ENVIRONMENTAL FACTORS AND GRAIN FILLING IN WHEAT

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To

Carl and Brigitta

PREFACE

The work reported in this thesis was carried out at the Phytotron, The Division of Plant Industry C.S.I.R.O. Canberra.

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The work carried out in this thesis, unless otherwise acknowledged, is my own and has not been submitted for a degree at any other University.

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ABSTRACT

Controlled environmental conditions were used to examine the effects of cultivar, day and night temperature and light intensity after anthesis on grain setting and on the rate and duration of grain filling. A brief examination of some factors which may influence the cessation of grain filling were also studied.

In the majority of cases, after an initial lag period, grain dry weight increased linearly until final grain weight was approached. Grain growth rate (per grain) not only varied among the cultivars but also in the extent these were influenced by conditions after anthesis. Growth rate per ear was, in many cases, broadly proportional to grain number per ear as differences between cultivars in grain growth rate (per grain) were much smaller than those in grain number.

Grain growth rates increased with a rise in temperature but in some cultivars under winter irradiance and at a high night temperature it decreased. In cultivars in which light intensity had a marked effect on grain number per ear, it had relatively little effect on growth rate per grain. When grain number was less affected by light intensity,growth rate per grain was highly responsive, especially in the more distal florets. Both response types displayed a close relation between leaf photosynthetic rate as influenced by light intensity and the rate of grain growth per ear.

The duration of linear grain growth, was scarcely influenced by light intensity, but was greatly reduced as temperature rose.

Under most conditions the cessation of grain growth did not appear to be due to the lack of assimilates. No relationship could be discerned between absolute nitrogen and phosphorus contents of

grains and the duration of grain filling. Examination of the water content of grains throughout the filling period may suggest a "block" of water movement into the grain at maturity.

CHAPTER I

INTRODUCTION

1.1 RATE AND DURATION OF GRAIN FILLING

After anthesis, grain size and ultimate yield in wheat will be determined by both the rate of grain filling and its duration. Considering how important these yield parameters are, surprisingly little attention has been paid to them. Many of the earlier experiments included only three or four harvests during the filling period making it difficult to define its rate and duration with sufficient precision for comparisons between cultivars and conditions. Hence the major objective of the experiments described here was to study the effect of day and night temperature and light intensity on the rate and duration of grain filling (dry matter accumulation) in several wheat cultivars. Frequent harvests were taken during the period from anthesis to ripe grain.

Large differences between cultivars in the rate of grain filling per ear have been observed, associated to a large degree with differences in grain number per ear (Ra 71). However, pronounced differences between cultivars in growth rate of grains have also been observed: in the experiments of Asana and Williams (As 65) faster rates were associated with larger, but fewer, grains per ear.

Grains in different positions within an ear grow at different rates. Thus Rawson and Evans (Ra 70) demonstrated that grains in second florets which are initially smaller than those in the first floret may grow faster and end up larger than these. Also, grains in upper spikelets grew more slowly than those below them and received much less assimilate from both the flag and penultimate leaves. Bremner (Br 72) observed that when the supply of assimilates was reduced by shading and defoliation growth was most severely reduced in upper spikelet grains. Thus within spikelets when the overall grain growth reduction was 60%, growth of first (a), second (b) and third (c) grains in a central spikelet was reduced by about 50%, 60% and 70% respectively. That is, grains were increasingly affected by leaf removal with progression from the base to apex of the spikelet. Therefore growth rates of individual grains in different positions within an ear responded differently to environmental conditions after anthesis.

In this study the influence of temperature on the rate and duration of individual grains from three selected spikelet positions throughout an ear were examined in order to determine which grains would be more adversly affected under high temperature. This aspect was also examined at high day and at high night temperatures and under low light intensity for individual grains from the central spikelets only.

Differences between cultivars in duration of grain filling have been observed by Asana and Joseph (As 64), Stoy (St 65) and Rawson and Evans (Ra 71). However Marcellos and Single (Ma 72) observed no difference in duration among the four cultivars they examined, but demonstrated a pronounced reduction in the time from anthesis to maturity as temperature increased, an important response not evident in the earlier experiments of Asana and Williams (As 65). Moreover the results of Asana and Williams (As 65) suggest that at high temperatures grain size was reduced mainly due to day temperature where no significant effect of 'night' temperature on grain weight could be observed, but Peters et al. (Pe 71) found that a rise in night temperature reduced grain yield by reducing the period of grain filling.

The results presented by Welbank et al. (We 68) indicate a fall in the duration of grain filling as incident radiation rises. This could be due to higher temperatures being associated with higher radiation, or alternatively to an abbreviation of grain growth at higher levels of radiation and photosynthesis. The experiments here aimed to distinguish between these alternatives in order to clarify the effect of day and night temperatures and irradiance on the duration as well as the rate of grain filling.

1.2 CESSATION OF GRAIN FILLING

After anthesis, most of the carbohydrate in the grains results from current photosynthesis (Ca 65), and increased leaf longevity could be important, if the enhanced supply should be associated with an increase in the growth rate of the grain and an extension of its period of growth (Bi 69). The problem, however, is that characteristics conferring high yields are likely to differ substantially from one environment to another and before striving for an ideotype more information is required about the basis of yield limitation.

The pronounced effect of high temperature in reducing the duration of grain growth must be a major factor in reducing grain yields in wheat grown at high temperatures, and therefore the factors causing cessation of grain filling require further analysis. In this investigation several aspects were examined: The flag and three lower leaves and the ear were rated for greenness in order to determine whether failure of assimilate supply could be related to the cessation of grain filling. Also phosphorus, nitrogen, calcium and water contents of grains were determined in some of the experiments to examine whether a relation between any of these factors and the cessation of grain filling could be established.

1.3 GRAIN SET

Environmental conditions prior to anthesis influence both the number and size of ears in a wheat crop and determine the potential number of grains (reviewed Au 75, Ev 74, Wa 74). Conditions at anthesis and during the next few days then determine how many grains are set, high temperature and low light intensities at this stage being particularly unfavourable (Wa 70).

Here, for the temperature and light treatments imposed at or just after first anthesis the pattern and numbers of grain set throughout an ear were examined in order to observe (i) which grains throughout an ear were least favoured to set and (ii) for those cultivars which had a greater modification of grain set at or just after first anthesis whether this had any influence on their subsequent growth rates. This is of course important when the role of environmental factors on the subsequent rate and duration of grain growth is to be considered.

1.4 SCOPE OF THE STUDY

The environmental factors examined here were temperature light intensity and very briefly thermoperiod. The effect of factors such as CO_2 supply, mineral nutrients, water supply, soil structure, atmospheric pollutants disease and lodging were not examined and attempts were made to ensure that the latter factors were "most favourable" for growth.

The study although not directly related to a specific aspect of crop production is nevertheless fairly basic to an understanding of the control and improvement of yield.

CHAPTER 2

EXPERIMENTAL DESIGN AND METHODS

2.1 DESIGN AND PLANT MATERIAL

Environmental factors limiting grain filling in the modern bread wheat (Triticum aestivum L) were studied in four experiments. The objectives were (a) to examine the effect of temperature, light intensity and briefly thermoperiod on grain set, (b) to assess the relative importance of differences between cultivars in the rate and duration of grain filling and the effect of day and night temperature, light intensity and thermoperiod on these, (c) to examine the trends in nitrogen and phosphorous contents of grains in relation to dry matter for each cultivar and the effect of temperature on these, and (d) to examine the calcium and water content of grains during grain filling and maturation.

The cultivars selected varied in average spikelet number and grains per spikelet. Triple Dirk, Timgalen, WW15 and Late Mexico 120 were used in experiments I and II. Triple Dirk and Sonora were used in experiment III and Late Mexico 120 and Sonora were used in experiment IV (Table 2.1). Triple Dirk and Timgalen are Australian cultivars. Triple Dirk is an early maturing, tall and slightly awned wheat. It is no longer grown commercially but is used in this study to extend results obtained elsewhere (Ra 70). Timgalen is a medium-early maturing wheat of medium height and of medium awned ears. (Ma 68). Sonora (early-maturing), WW15 (medium-early maturing) and Late Mexico 120 (late-maturing) are semi-dwarf heavily awned Mexican wheats.

Table 2.1 Summary of treatments and sampling Experiments I - IV

Cultivar and pretreatment	Treatments during grain filling	Sampling
EXPERIMENT I Cultivars Triple Dirk, Timgalen, WW15 and Late Mexico 120 Seeds vernalized Three weeks Date Sown Spring 5/11/71 Growing environment. In a phytotron glasshouse (Mo 62) with day temperature (08.30 - 16.30) at 21°C and night temperature (16.30 - 08.30) at 16°C - abbreviated 21/16°*C Photoperiod The natural day length was extended to 16h with low light of 500 lux intensity from incandescent lamps. Mean daily radiation: (cal.cm^{-2} day^{-1}) Triple Dirk 504 ± 166, Timgalen 498 ± 159, WW15 501 ± 155, Late Mexico 120, 498 ± 155 (± S.D.) Date and span of first anther emergence Triple Dirk 17/12/71, Timgalen 24-25/12/71, WW15 25-30/12/71, Late Mexico 120 7-12/1/72. Time from sowing to anthesis (days) Triple Dirk 36, Timgalen 44, WW15 49, Late Mexico 120 62.	Commencement of temperature treatments At first anthesis Temperature treatments 18/13°C phytotron glasshouse 21/16°*C phytotron glasshouse 30/25°C phytotron glasshouse Photoperiod and thermoperiod as for pretreatment. In each glasshouse the plants were under a mean daily radiation of 573 ± 195 cal.cm^{-2}day^{-1}(1) = 1.32 x 10^{7} ± 0.45 x 10^{7} J m^{-2} day^{-1} (400-700nm) Specific values of mean daily radiation from first anthesis to maturity (cal. cm^{-2} day^{-1}) 18/13°C: Triple Dirk 420 ± 145, Timgalen 406 ± 136, WW15 404 ± 140. 21/16°*C: Triple Dirk 420 ± 145, Timgalen 423 ± 148, WW15 404 ± 144, Late Mexico 120 378 ± 121. 30/25°C: Triple Dirk 452 ± 140, Timgalen 433 ± 156, WW15 404 ± 144, Late Mexico 120 377 ± 142	From first anthesis, eight plants were taken randomly for each treatment at three day intervals till the tenth harvest after which sampling was every sixth day. Harvest were continued till plants reached grade 3 on the senescence scale (2)

(1) the mean daily radiation during rapid grain filling that is, during the linear phase and will be quoted throughout the study (2) Definition of senescence scale (Table 2.3)

Table 2.1 (Cont.)

Cultivar and pretreatment	Treatments during grain filling	Sampling
EXPERIMENT II Cultivars Triple Dirk, Timgalen, WW15, Late Mexico 120. Seeds vernalized (1) Six weeks. Date Sown Autumn 22/3/72 Growing environment and photoperiod as in experiment I. Mean daily radiation (2) (cal. cm^{-2} day^{-1}) 311 $\pm$ 89 Date and span of first anther emergence Triple Dirk 6-7/5/72, Timgalen 8-12/5/72, WW15 6-12/5/72, Late Mexico 120 7-9/5/72 Time from sowing to anthesis (days) Triple Dirk 35, Timgalen 40, WW15 40, Late Mexico 120 37.	Commencement of temperature treatments At first anthesis. Temperature treatments 15/10°C (3) phytotron glasshouse 21/16°*C phytotron glasshouse 30/25°C phytotron glasshouse Photoperiod and thermoperiod as for pretreatment. In each glasshouse the plants were under a mean daily radiation of approximately 251 $\pm$ 83 cal cm^{-2} day^{-1} (4) $=5.78\times10^{6} \pm 1.91\times10^{6}$ J m^{-2} day^{-1} (400-700nm) Specific values of mean daily radiation from first anthesis to maturity (2) 15/10°C 193$\pm$60 cal. cm^{-2} day^{-1} 21/16°*C 194$\pm$61 cal. cm^{-2} day^{-1} 30/25°C 198$\pm$65 cal. cm^{-2} day^{-1}	As in experiment I.

(1) The longer period of six weeks was applied in experiment II as in experiment I three weeks of vernalization had not been sufficient to synchronize flowering times of the cultivars. (2) No significant difference between the cultivars. (3) The lower temperature regime of 15/10°C was employed since in experiment I differences in most aspects of grain development were slight. (4) Mean daily radiation during the linear phase of grain filling, this value will be quoted throughout the study.

Table 2.1 (Cont.)

Cultivar and pretreatment	Treatments during grain filling	Sampling
EXPERIMENT III Cultivars Triple Dirk and Sonora Seeds were not vernalized Date Sown Winter 14/8/73 Growing environment and photoperiod as in experiment I Mean daily radiation (1) (cal. cm^{-2} day^{-1}) 290 ± 101 Date and span of first anther emergence Triple Dirk 1-3/10/73, Sonora 29-9 to 2-10/73. Time from sowing to anthesis (days) Triple Dirk 56, Sonora 55	For each cultivar one group of plants remained in the pretreatment glasshouse till maturity, denoted as 21/16°*C. Also an additional group of Triple Dirk plants remained in the pre-treatment glasshouse. These were used for determination of calcium uptake, water content and fresh volume of grains. Photoperiod and thermoperiod as for pretreatment. Mean daily radiation (1,2) was 373±85 cal. cm^{-2} day^{-1} $= 6.53x10^6 \pm 1.96x10^6$ J m^{-2} day^{-1} (400-700nm) LIGHT INTENSITY TREATMENTS (values given at ear level). Commencement of treatments four days after first anthesis. Treatments were conducted in artifically lit cabinets (Mo 62) Treatments (1) 8070 lux, $1.31x10^6$ J m^{-2} day^{-1} (400-700nm) (2) 16140 lux, $2.52x10^6$ J m^{-2} day^{-1} (400-700nm) (3) 34432 lux, $5.92x10^6$ J m^{-2} day^{-1} (400-700nm) (4) 48420 lux, $8.29x10^6$ J m^{-2} day^{-1} (400-700nm) In each cabinet day temperature was at 21°C (08.30-16.30) and night temperature was at 16°C (16,30-08.30). Light was switched on at 08.30, plants were under 12h fluorescent plus incandescent this was extended to 16h under incandescent, followed by 8h darkness.	For the calcium and water study etc., eight replicates per sample were collected at 2-3 day intervals commencing from 10 days after first anthesis to maturity. For the remaining treatments eight replicates per sample were collected at 5 day intervals from first anthesis to maturity (grade 3 on senescence scale).

