mexico 120 by seed vernalization, also demonstrated the dependence of grain yield on spikelet number under these conditions.

The dependence of yield per ear on spikelet number in a single variety suggests that the size of the photosynthetic system is not the factor limiting yield, at least in Triple Dirk and Late Mexico 120 under these conditions, and that it is the number of grains set that is of prime importance. This was particularly shown in Triple Dirk when an increase in the size of the ear and in grain number and yield was accompanied by a reduction in the size of the flag leaf. Clearly the photosynthetic apparatus became more productive as spikelet number increased from 17 to 23. The lower leaves may have been the source of this additional assimilate, but as plants were grown at 2–3-in. centres, unusually high illumination of these leaves is unlikely to have been a contributing factor.

(b) *Duration of Developmental Phases and Spikelet Number*

Lupton and Kirby (1968) suggested that there is great scope for crop improvement by altering the relative lengths of successive phases in the growth of cereals, and indicated that an extension of the time during which the ear is developing may cause an increase in the number of spikelets produced. The present trial with 12 wheat cultivars (expt. 1) demonstrated that those cultivars which took longer to floral initiation and longer to develop from initiation to terminal spikelet appearance also formed more spikelets (Table 2) per ear. The duration of the period from initiation to terminal spikelet differentiation was particularly related to the number of spikelets produced.

There was a much greater varietal range in spikelet number at 21/16°C than at 15/10°C, the reduction in spikelet number at the lower temperature being most pronounced for varieties with a greater number at 21/16°C. These varieties—Heron, Pinnacle, Festiguay, Nainari, Pitic, and Mexico 120—all have some response to vernalization and it is probable that 10°C was in part fulfilling this requirement (Gott 1961). The response to cold by these varieties was shown as a relative reduction in the lengths of the periods to initiation and to terminal formation together with a related decrease in spikelet number.

Vernalization of Late Mexico 120, a variety with a much greater response to cold than the wheats mentioned above, reduced the length of the period from sowing to initiation with a corresponding reduction in spikelet number. As noted by Cooper (1956), there was little effect of vernalization on the duration of the phase from floral initiation to ear emergence which was completed relatively rapidly. Plants not vernalized produced leaf primordia at about one per day and, as leaves emerged at approximately one per week, more and more unexpanded leaf primordia accumulated on the apex (see Evans 1960). The number of these primordia or potential spikelet sites present when the apex became floral largely determined the final number of spikelets. With longer cold treatment the apex became competent to flower earlier, fewer potential spikelet sites had been established, and spikelet number was reduced.

Clearly in Late Mexico 120, vernalization response is the factor dominating the flowering mechanism and, once the apex is competent to flower, the process is completed rapidly by the production of a terminal spikelet. However, for those varieties with a small response or no response to cold, the day-length response is relatively more important. Triple Dirk for example did not accumulate leaf primordia prior to floral initiation under the conditions of the experiments, and therefore the final spikelet number was dependent on the duration of the period after initiation during which spikelet sites were established. If production of the terminal spikelet was delayed, more spikelets were formed.

These studies on the control of spikelet number by photoperiod manipulation demonstrate that, while there may be a common long-day stimulus for both floral initiation and terminal spikelet production, the processes have a different quantitative requirement. For Triple Dirk, 2 LD was sufficient to cause floral initiation, but with this treatment a terminal spikelet was not produced for a further 28 days; 12 LD scarcely advanced the time of initiation but reduced the period to terminal spikelet appearance to 17 days. Additional long days given after initiation could make up the balance and accelerate terminal production. It seems that the flowering processes are not necessarily all triggered at the time of floral initiation.

The relative sensitivity of the two processes, initiation and terminal spikelet production, may differ between varieties. Sunset, for example, required 13 days growth before double ridges appeared (Table 2), and a further 5 days to produce a terminal spikelet. Triple Dirk became floral at approximately the same time but took twice as long to produce a terminal spikelet. Conclusions of this nature may not be drawn for the varieties with higher spikelet numbers (Table 2), as the vernalization response becomes a confusing factor.

Selection for sensitivity may be used to increase spikelet number and consequently grain yield per ear in different environments. In cold areas where a vernalization response would be quickly satisfied, selection for rapid floral initiation and for late terminal production would result in more spikelets per spike. In warmer areas, vernalization response could be selected for so that initiation occurred late but spikelet number remained high. However, if some aspect of the environment, such as water, is strictly limiting at the time of seed set, then increased spikelet number may confer little advantage.

V. Conclusion

It is clear that spikelet number in wheat can be an important determinant of grain yield per ear and may be increased only by an extension of the growing period. When increased spikelet number is conferred by a response to vernalization, the period up to inflorescence initiation is the most important. When day length controls spikelet number, on the other hand, it is the duration of the period from initiation to terminal spikelet formation that appears to be critical.

If short-season wheats are required, and if their production involves a reduction of the phase up to terminal spikelet formation, then a price must be paid in spikelet number and consequently in yield.

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