(1) No significant difference between the cultivars
(2) Mean daily radiation during the linear phase of grain filling

TABLE 2.1 (cont.)

Cultivar and pretreatment	Treatments during grain filling	Sampling
EXPERIMENT IV Cultivars Sonora & Late Mexico 120 Seeds vernalized Four weeks Date Sown Autumn 1/4/74 Growing environment and photoperiod as in experiment I. Mean daily radiation: (cal. cm^{-2} day^{-1}) Sonora 203 ± 100, Late Mexico 120 199 ± 94. Date and span of first anther Emergence: Sonora 15-19/5/74, Late Mexico 120 22-30/5/74. Time from sowing to anthesis (days) Sonora 45, Late Mexico 120 56.	For each cultivar one group of plants remained in the pretreatment glasshouse till maturity, denoted as 21/16°*C. Thermoperiod and photoperiod as for pretreatment. Mean daily radiation[(1)] was 246±78 Cal cm^{-2} day^{-1} = $5.6x10^6 \pm 1.80x10^6$ J m^{-2} day^{-1} (400-700 nm) Specific values of mean daily radiation from first anthesis to maturity (cal. cm^{-2} day^{-1}) Sonora 163±68, Late Mexico 120 161±66. TEMPERATURE TREATMENTS Commencement of treatments Five days after first anthesis[(2)] Treatments were conducted in artifically lit cabinets (Mo62) Treatments (1) 21/16°C (2) 21/25°C (3) 30/16°C (4) 30/25°C. At ear level, each cabinet had a mean daily radiation of $5.92x10^6$ J m^{-2} day^{-1} (400-700nm) Photoperiod: as in experiment III Thermoperiod 12h. day temperature (08.30 - 20.30), 12h night temperature (20.30-08.30)	Eight plants were harvested at five day intervals for each treatment from first anthesis to maturity (grade 3 on senescence scale)

(1) Mean daily radiation during the linear phase of grain filling
(2) Plants were transferred five days after first anthesis in order to minimize the effect of temperature on grain set.

2.2 VERNALIZATION

In experiments I, II and IV seeds were vernalized in an attempt to synchronize flowering both within and between cultivars. The seeds were maintained at 2 - 4°C on wet filter paper in petri dishes in the dark for three, six and four weeks in experiment I, II and IV respectively (Table 2.1).

2.3 GROWING CONDITIONS BEFORE ANTHESIS

The seeds were sown at a uniform depth (approximately 1cm) in a 50:50 mixture of perlite and vermiculite to give three plants in each 12cm pot. In experiments I, II and III where the seeds had been vernalized the radicles had emerged.

In all experiments the plants remained in a phytotron glasshouse at 21/16°C until first anthesis of the main stem ear. Details of thermoperiod, photoperiod and incident radiation are summarized in Table 2.1 (pretreatment). As the experiments were conducted at different seasons the incident radiation varied considerably.

Plants were watered each morning with a modified Hoagland's nutrient solution and each afternoon with water. Tillers were removed periodically to reduce each plant to the main culm in order to minimize shading and water stress. The density was equivalent to 2.1 x 10^6 ears per hectare. All plants were staked at anthesis to prevent lodging. Plants were re-arranged at regular intervals to minimize the effects of the slight radiation gradient in the phytotron glasshouse.

2.4 TREATMENTS FROM FIRST ANTHESIS TO MATURITY

First anthesis here is defined as the emergence of the first anther from an ear (day 0). As plants reached first anthesis their stems were tagged with dated labels (Table 2.2). Plants of each cultivar were then assigned randomly to treatments. All experiments included the treatment 21/16°*C in which the plants remained in the same phytotron glasshouse with the thermoperiod and photoperiod the same as for the pre-anthesis period.

Temperature treatments were examined in experiments I, II and IV. In experiments I and II treatments commenced at first anthesis, where temperature regimes were selected such that the night temperature was always 5°C less than the day temperature. That is, in experiment I the regimes were 18/13°C, 21/16°*C and 30/25°C and in experiment II they were 15/10°C, 21/16°*C and 30/25°C. In experiment I plants reached anthesis in December and filled their grains in a mid-summer period of high solar radiation ($1.32 \times 10^7 \pm 0.45 \times 10^7$ J m $^{-2}$ day $^{-1}$ (400-700nm)) whereas in experiment II plants reached anthesis in May, so that grain filling occurred in mid-winter under low solar radiation ($5.78 \times 10^6 \pm 1.91 \times 10^6$ J m $^{-2}$ day $^{-1}$ (400-700nm)). Details of photoperiod and thermoperiod are summarized in Table 2.1.

In experiment IV temperature treatments were commenced five days after first anthesis. Here increases of (a) 9°C in the night temperature were examined for two different day temperatures that is (i) 21/16°C to 21/25°C and (ii) 30/16°C to 30/25°C (b) 9°C in the day temperature were examined for two different night temperatures that is (i) 21/16°C to 30/16°C and (ii) 21/25°C to 30/25°C. These were cabinet treatments under 5.92×10^6 J m $^{-2}$ day $^{-1}$ (400-700nm), where the thermoperiod included a 12h day temperature (Table 2.1). Furthermore the influence of extending the day temperature by four hours (from eight to twelve hours) at 21/16°C under approximately 5.92×10^6 J m $^{-2}$ day $^{-1}$ (400-700nm) was examined (Table 2.1 experiment IV).

Light intensity treatments were examined in experiment III.

Treatments commenced four days after first anthesis. Plants were transferred to their respective artifically lit cabinets at 21/16°C at intensities of 8,070, 16,140, 34,432 and 48,420 lux. Details of thermoperiod and photoperiod are summarized in Table 2.1 experiment III.

The total radiant energy received each day above the glasshouse roof was measured by means of a Kipp Solarimeter connected to a CSIRO solar integrator. Total radiant energy in the phytotron glass-houses was reduced by 20-22% due to absorption and reflection.

Lighting in the cabinets was from fluorescent tubes supplemented by incandescent lamps. Light intensities were monitored with an Eppley pyrometer (400-700nm).

In each cabinet the experimental plants were surrounded by a zone of guard plants of similar age and pretreatment. As sample plants were removed additional guards were put into the gaps so as to maintain the same population of plants throughout the experimental period. When cultivars varied in height the shorter one(s) were raised so that their ears were at the same level as those of the taller cultivars.

2.5 SAMPLING AND ATTRIBUTES RECORDED EXPERIMENTS I - IV.

In each treatment randomly selected groups of eight plants were harvested at regular intervals (summarized in Table 2.1) and twelve at maturity. After harvesting each main culm was cut into the parts required (attributes for each experiment are summarized in Table 2.2) and each part was placed into a separate labelled envelope. These were dried at 80°C for 48h and then their dry weights were recorded onto computer data sheets.

The attributes recorded vary between experiments as outlined in Table 2.2. The notation adopted for the definition of floret a b c and d grains within a spikelet is illustrated by the diagram of the

Table 2.2 Summary of attributes recorded and determined in experiments I - IV

In all experiments all plants were observed daily to determine first anthesis (day 0). Further in experiments I and II for each temperature treatment 10 replicates were examined daily (11.30 - 12.30 pm) to determine the patternand time (from that of the earliest floret to reach anthesis) of anther emergence throughout an ear. Within each cultivar within each experiment ears with the same number of spikelets were selected.

EXPERIMENT I

A. Senescence during grain filling. A greenness rating (Table 2.3) was recorded at each alternative harvest for the ear, flag and three lower leaves, sheaths and stem of the main clum plant.

B. The number of spikelets and grains per ear were recorded for all ears.

C. Pattern of grain set throughout an ear. Replicates to determine the pattern of grain set varied between 13 and 36. Replicates were examined from harvests which had progressed at least two weeks after first anthesis as the pattern of grain set was unlikely to be further modified after this period under the experimental conditions of experiment I. Moreover within each cultivar ears with the same number of spikelets were selected from each temperature treatment

D. Dry Weight Measurements

(i) Main culm for each main culm the dry weight of the top, second and lower internodes were recorded.

(ii) Individual ears (grains + structure)

(iii) Total grain weight of individual ears

(iv) Grains from individual florets: for each ear dry matter accumulation in the a,b,c and d florets of the three selected spikelet positions: upper central and lower (Figure 2.1) were determined.

Table 2.2 (cont.)

EXPERIMENT II Same as experiment I for A, B and C. In C the number of replicates varied between four and twelve ears. Same as experiment I for D (ii) - (iv), where for D(iv) dry matter accumulation in the a,b,c and d grains was determined for the central spikelets only. E. Nitrogen and phosphorus contents; were determined for the floret a and c grains from the central spikelets for each temperature treatment.
EXPERIMENT III Same as experiment I for A,B,C & D. In C the number of replicates varied between four and twelve ears and for D(iv) dry matter accumulated in the a,b,c, and d grains was determined for the central spikelets only. F. For Triple Dirk at 21/16°*C fresh volume, water content and calcium content of grains for the floret a grains from the central spikelets was determined.
EXPERIMENT IV Same as experiment I for A and B. C and D(i) were determined only for Sonora. D (ii - iv) were recorded for both cultivars, where D(iv) was recorded for grains from the central spikelets only.

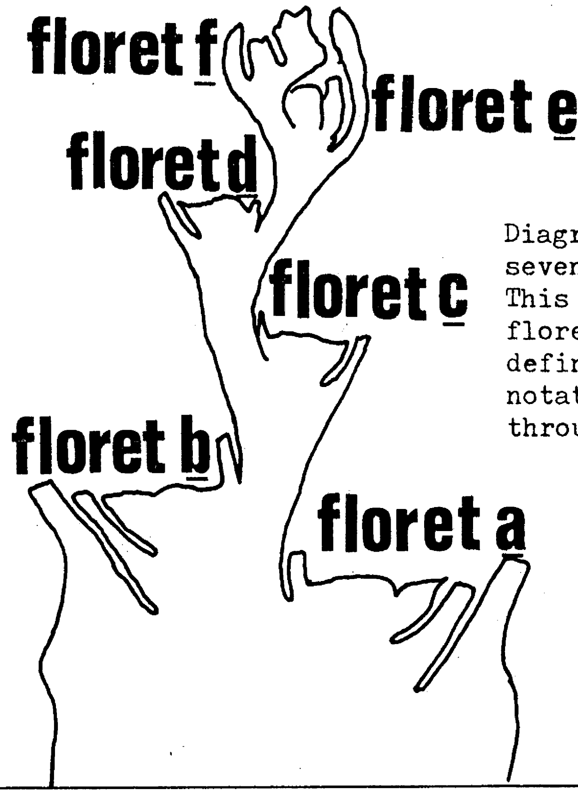


Diagram of the rachilla of the seventh spikelet from (Ha 71). This diagram illustrates how floret a,b,c and d grains were defined within a spikelet. This notation was used for all spikelets throughout an ear.

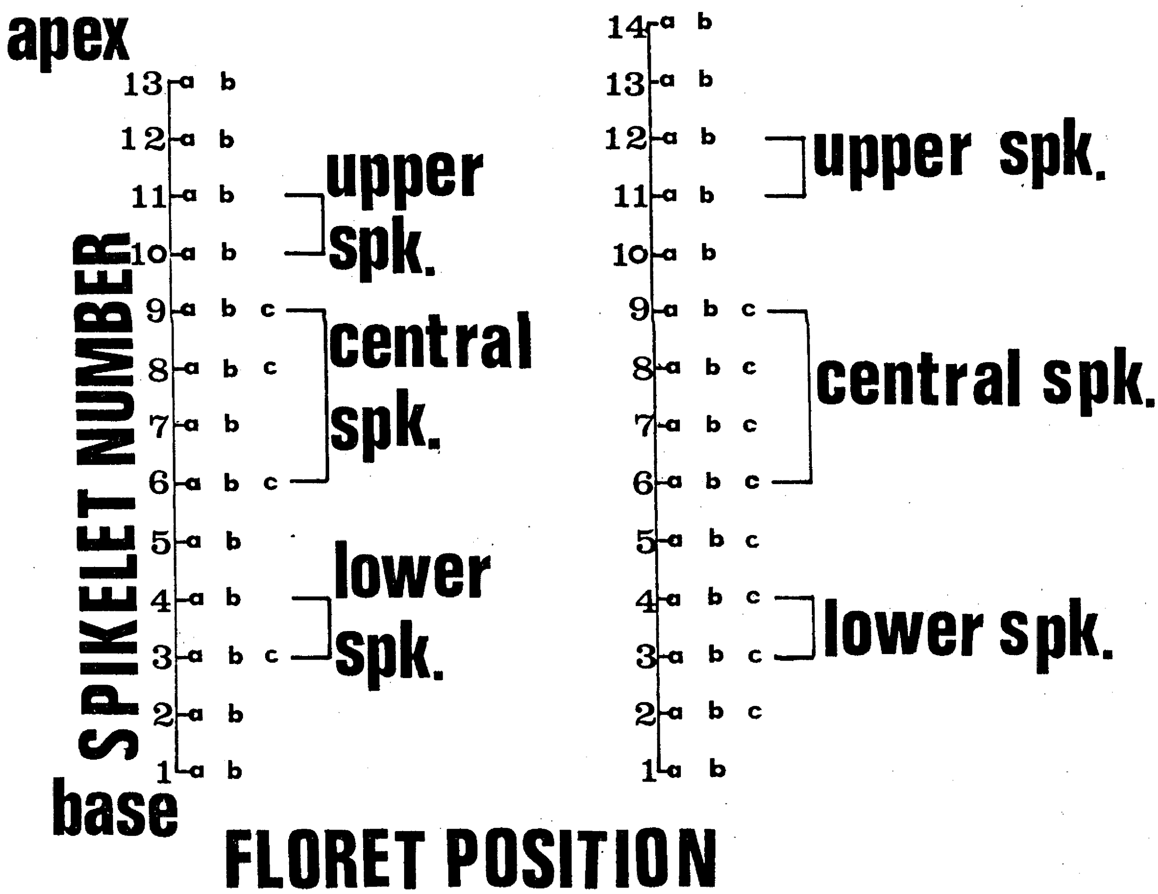


Figure 2.1 The braces define the positions of the upper, central and lower spikelets within an ear. The upper spikelets are only comprised of two spikelets always the third and fourth spikelets below the apex of the ear. The central spikelets are only comprised of the four middle spikelets. For an ear with an odd number of spikelets the central spikelets were biased towards the upper spikelets. The lower spikelets are only comprised of two spikelets, always the third and fourth spikelets above the base of the ear.

rachilla of the seventh spikelet from (Ha 71) in Fig. 2.1. This notation was used for all spikelets throughout an ear.

In relation to D(iv) Table 2.2, a position mean dry weight of grains for each individual floret position (a, b, c, and d) was calculated over two, four, and two grains respectively in the upper, central and lower spikelets (Fig. 2.1.). If a grain failed to set in a selected spikelet (for example in Fig. 2.1 for the ear with 13 spikelets, only three c grains set in the central spikelets) then the position mean dry weight was calculated for those which had set (for the above example for the floret c grains the position mean dry weight was calculated for the three grains). In upper and lower spikelets when one of the two grains in any of the individual floret positions (a b or c) failed to set the dry weight of the remaining grain was used to represent the position mean dry weight. Finally, position mean dry weights of grains for each harvest were calculated.

"Position mean dry weight" will be abbreviated to "mean dry weight" of floret a, b, c or d grains, upper, central or lower spikelets. Recall (Table 2.2) that mean dry weight of grains for individual florets were determined in the upper, central and lower spikelets in experiment I, for the remaining experiments, these were calculated for the central spikelets only.

2.5.1 Observations on Senescence

In all experiments, for all treatments at regular intervals (Table 2.2) plant parts were visually rated for senescence. Changes in the photosynthetic surface of plants parts were estimated for each replicate on the basis of categories of greenness as indicated in Table 2.3.

Table 2.3 Visual Rating for Senescence

Visual Rating		Approximate percent green colour
0	totally green	100 - 90
<- 0-1		90 - 80
-> 0-1		80 - 70
1	more green than yellow	70 - 60
<- 1-2		60 - 50
-> 1-2		50 - 40
2	more yellow than green	40 - 30
<- 2-3		30 - 20
-> 2-3		20 - 10
3	totally yellow	10 - 0

For some plants in experiment III, these visual ratings were compared with measurements of respiration and photosynthesis on the same leaves and ears using a gasometric method which has been described by Rawson and Evans (Ra 71).

2.5.2 Determinations of Nitrogen and Phosphorus Contents of Grains

In experiment II nitrogen and phosphorus contents for floret a and c grains of the central spikelets were determined.

For each harvest two replicates were randomly selected. The grains for each were bulked, dried, counted, weighed and then ground. An aliquot of known weight from each replicate was digested using a modified Kjeldahl procedure (Wi 67).

Nitrogen and phosphorus were determined colorimetrically on prepared digestions by J.R. Twine at C.S.I.R.O. Division of Plant Industry (Wi 67) and for each digestion two readings were taken. For both elements determinations had a maximum variation of 5% for readings on the same digestion. Thus the error compared favourably with those obtained by conventional chemical methods for nitrogen and phosphorus (Wi 67).

2.5.3 Determination of Fresh Volume, Water and Calcium Contents of Grains.

These were determined for floret a grains of the central spikelets for cv. Triple Dirk in experiment III (Table 2.2).

The volume of fresh grains was determined by the pyknometer method. Care was taken to make sure that bubbles of air were not attached to the grains and, to guarantee uniform temperature readings, specific gravity bottles filled with distilled water were set up the previous night in a water bath (21°C). From tests conducted at each collection (Table 2.2) it was evident that the grains absorbed negligible amounts of water during the three minutes it took to determine the volume of each replicate.

After their volumes had been determined the grains were dried at 80°C for 48h. The difference between the fresh and dry weights represents the water content.

For calcium determination the grains from each collection were bulked, counted, weighed and then ground. Calcium was determined by Atomic-absorption Spectrophotometry as proposed and carried out by D.J. David at C.S.I.R.O. (Da 59).

2.6 GRAIN GROWTH CURVES: DERIVATION OF LAG RATE AND DURATION.

Growth curves, that is, dry weight versus time (days from first anthesis) were plotted for individual grains.

With a few exceptions (Appendix A p 78) a constant feature of a grain growth curve was a prolonged phase in which grain growth proceeded at very nearly a constant rate until grain filling was almost complete. This is illustrated in Figure 2.2 for Triple Dirk in experiment II for floret a grains of the central spikelets for three temperatures. Grains in other positions in the ear, in upper florets or spikelets for example also displayed linear growth as did whole ears of most cultivars.

The prolonged period of linear grain growth made possible objective estimates of both rate and duration of grain growth. The rate was derived from the line of best fit during the linear phase, while the duration was derived by extrapolation of that line to its intercepts with ovary weights at anthesis and maturity respectively. The former intercept gives a measure of the initial lag in grain growth (Fig. 2.3).

To the linear phase of grain growth a line of best fit was estimated by the method of least squares. In order to minimize the subjectivity of the choice of end-points of the linear phase, initially four data points in the middle region of the linear phase of grain growth were selected. A least squares fit was determined and a correlation coefficient calculated. The middle region was then progressively extended by the inclusion of data points first at one end then the other. Each time an additional data point was added a least square fit and a correlation coefficient were determined. This procedure was continued until inclusion of a data point no longer gave a good least square linear fit in relation to the ones previously calculated. This data point was then discarded and the slope of the line of best fit was defined as the growth rate.

Confidence intervals of 95% were determined for the sample regression coefficients. The magnitude of the 95% confidence interval was used as a measure of variability for the growth rate parameter. When any two growth rate parameters differed by less than 2 x the standard deviation a t-test for the significance of the difference was used (at 95% confidence level).

Two factors contribute to the error of the estimated measurement of duration as defined in Fig. 2.3. First the mature dry grain weight (or mature dry weight of ears) is a mean value and its standard deviation determines part of the error. In Fig. 2.3 this is referred to as the "first-error". Second the variation of the slope of the fitted line at 95% confidence level contributes the other part of the error, "the second error", in Fig. 2.3. Generally these errors varied from one to four days. The "second error" also influences estimates of the lag.

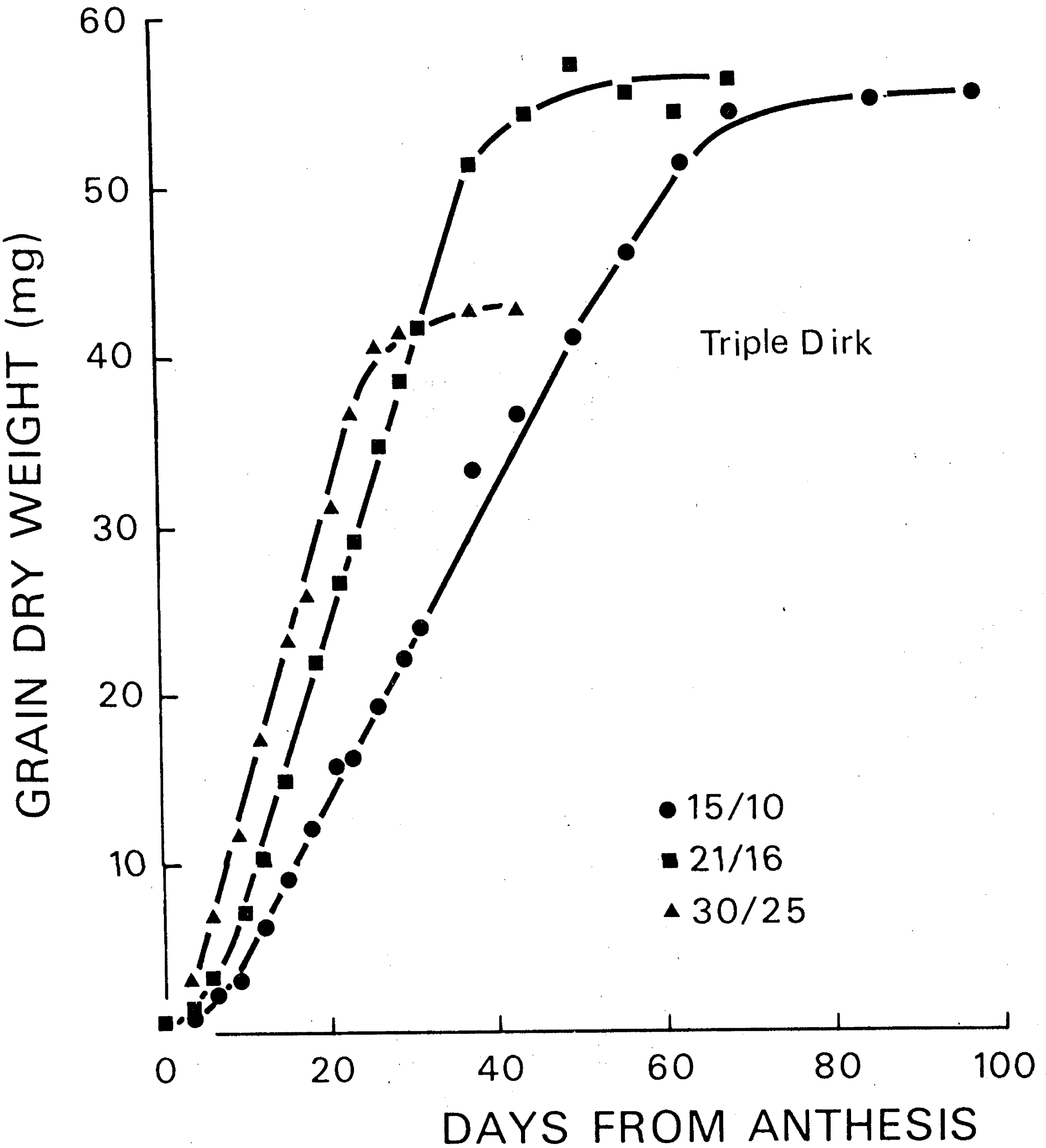


Figure 2.2 Experiment II. Increases in dry weight of floret a grains from the central spikelets with time from anthesis in three temperature regimes for Triple Dirk.

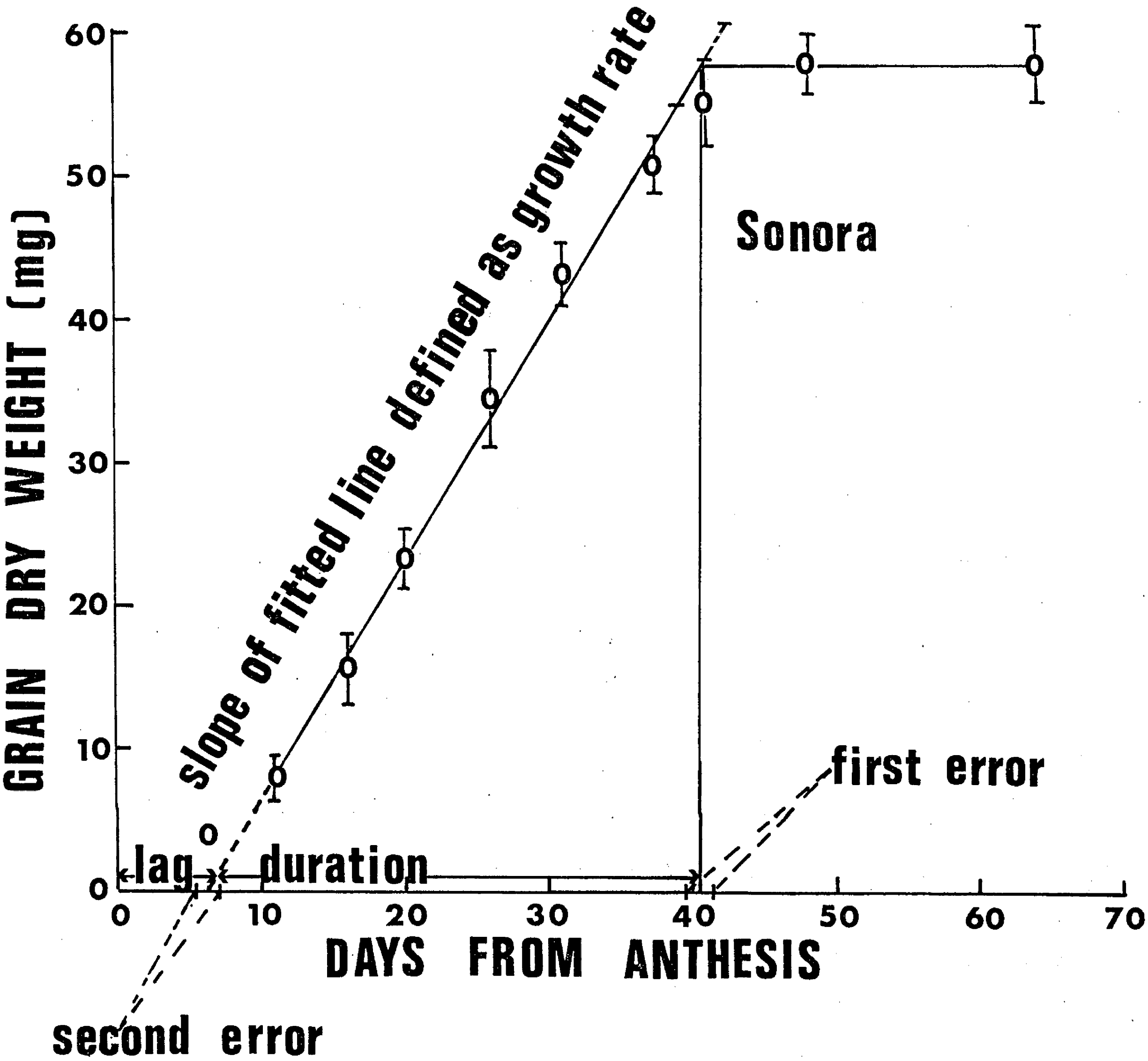


FIGURE 2.3. The diagram illustrates the procedure used to define the lag, rate and duration of grain filling. The growth curve used belongs to Sonora floret a from the central spikelets at 21/16°C under 48,420lux in experiment III. The errors are associated with estimates of maximum dry weight and with the slope of the fitted line (see text)

CHAPTER 3

GRAIN SET

Not all florets reaching anthesis set grains (Ev 72) and this can be further modified by environmental conditions at or just after first anthesis. High temperature and low light intensities at this stage are particularly unfavourable (Wa 70).

In this chapter the effect of environmental conditions at or just after first anthesis on the number and pattern of grain set throughout an ear are examined. In experiment I and II temperature treatments were commenced at first anthesis and in experiment IV five days after first anthesis. Light intensity treatments were commenced four days after first anthesis, in experiment III (Table 2.1). The information on grain set is also necessary if proper interpretation of the rate and duration of grain filling is to be assessed for the various treatments.

Ear size, the number of spikelets per ear and the mean number of grains set per spikelet are given for each experiment. Also leaf blade areas for the three youngest leaves at anthesis on the main culm are tabulated for each cultivar in experiments I, III and IV.

3.1 EAR SIZE AND LEAF BLADE AREA AT ANTHESIS

Environmental conditions prior to anthesis influence both the number and size of ears in a wheat crop and hence the potential number of grains (reviewed Au 75, Ev 74, Wa 74).

Prior to anthesis both vernalization and incident radiation differed between the experiments (Table 2.1). Consequently for some cultivars, ear size varied considerably between experiments. For example from Table 3.1 at 21/16°*C Late Mexico 120 set 26.5 ± 0.5, 16.5 ± 0.5 and 18.5 ± 0.5 spikelets per ear and 2.6 ± 0.05, 1.9 ± 0.01 and 1.6 ± 0.02 grains per spikelet in experiments I, II and IV respectively. Triple Dirk set 13.5 ± 0.5, 12.5 ± 0.5 and 14.5 ± 0.3

spikelets per ear and 1.8 $\pm$ 0.08, 1.4 $\pm$ 0.03 and 2.0 $\pm$ 0.03 grains per spikelet in experiments I, II and III, at 21/16°*C respectively.

Generally the greater the number of spikelets, the larger was the leaf blade area of the flag and two lower leaf blades (flag blade, blade 1, blade 2) at anthesis, (Figure 3.1).

This relationship held for the comparison between experiments of any one cultivar, for example Late Mexico 120 between experiments I and IV, Triple Dirk between experiments I and III and except for Triple Dirk for the comparison between cultivars between the experiments. Triple Dirk was exceptional in that it had markedly larger leaf areas at anthesis in relation to its spikelet numbers.

Vegetative nodes were counted in experiment I only, and they appear to be correlated with spikelet number per ear. Thus as spikelet number per ear increased from 13.5 to 14.5 to 17.5 for Triple Dirk, Timgalen and WW15 respectively, the total number of vegetative nodes increased from 6.6 $\pm$ .5 to 8.1 $\pm$ .3 to 9.3 $\pm$ .4. However such a strict correlation was not always the case as Late Mexico 120 set up to 28 spikelets per ear yet its total number of vegetative nodes was comparable to that of WW15 (Table 3.1a).

3.2 PATTERN AND TIME OF ANTHER EMERGENCE AS INFLUENCED BY TEMPERATURE. EXPERIMENTS I AND II.

For any one cultivar the pattern of anther emergence was similiar in experiments I and II inspite of the smaller spikelet numbers in experiment II, especially for Late Mexico 120 (Table 3.1a and b). Slight differences between cultivars however occurred. For Triple Dirk, WW15 and Late Mexico 120 the patterns were similiar: the first anther emerged from a floret <u>a</u> position half to two-thirds up from the base of an ear. The next <u>a</u> florets to anthese emerged from the upper and then

TABLE 3.1 EXPERIMENTS I - IV: The mean number of (i) spikelets per ear (ii) grains set per ear and (iii) grains set per spikelet. For EXPERIMENTS I, III and IV: Leaf blade areas at anthesis for the flag and two lower leaves are presented.

TABLE 3.1 (a) EXPERIMENT I

Cultivar		Triple Dirk	Timgalen	WW15	Late Mexico 120
Mean number of spikelets per ear[(1)] (± S.E.)		13.5 ± 0.5	14.5 ± 0.5	17.5 ± 0.5	26.5 ± 0.5
Mean number of grains per ear[(2)] (± S.E.)	18/13°C	26.6 ± 0.5	32.0 ± 0.5	46.5 ± 0.5	
	21/16°*C	25.7 ± 0.4	31.6 ± 0.7	46.5 ± 0.5	69.3 ± 0.5
	30/25°C	22.7 ± 0.3	31.8 ± 0.5	44.8 ± 0.6	64.3 ± 0.6
Mean number of grains per spikelet[(3)] (± S.E.)	18/13°C	2.0 ± 0.04	2.2 ± 0.02	2.6 ± 0.03	
	21/16°C	1.8 ± 0.08	2.2 ± 0.05	2.6 ± 0.06	2.6 ± 0.05
	30/25°C	1.7 ± 0.08	2.2 ± 0.09	2.5 ± 0.09	2.4 ± 0.07
Mean leaf blade areas at anthesis cm^2 (± S.E.)	flag	31.8 ± 0.7	20.4 ± 0.1	31.5 ± 1.7	38.3 ± 1.0
	leaf 1	24.7 ± 0.6	18.9 ± 0.3	21.3 ± 1.2	33.2 ± 1.4
	leaf 2	19.7 ± 0.5	15.6 ± 1.1	15.6 ± 1.1	28.6 ± 1.0
Mean number of vegetative nodes (± S.E.)		6.6 ± 0.5	8.1 ± 0.3	9.3 ± 0.5	8.9 ± 0.3

(1) For each cultivar this mean value denotes the mean number of spikelets per ear in all treatments. (2) For each treatment the sample selected to determine the mean included the ears from all harvests from two weeks after first anthesis to maturity. (3) (Mean number of spikelets per ear)$^{-1}$x(mean number of grains per ear).

TABLE 3.1(b) EXPERIMENT II

Cultivar		Triple Dirk	Timgalen	WW15	Late Mexico 120
Mean number of spikelets per ear (1) ($\pm$ S.L.)		12.5 $\pm$ 0.5	12.5 $\pm$ 0.5	14.5 $\pm$ 0.5	16.5 $\pm$ 0.5
Mean number of grains per ear (2) ($\pm$ S.E.)	15/10°C 21/16°*C 30/25°C	20.9 $\pm$ 1.5 18.1 $\pm$ 1.0 17.4 $\pm$ 0.3	22.0 $\pm$ 0.5 21.1 $\pm$ 0.5 21.4 $\pm$ 0.5	33.5 $\pm$ 1.4 33.6 $\pm$ 1.9 30.6 $\pm$ 1.3	32.3 $\pm$ 1.2 30.8 $\pm$ 1.0 28.8 $\pm$ 0.9
Mean number of grains per spikelet (3) ($\pm$ S.E.)	15/10°C 21/16°*C 30/25°C	1.8 $\pm$ 0.03 1.4 $\pm$ 0.03 1.3 $\pm$ 0.01	1.8 $\pm$ 0.02 1.7 $\pm$ 0.02 1.8 $\pm$ 0.00	2.3 $\pm$ 0.04 2.2 $\pm$ 0.07 2.1 $\pm$ 0.04	2.0 $\pm$ 0.02 1.9 $\pm$ 0.01 1.8 $\pm$ 0.01

(1) For each cultivar this mean value denotes the mean number of spikelets per ear in all treatments. (2) For each treatment the sample selected to determine the mean included the ears from all harvests from two weeks after first anthesis to maturity. (3) (Mean number of spikelets per ear)$^{-1}$x(mean number of grains per ear).

TABLE 3.1(c) EXPERIMENT III

Cultivar		Triple Dirk	Sonora
Mean number of spikelets per ear (1) (± S.E.)		14.5 ± 0.3	17.0 ± 0.4
Mean number of grains per ear (2) (± S.E.)	21/16°*C	29.1 ± 0.6	42.7 ± 0.4
	8070 lux	24.5 ± 0.8	39.7 ± 0.8
	16140 lux	24.7 ± 0.5	42.8 ± 1.2
	34432 lux	31.2 ± 0.4	46.1 ± 0.4
	48420 lux	30.6 ± 0.5	45.9 ± 1.2
Mean number of grains per spikelet (3) (± S.E.)	21/16°*C	2.0 ± 0.03	2.5 ± 0.03
	8070 lux	1.6 ± 0.03	2.3 ± 0.02
	16140 lux	1.6 ± 0.01	2.5 ± 0.02
	34432 lux	2.0 ± 0.02	2.7 ± 0.04
	48420 lux	2.1 ± 0.00	2.7 ± 0.03
Mean leaf blade areas at anthesis cm^2 (± S.E.)	flag	39.4 ± 3.0	34.9 ± 1.4
	leaf 1	37.4 ± 0.7	25.1 ± 1.1
	leaf 2	31.7 ± 1.0	19.5 ± 0.8

(1) For each cultivar this mean value denotes the mean number of spikelets per ear in all treatments.

(2) For each treatment the sample selected to determine the mean included the ears from all harvests from two weeks after first anthesis to maturity.

(3) (Mean number of spikelets per ear)$^{-1}$ x (Mean number of grains per ear).

TABLE 3.1(d) EXPERIMENT IV

Cultivar	Late Mexico 120		Sonora
Mean number of spikelets per ear[1] (± S.E.)		18.5 ± 0.5	15.0 ± 0.6
Mean number of grains per ear[2] (± S.E.)	21/16°*C	29.2 ± 1.6	28.5 ± 0.7
	21/16°C	29.4 ± 1.7	30.0 ± 0.8
	21/25°C	30.3 ± 2.0	28.9 ± 1.4
	30/16°C	29.0 ± 1.6	28.8 ± 1.2
	30/25°C	29.0 ± 1.2	28.9 ± 1.1
Mean number of grains per spikelet[3] (± S.E.)	21/16°*C	1.6 ± 0.02	2.0 ± 0.01
	21/16°C	1.6 ± 0.08	2.1 ± 0.06
	21/25°C	1.7 ± 0.06	2.0 ± 0.04
	30/16°C	1.6 ± 0.04	2.0 ± 0.02
	30/25°C	1.6 ± 0.04	1.9 ± 0.04
Mean leaf blade areas at anthesis cm^2 (± S.E.)	flag	34.8 ± 1.2	26.9 ± 1.3
	leaf 1	27.1 ± 0.6	18.8 ± 0.4
	leaf 2	20.0 ± 1.4	10.6 ± 1.0

(1) For each cultivar this mean value denotes the mean number of spikelets per ear in all treatments.

(2) For each treatment the sample selected to determine the mean included the ears from all harvests from two weeks after first anthesis to maturity.

(3) (Mean number of spikelets per ear)$^{-1}$x(Mean number of grains per ear).

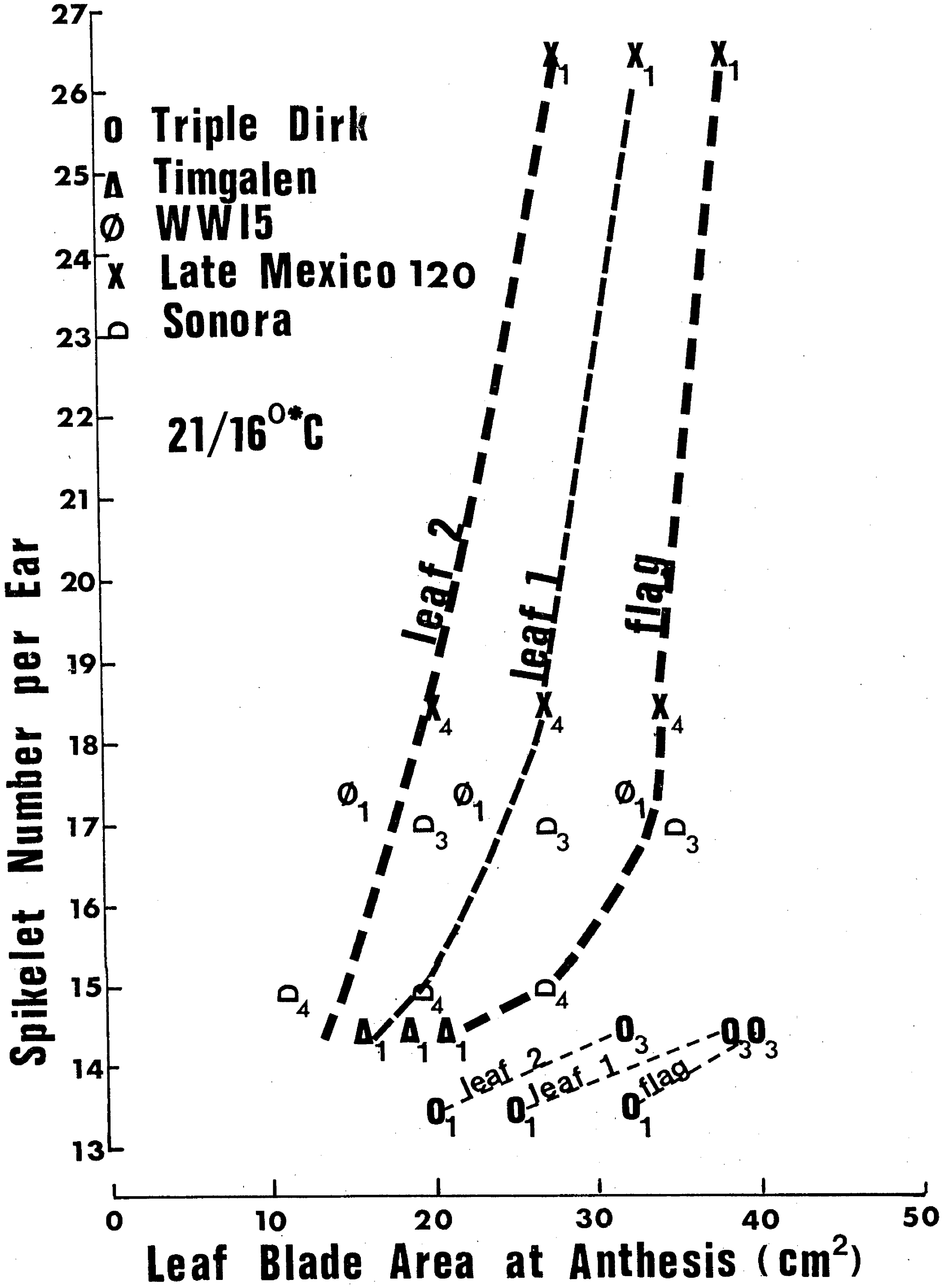


Figure 3.1 Experiments I, III and IV. Areas of the flag leaf blade and two lower blades (1 and 2) at 21/16°*C. The subscripts 1, 3 and 4 refer to blade measurements in experiments I, III and IV respectively. Each data point represents the mean of 10 replicates.

from the lower spikelets. This is illustrated in figures 3.2 a,b, e,f,g and h.

A similiar pattern was observed for the floret b positions whose anthers emerged one to two days later than their respective floret a positions.

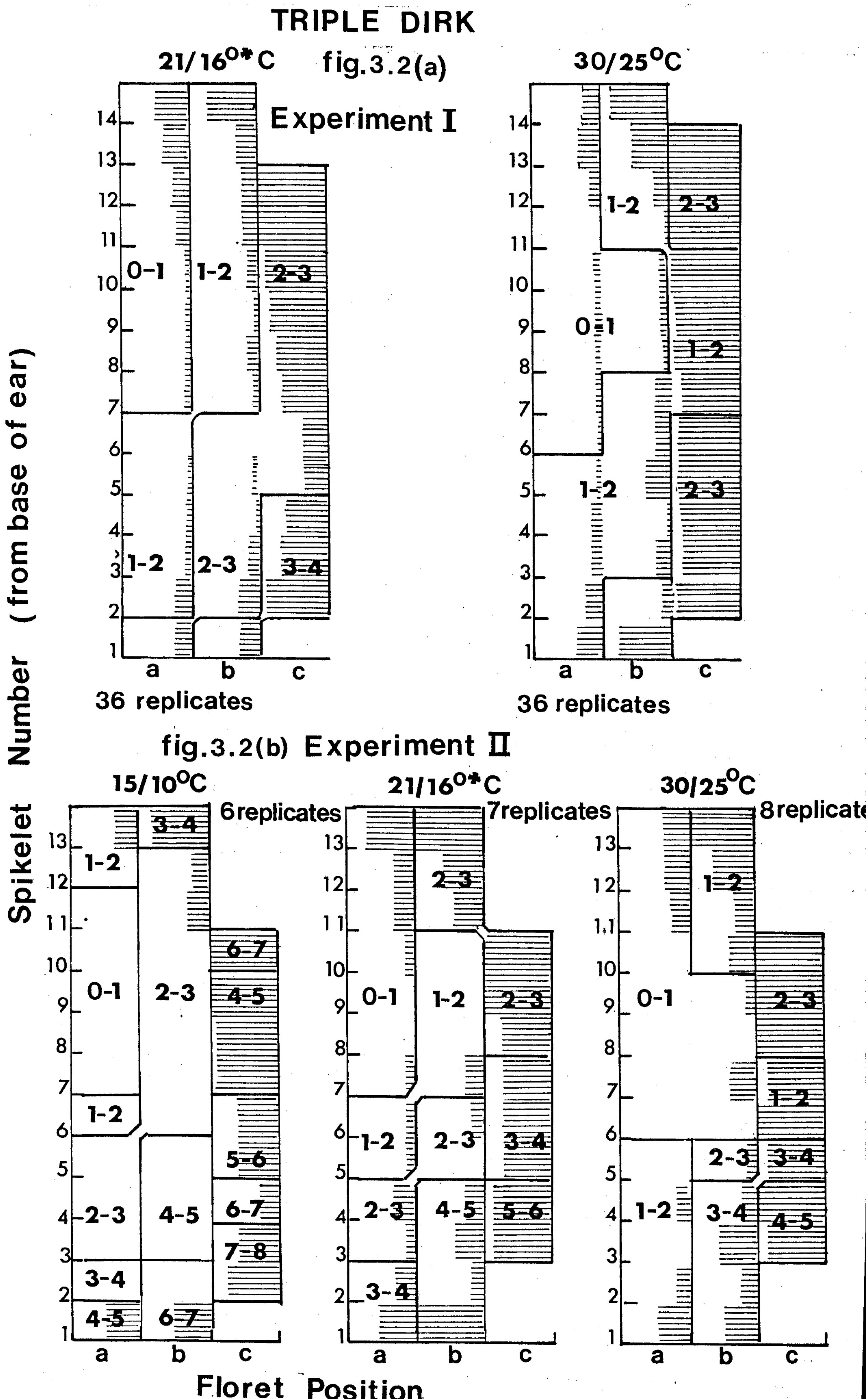
However for Timgalen a different pattern was evident: the first anther emerged from a floret a position approximately four-fiths up from the base of the ear and gradually anthers emerged progressively towards the base. Again the same pattern was observed for the floret b positions whose anthers emerged one to two days later than those in the respective floret a positions (Figure 3.2 c & d).

The patterns of anther emergence were not significantly altered by either increasing or decreasing the temperature from 21/16°*C at first anthesis in either experiment. Nor were they altered by the drop in incident radiation in experiment II. However the time taken for the complete anthesis of an ear was influenced by temperature. Generally the effect was most marked for florets in lower spikelets and more distal florets.

For a particular temperature treatment, within each experiment, the time taken for complete anthesis of an ear did not vary significantly between the cultivars. At 21/16°*C anthesis of an ear was completed within four to five days in experiment I under high summer solar radiation, and six to seven days in experiment II, under low winter solar radiation. When the temperature was increased from 21/16°*C to 30/25°C, anther emergence was completed one to two days earlier, when it was decreased to 18/13°C in experiment I and 15/10°C in experiment II, it was slower by one to two days.

Under the lower incident radiation of experiment II at 21/16°*C and 30/25°C anther emergence was marginally slower, by one to two

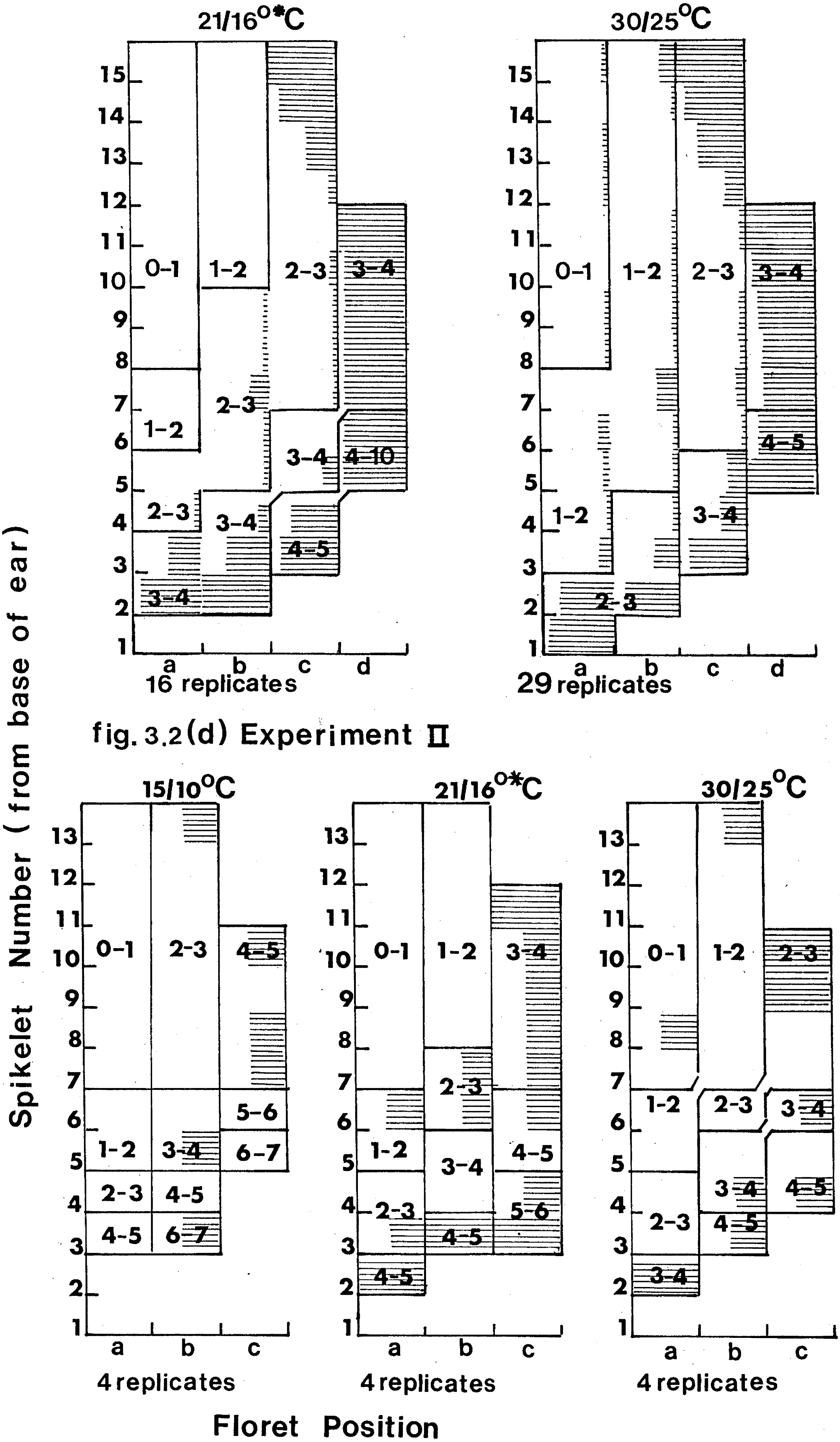
Figure 3.2 Experiments I and II. Profiles of time of anthesis and grain set at maturity within ears. The numbers indicate average days to anthesis of a particular floret after that in the earliest floret. The hatched areas indicate percent failure of grain set for the number of replicates used for each treatment and cultivar.



TIMGALEN

fig.3.2(c) Experiment I

fig.3.2(d) Experiment II



W W15

fig. 3.2 (e) Experiment I

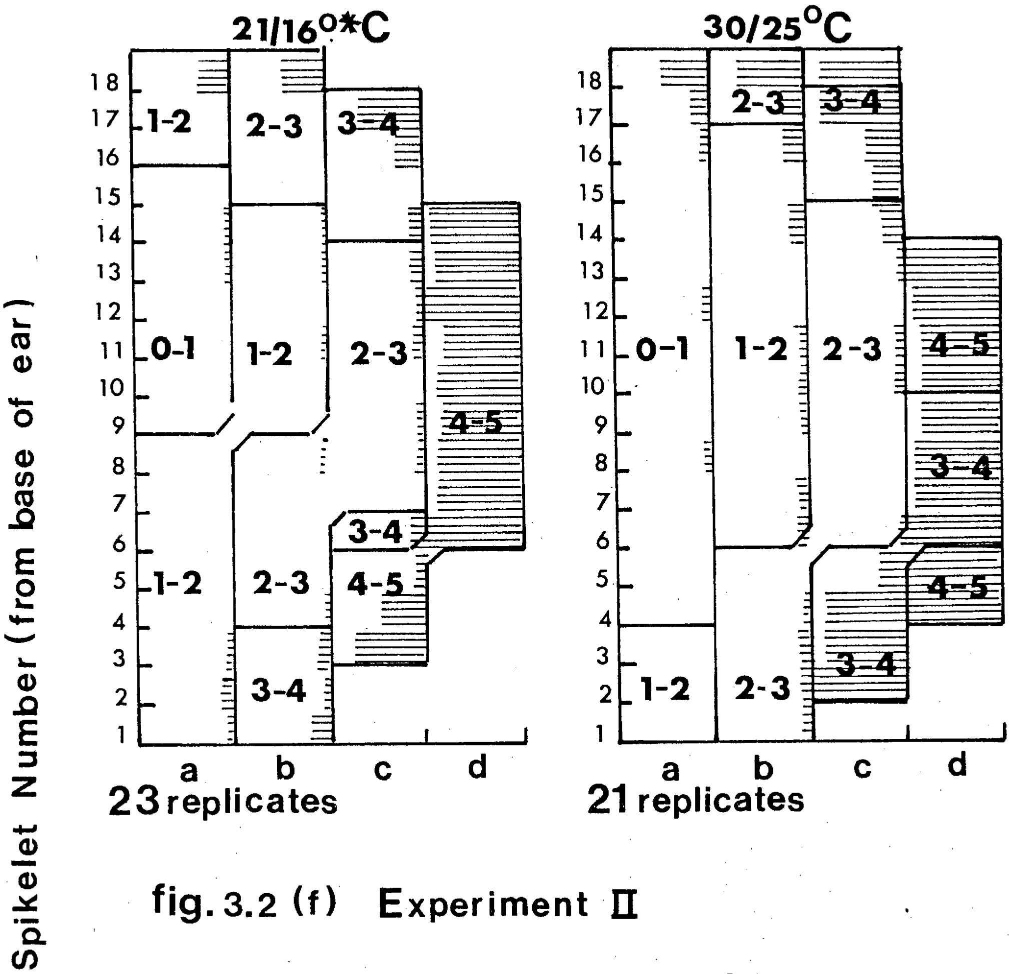
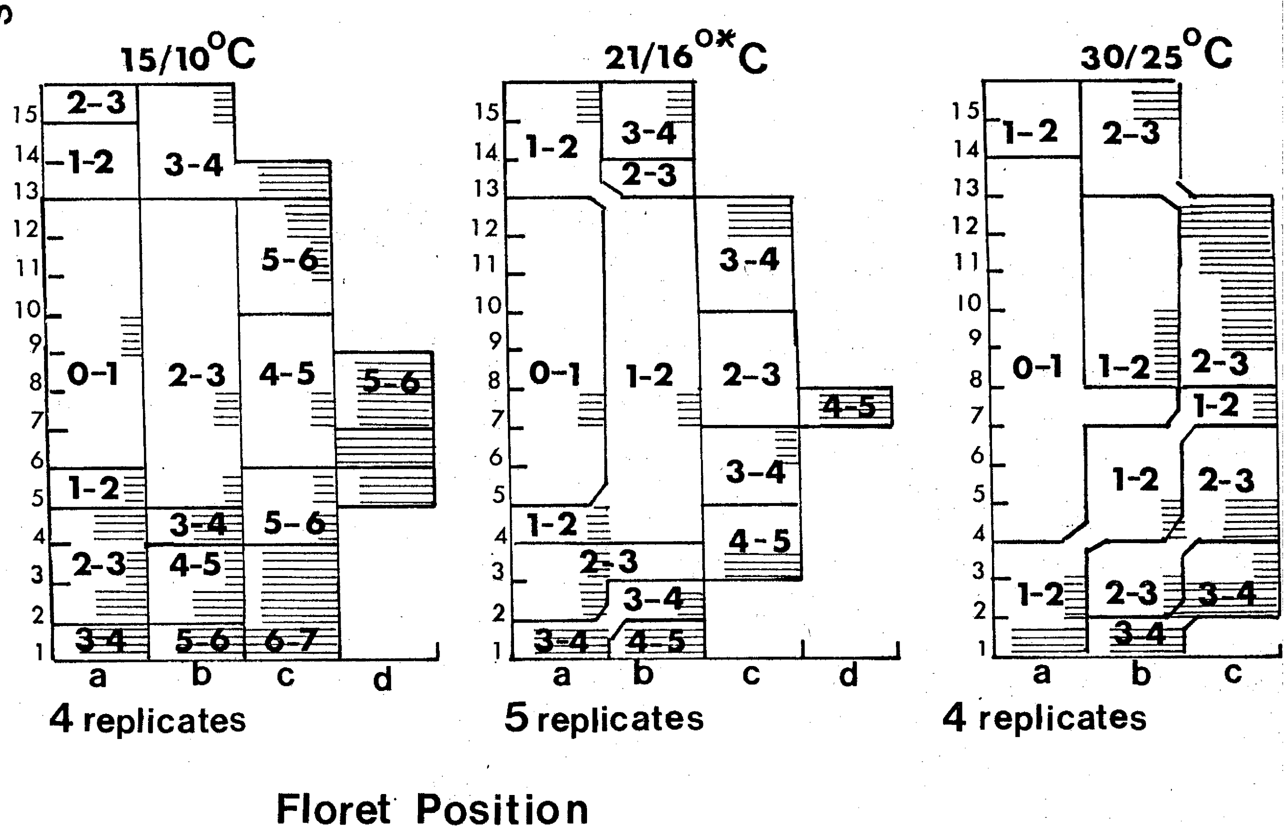


fig. 3.2 (f) Experiment II



Late Mexico 120

fig. 3.2(g) Experiment I

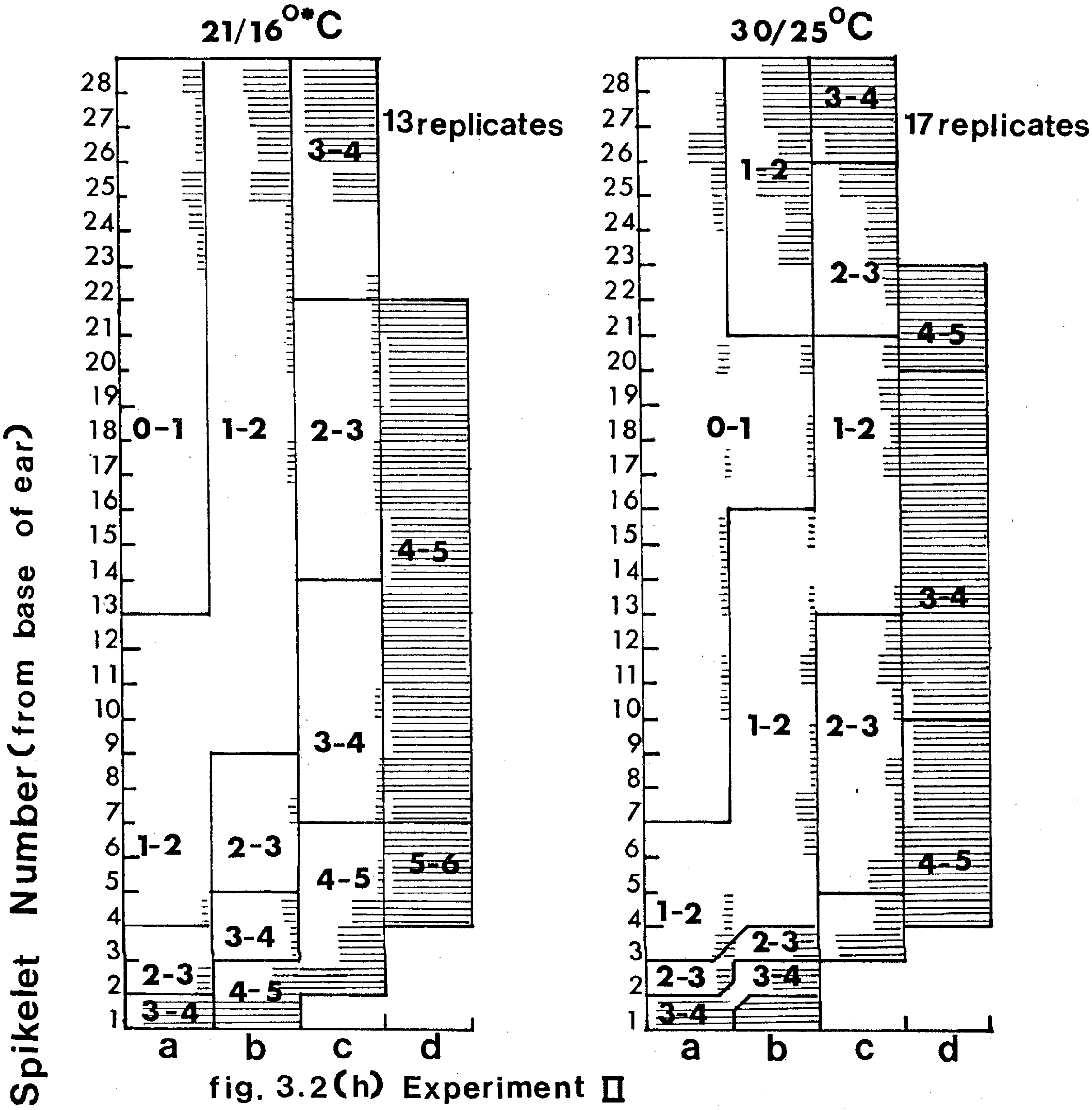
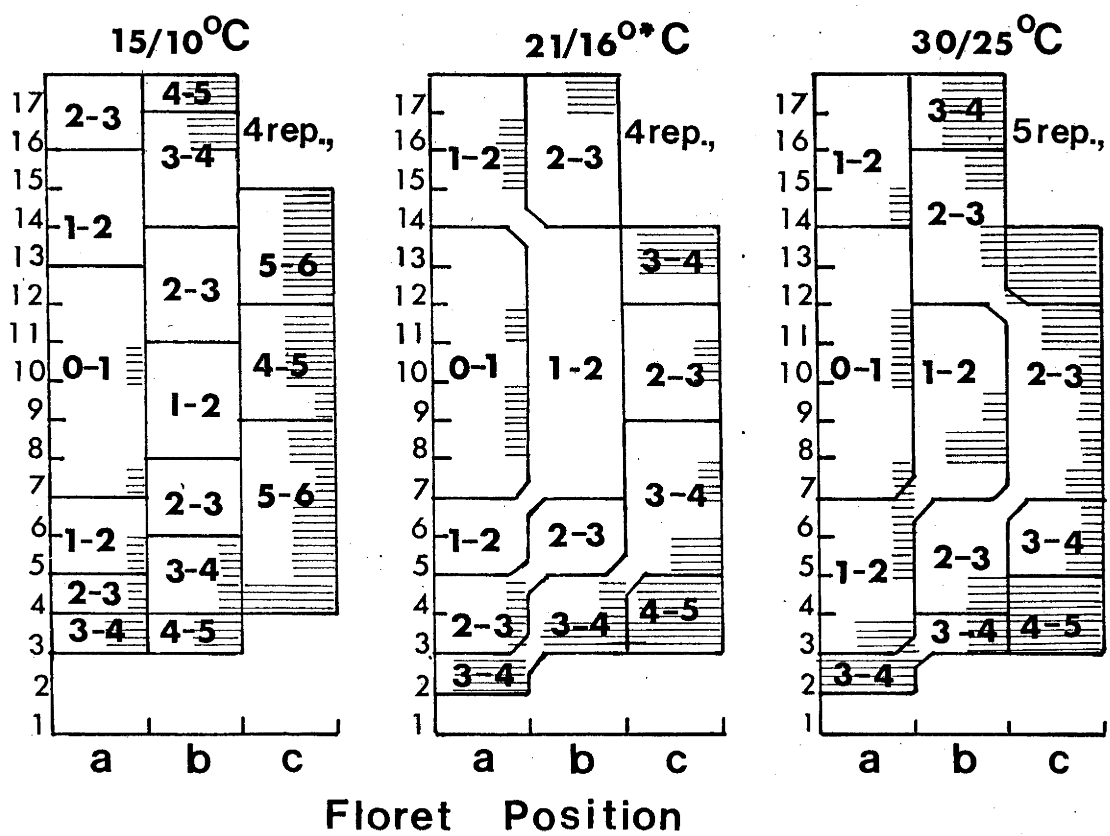


fig. 3.2(h) Experiment II



days, than for the comparable floret positions in experiment I.

3.3 THE EFFECT OF TEMPERATURE ON THE NUMBER AND PATTERN OF GRAIN SET. EXPERIMENTS I AND II.

In this section the data on number and pattern of grains set at maturity for ears of a prescribed spikelet number are presented (Table 2.2). Therefore the mean values for number of grains per ear differ slightly from those in Table 3.1, which are the treatment means. For the patterns of grain set more emphasis is placed on data from experiment I where a greater number of replicates were used. (Fig. 3.2 a-h)

In all cultivars the mean number of florets per ear reaching anthesis was not significantly altered by either increasing or decreasing the temperature from 21/16°*C at first anthesis (Table 3.2). Thus for Timgalen in experiment I the mean number of florets reaching anthesis was 42.1 $\pm$ 4.0, 42.8 $\pm$ 4.0, and 44.0 $\pm$ 4.0 at 18/13°C, 21/16°*C and 30/25°C respectively. However the number of grain set per ear was influenced by temperature changes at first anthesis for some cultivars, (Table 3.2).

From the data of Table 3.2, it is apparent that a cultivar responded similarly in both experiments to a change in temperature at first anthesis. At the higher temperature of 30/25°C a marginally smaller number of grains set in Triple Dirk, WW15 and Late Mexico 120, than at the lower temperatures of 21/16°*C and 18/13°C in experiment I and 15/10°C in experiment II. Moreover a small increase in the number of grain set was recorded for Triple Dirk and Late Mexico 120 but not WW15 when the temperature was lowered from 21/16°*C to 18/13°C in experiment I and 15/10°C in experiment II. There are no data for Late Mexico 120 at 18/13°C since too few plants reached anthesis

TABLE 3.2 EXPERIMENTS I and II. The mean number of florets reaching anthesis and the mean number of grains set per ear for four cultivars.

Experiment No. Temperature treatment.		Cultivar number of Spikelets per ear	Mean number of florets reaching anthesis per ear($\pm$ S.D.)	Mean number of grains set per ear
I	18/13°C	Triple Dirk	38.0 $\pm$ 1.8	27.2
	21/16°*C	14	36.5 $\pm$ 2.1	25.8
	30/25°C		35.8 $\pm$ 1.0	23.3
I	18/13°C	Timgalen	42.1 $\pm$ 4.0	33.3
	21/16°*C	15	42.8 $\pm$ 3.5	32.7
	30/25°C		44.0 $\pm$ 4.0	33.3
I	18/13°C	WW15	54.8 $\pm$ 2.9	48.2
	21/16°*C	18	53.7 $\pm$ 4.3	47.8
	30/25°C		53.1 $\pm$ 4.3	44.9
I	21/16°*C	Late Mexico	92.5 $\pm$ 4.7	72.0
	30/25°C	120,28	94.3 $\pm$ 4.9	67.1
II	15/10°C	Triple Dirk	33.6 $\pm$ 1.8	25.3
	21/16°*C	13	32.0 $\pm$ 2.1	21.3
	30/25°C		33.2 $\pm$ 1.8	20.1
II	15/10°C	Timgalen	28.0 $\pm$ 0.7	25.0
	21/16°*C	13	29.0 $\pm$ 1.0	23.5
	30/25°C		29.0 $\pm$ 0.8	24.0
II	15/10°C	WW15	40.3 $\pm$ 4.7	35.0
	21/16°C	15	39.4 $\pm$ 2.5	35.0
	30/25°C		39.0 $\pm$ 1.4	33.0
II	15/10°C	Late Mexico	40.5 $\pm$ 3.2	37.5
	21/16°C	120, 17	42.7 $\pm$ 3.2	34.5
	30/25°C		41.3 $\pm$ 1.7	29.6

within a reasonable period.

Timgalen differed from the other cultivars in that the number of grains per ear was not significantly altered by any of the temperature treatments in either experiment: approximately 33 grains set in each temperature regime in experiment I and 24 to 25 in experiment II.

In experiment I for all temperature treatments Triple Dirk set the least number of grains per ear, 27 and 23 (at 18/13°C and 30/25°C), followed by Timgalen then WW15 and Late Mexico which set the most, 72 and 67 (at 21/16°*C and 30/25°). However in experiment II, due mainly to fewer spikelets per ear, the number of grains set was similar for Triple Dirk and Timgalen being 25 in both cultivars at 15/10°C and 20 and 24 respectively at 30/25°C. WW15 and Late Mexico 120 set more grains than the other cultivars, 35 and 33 in the former and 38 and 30 in the latter (at 15/10°C and 30/25°C) (Table 3.2).

The positions within an ear in which florets reached anthesis but failed to set grains are indicated by the hatched areas in Figure 3.2 a-h. A detailed examination of the number of grains set in each of the floret a,b,c and d positions from the apex to the base of an ear is presented in Table 3.3.

For Triple Dirk, WW15 and Late Mexico 120 the small decrease in the number of grains per ear at the higher temperature of 30/25°C was largely due to grains failing to set in the outer floret positions. Invariably the number setting in the floret a position was not significantly altered by any of the temperature treatments. Thus for example, from Table 3.3, for Late Mexico 120 in experiment II when comparing the number of grains set between 15/10°C and 30/25°C a decrease of eight grains per ear was noted at 30/25°C, this was accounted by 1.3, 2.4 and 4.2 grains failing to set in the floret a,b and c positions respectively.

TABLE 3.3 EXPERIMENTS I and II. Mean number of (i) florets reaching anthesis and (ii) grains set for the floret a, b, c and d positions respectively.

EXPERIMENT I

Cultivar Temperature treatment and number of spikelets per ear		Each floret position is averaged from the tip to the base of the ear							
		a Florets		b Florets		c Florets		d Florets	
		Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set
Triple Dirk									
18/13°C	14	13.8 ± 0.4	12.0	13.8 ± 0.4	11.6	10.8 ± 0.8	3.6	0.6 ± 0.9	0
21/16°*C	14	13.5 ± 0.7	11.6	13.0 ± 1.4	11.2	10.5 ± 1.4	3.1	0	0
30/25°C	14	13.3 ± 0.5	12.1	13.0 ± 0.8	10.2	9.2 ± 1.1	1.0	0	0
Timgalen									
18/13°C	15	12.7 ± 0.6	12.5	12.8 ± 0.8	11.5	11.0 ± 0.9	8.6	5.5 ± 0.6	0.8
21/16°*C	15	12.7 ± 0.6	12.5	12.8 ± 0.8	11.6	11.7 ± 0.8	8.3	5.7 ± 1.0	0.3
30/25°C	15	13.0 ± 1.2	12.8	13.7 ± 0.6	11.7	10.7 ± 1.5	8.0	6.7 ± 3.5	0.8
WW15									
18/13°C	18	17.3 ± 0.6	17.4	17.5 ± 0.6	17.5	14.5 ± 1.0	12.8	5.5 ± 3.4	1.5
21/16°*C	18	17.6 ± 0.5	17.4	16.6 ± 1.1	17.0	14.2 ± 1.5	12.0	4.3 ± 3.6	1.4
30/25°C	18	17.7 ± 0.6	17.3	17.3 ± 0.6	16.1	14.0 ± 1.0	11.0	4.0 ± 2.7	0.6
Late Mexico 120									
21/16°*C	28	27.0 ± 1.4	26.1	27.0 ± 1.4	24.1	24.5 ± 0.7	21.2	13.5 ± 2.2	0.7
30/25°C	28	27.0 ± 0.0	25.3	27.0 ± 0.0	22.6	26.0 ± 0.0	18.9	15.0 ± 4.2	0.3

TABLE3.3 EXPERIMENTS I AND II. Mean number of (i) florets reaching anthesis and (ii) grains set for the floret a,b,c and d positions respectively.

EXPERIMENT II

Cultivar Temperature treatment and number of spikelets per ear		Each floret position is averaged from the tip to the base of the ear							
		a Florets		b Florets		c Florets		d Florets	
		Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set	Mean number of florets reaching anthesis (± S.D.)	Mean number of grains set
Triple Dirk									
15/10°C	13	12.8 ± 0.5	12.2	12.6 ± 0.5	11.0	7.8 ± 1.1	2.2	0	0
21/16°*C	13	12.8 ± 0.5	11.1	12.4 ± 0.5	8.7	6.9 ± 1.2	1.4	0	0
30/25°C	13	12.5 ± 0.5	11.1	12.5 ± 0.5	8.7	7.6 ± 1.5	0.4	0	0
Timgalen									
15/10°C	13	11.0 ± 0.0	11.0	11.0 ± 0.0	9.5	6.0 ± 0.0	4.5	0	0
21/16°*C	13	11.3 ± 0.6	10.5	10.7 ± 0.6	8.0	7.0 ± 1.5	4.5	0	0
30/25°C	13	11.5 ± 0.7	10.5	11.0 ± 0.0	9.5	7.3 ± 0.6	4.0	0	0
WW15									
15/10°C	15	14.3 ± 1.2	11.7	13.3 ± 1.5	12.7	10.0 ± 0.9	9.0	3.0 ± 2.0	1.7
21/16°*C	15	14.6 ± 0.6	13.0	14.0 ± 0.7	13.4	10.8 ± 0.8	8.4	1.0 ± 0.5	0.2
30/25°C	15	14.5 ± 0.6	14.0	13.8 ± 0.5	12.8	10.3 ± 1.1	6.3	0	0
Late Mexico 120									
15/10°C	17	15.0 ± 0.0	14.5	14.0 ± 0.8	14.0	11.0 ± 2.8	9.0	0	0
21/16°*C	17	15.2 ± 0.9	13.5	14.3 ± 0.8	13.5	10.5 ± 0.5	7.5	1.2 ± 1.5	0
30/25°C	17	15.2 ± 0.8	13.2	14.5 ± 0.5	11.6	11.6 ± 2.9	4.8	0	0

As concluded by Evans (Ev 72) the position of the floret within the ear appears to be more important than the time of anthesis (from that of the earliest floret to reach anthesis)in determining its grain set. Namely florets in lower spikelets have an advantage over those in upper spikelets, even though the former may anthese later. For example at 21/16°*C some florets in the upper spikelets which had reached anthesis on day 2 to 3 failed while some florets anthesing on day 3 to 4 in the lower part of the ear set grain. This was common to all cultivars in both experiments.

Triple Dirk, Timgalen and WW15 responded to high temperature by aborting some grains, mainly from the outer floret positions, this was not the case for Timgalen. At 30/25°C Timgalen did not abort any grains but some grains anthesing within two days in the floret a and b positions of central spikelets failed to set grains where they normally did at lower temperatures. This was compensated by more grains setting in the lower spikelets where they did not normally set as many at the lower temperatures (Figure. 3.2c). This "spreading out" of grains within each floret position (apex to base of an ear) was noted to occur at a much lesser extent for Triple Dirk WW15 and Late Mexico 120.

3.4 THE EFFECT OF LIGHT INTENSITY ON THE NUMBER AND PATTERN OF GRAIN SET FOR TRIPLE DIRK AND SONORA. EXPERIMENT III.

Low light intensity imposed four days after first anthesis influenced grain set at maturity to a considerable extent in Triple Dirk and to a lesser extent in Sonora. Thus for example when comparing grain set at the lowest and highest light intensities (8070 lux, 48420 lux) grain numbers were 24.5 ± 2.2 and 30.6 ± 1.3 respectively in Triple Dirk and 39.7 ± 2.2 and 45.9 ± 3.5 respectively in Sonora.

At the lowest intensity (8,070 lux) the ~~21%~~ 20% and ~~10%~~ 14% failures in Triple Dirk and Sonora respectively were due mainly to grains failing to set in the outer florets, especially in the upper spikelets (Figure 3.3a and b).

For example the 21% failure of grain set in Triple Dirk at 8070 lux was accounted for by 3% and 18% failure of the total 21%, in the floret b and c positions, and of this 3% failure in the floret b position 95% was due to grains failing to set in the upper spikelets, numbers 9-15 (Figure 3.3).

Such adjustment of grain number according to conditions at anthesis has the consequence that, especially in cultivars like Triple Dirk, environmental conditions have far less effect on growth rate <u>per grain</u> than on rate <u>per ear</u>, and final grain size is thereby buffered against extreme variation. In Sonora the outer floret grains did not abort so readily and the growth rate per grain was correspondingly far more responsive to light intensity (4.3).

3.5 THE EFFECT OF DAY/NIGHT TEMPERATURES AND THERMOPERIOD ON THE NUMBER OF GRAINS SET PER EAR FOR CVS. SONORA AND LATE MEXICO 120 THE EFFECT OF DAY/NIGHT TEMPERATURES ON THE PATTERN OF GRAIN SET FOR CV. SONORA. EXPERIMENT IV.

The 21/16°*C glasshouse treatment had a day temperature of eight hours duration (Table 2.1) and was under a mean daily radiation of $5.6 \times 10^6 \pm 1.8 \times 10^6$ J m $^{-2}$ day $^{-1}$ (400-700nm). But the treatments in cabinets, 21/16°C, 21/25°C, 30/16°C and 30/25°C had a day temperature of 12h duration where each cabinet treatment and a mean daily radiation of 5.92×10^6 J m $^{-2}$ day $^{-1}$ (400-700nm) at ear level. Also transfers to the treatments were effected five days after first anthesis (Table 2.1).

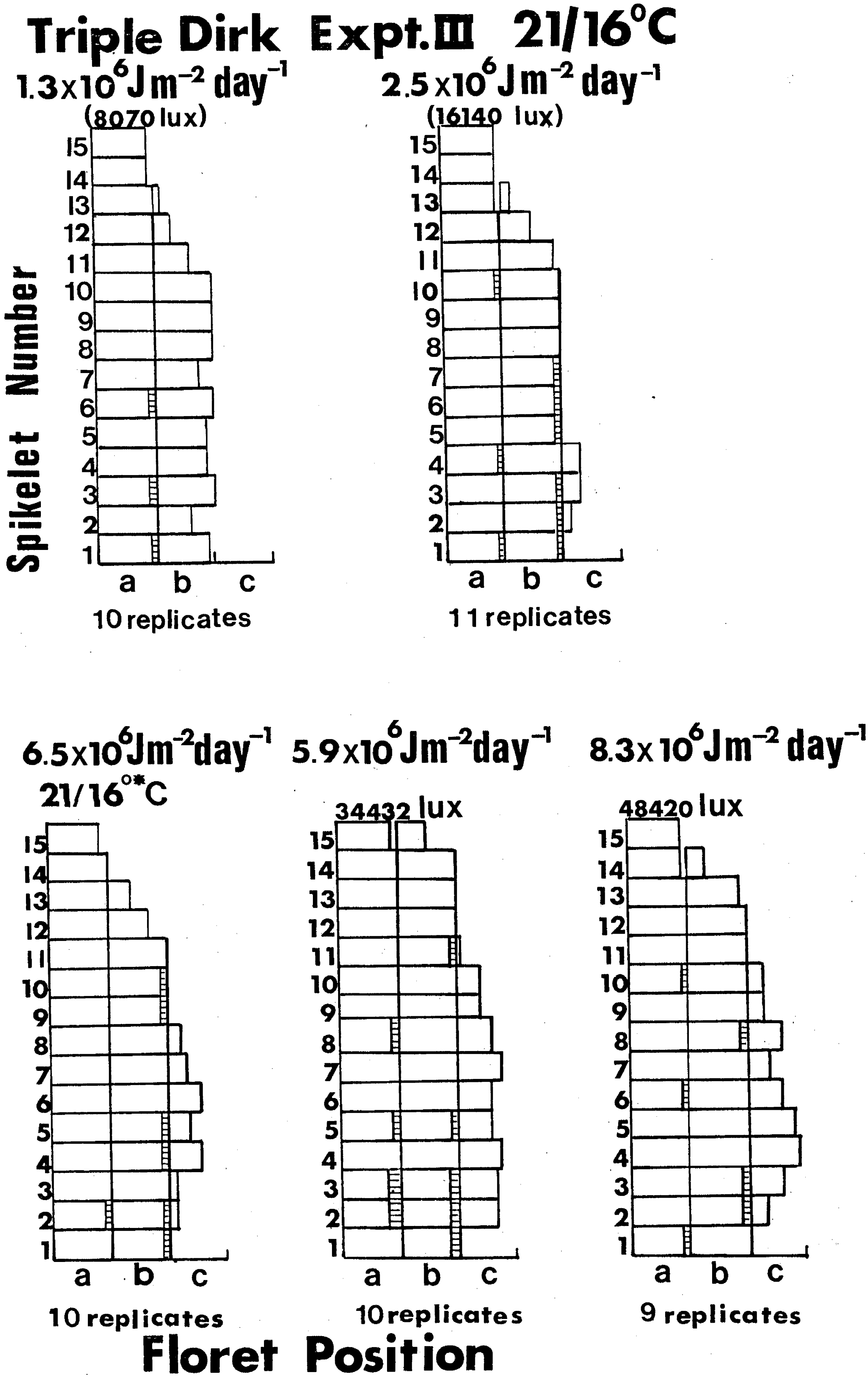
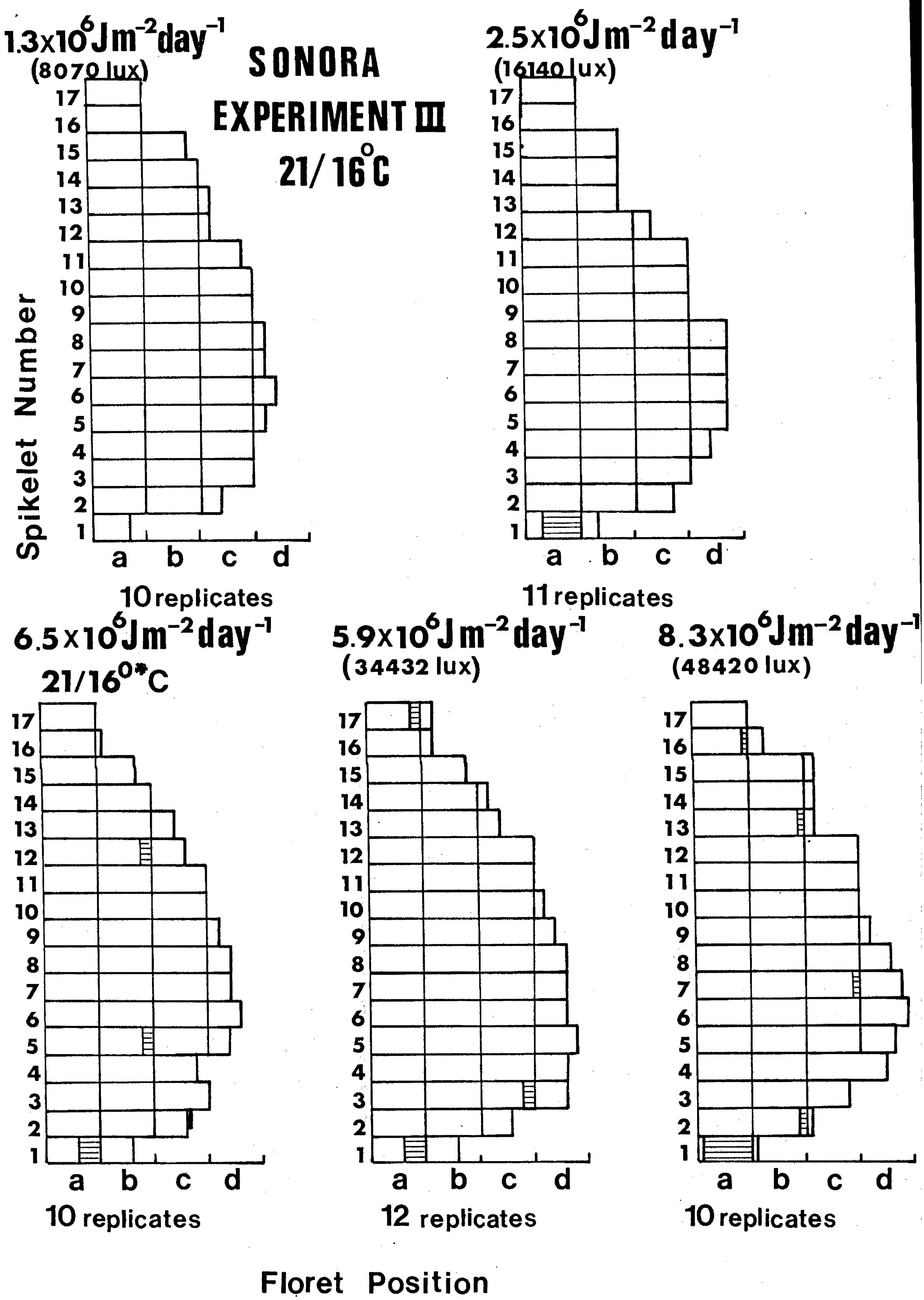


Figure 3.3 Experiment III. Profiles of grain set at maturity at different light intensities. All light readings are given in the 400-700n.m. range. The hatched areas indicate percent failure of grain set for the number of replicates examined.



SONORA
EXPERIMENT III
21/16°C
1.3x10⁶Jm⁻²day⁻¹
(8070 lux)
10 replicates
2.5x10⁶Jm⁻²day⁻¹
(16140 lux)
11 replicates
6.5x10⁶Jm⁻²day⁻¹
21/16°*C
10 replicates
5.9x10⁶Jm⁻²day⁻¹
(34432 lux)
12 replicates
8.3x10⁶Jm⁻²day⁻¹
(48420 lux)
10 replicates
Spikelet Number
a b c d
Floret Position

Neither extending the day temperature nor altering the temperature influenced the grain number in either cultivar, where in both cultivars grain numbers were approximately 29-30 grains per ear (Table 3.1d). However the cultivars differed in their mean number of grains set per spikelet Sonora setting approximately 2.0 and Late Mexico 120 1.6.

It is evident from Figure 3.4 that the pattern of grain set in Sonora at 21/16°C, 21/25°C, 30/16°C and 30/25°C was similar for the floret a and b positions. However in the floret c position, especially at the higher temperatures of 21/25°C and 30/25°C,* some grains failed to set in the central spikelet positions. This was compensated by grains setting further apart in the c floret positions, a similiar response to that observed for Timgalen in the basal floret positions at 30/25°C in experiment I.

3.6 SUMMARY: NUMBER AND PATTERN OF GRAIN SET AS INFLUENCED BY ENVIRONMENTAL CONDITIONS AT OR JUST AFTER FIRST ANTHESIS.

For some cultivars environmental conditons during grain set also influence the final numbers of grains. The extent of this influence depends on the cultivar, the extremity of the environmental conditions and the period lapsed after first anthesis.

High temperature at 30/25°C imposed at first anthesis resulted in a marginally smaller number of grains setting per ear in Triple Dirk, WW15 and Late Mexico 120 but not for Timgalen (Section 3.3). When high temperature was imposed five days after first anthesis, grain set per ear was uninfluenced for Late Mexico 120 and Sonora (Section 3.5).

Low levels of light intensity imposed even four days after first anthesis reduced grain set per ear considerably in Triple Dirk but to a much lesser extent for Sonora (Section 3.4).

* The effect in this instance was also related to high night temperature.

fig.3.4 SONORA, EXPERIMENT IV, 5.9x10^6 J m^{-2} day^{-1}

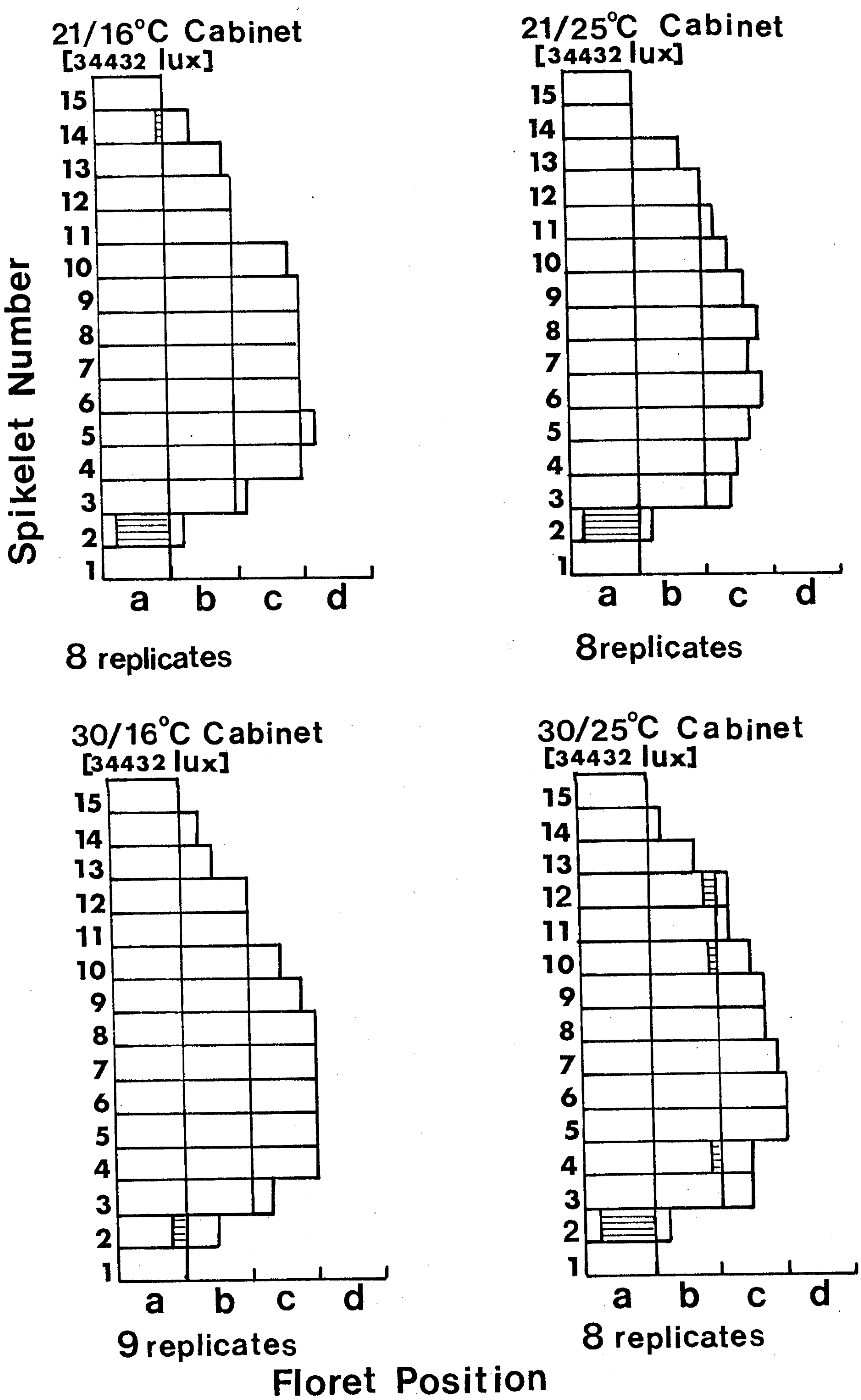


Figure 3.4 Experiment IV. Profiles of grain set at maturity for cv.Sonora at different temperature treatments. The hatched areas indicate percent failure of grain set for the number of replicates examined.

The failure of grains to set at high temperatures or low levels of light intensity is due mainly to failures in the outer floret positions, especially in upper spikelets under low incident radiation.

CHAPTER 4

THE EFFECT OF TEMPERATURE, LIGHT INTENSITY AND CULTIVAR ON THE RATE AND DURATION OF GRAIN FILLING FOR INDIVIDUAL GRAINS AND EARS.

4.1 INTRODUCTION

The introduction serves two functions, firstly, to briefly outline the major responses observed and secondly to indicate the order in which the results are presented.

Basically two components contribute to final weight per grain, that is, the rate and duration of grain filling. These two components varied with temperature and light intensity and they may vary with cultivar.

Either high temperature, 30/25°C, or low light intensity, 8,070 lux and 16,140 lux, reduced final grain weight but under high temperature the reduction was mostly due to a decrease in the duration of grain filling (Section 4.2) whereas under low light intensity it was mostly due to a slower growth rate (Section 4.3).

4.1.1 Temperature

For the different temperature regimes the rate and duration of grain filling generally showed an inverse relationship:- as temperature increased the duration of grain filling was shortened and the rate of grain filling increased. Whether the shortened duration was partially or fully compensated by an increase in the growth rate was influenced by the cultivar and was strongly dependent on the severity of the treatment. For temperatures below 21/16°*C a decrease in the duration of grain filling was largely compensated by an increase in the growth rate but at temperatures above 21/16°*C the reduction in the duration far outweighed any increase in the growth rate. Under high temperature combined with low winter irradiance, the growth rate as well as the duration of grain filling decreased in some cultivars (Section 4.2.1).

Both high day and high night temperatures reduced final grain weight. However a high day temperature appears to have a more adverse effect, largely due to a more severe reduction in the duration of grain filling (Section 4.2.2).

4.1.2 Light Intensity

Light intensity ranging from 2.5 to 13.2 x 10^6 Jm $^{-2}$ day $^{-1}$ (400-700nm) did not appear to influence the duration of grain filling but at the lowest level of 1.3 x 10^6 J m^{-2} day $^{-1}$ (400-700nm) the marked reduction in the growth rate was marginally compensated by a slight increase in the duration of filling (Section 4.3).

4.1.3 Cultivar

For the several wheat cultivars examined, in most cases, no consistent difference in the duration of grain filling was observed for individual grains from the central spikelets (Section 4.4). However not only were there marked differences between the cultivars in their grain growth rates but also in the way these were influenced by environmental conditions (Section 4.4). Among the cultivars no consistent relation between the number of grains per spikelet and grain growth rate was observed (Section 4.4).

4.1.4 Growth of Ears

Cultivar, temperature and light intensity all influenced the rate of growth of ears. The growth rate of ears was in many cases closely related to the number of grains per ear and to the rate of flag leaf photosynthesis as influenced by light intensity (Section 4.5 Fig.4.10). The duration of ear growth was scarcely influenced by light intensity but was greatly decreased as temperature rose, with pronounced effects on grain yield per ear (Section 4.5).

4.1.5 Individual Grains

Final dry weight of individual grains varied markedly with their position, a difference associated with either the rate or duration of filling or both. The effect of a treatment was not necessarily uniform for all grains and the extent of this response varied with the position of the grain within an ear. Moreover which grain positions were more adversely affected appeared to be influenced by the type of stress applied and also varied between the cultivars. Thus in Timgalen high temperature, 30/25°C, combined with high summer irradiance adversely affected grains in the basal floret a and b positions of the central spikelets more than those in the outer florets, whereas in both cultivars at 21/16°*C the effect of low light intensity was less in the basal grains and was most marked in the outer florets (Section 4.6).

4.1.6 Initial Lag

Initial lag was shorter at the higher temperatures. No consistent differences between the cultivars in the length of the initial lag period were evident at the two higher temperatures of 21/16°*C and 30/25°C, but at 15/10°C the lag was consistently longer in the two cultivars setting more grains per spikelet (Section 4.7,Apendix B p 79).

4.1.7 Presentation of the Results

The rate and duration of grain filling as influenced by temperature, light intensity and cultivar are firstly presented on a per grain basis and then on a per ear basis. The effect of temperature, light intensity and cultivar on the initial lag in grain growth is then presented.

Factors, that is, temperature, light intensity and cultivar influencing the rate and duration of grain filling, on a per grain basis, for grains from the central spikelets are presented in the following order

(i) Temperature:- firstly the results for the temperature treatments under summer (Experiment I) and winter (Experiment II) irradiance (Section 4.2.1), then the day/night temperature treatment results (Experiment IV, Section 4.2.2) and lastly the results for the treatment where the day temperature was extended during the photoperiod (Experiment IV, Section 4.2.3) are presented.

(ii) LightIntensity:- treatment results (Experiment III) are presented in Section 4.3.

Within each section, outlined above, simple flow charts illustrating the effect of a particular treatment on the rate and duration of grain filling are given.

(iii) Cultivar:- (a) Cultivar and temperature interactions and (b) cultivar and light intensity interactions and (c) cultivar and light and temperature interactions are summarized in Section 4.4.

Ear growth rate as influenced by cultivar, temperature and light intensity is presented in Section 4.5. The specific effects observed for individual grains as influenced by their floret position within the central spikelets are presented in Section 4.6 and initial lag in grain growth is presented in Section 4.7.

4.2 THE EFFECT OF TEMPERATURE ON THE RATE AND DURATION OF GRAIN FILLING FOR INDIVIDUAL GRAINS. EXPERIMENTS I, II AND IV.

4.2.1 Experiments I and II. The Effect of Increasing the Temperature under Summer (Experiment I) and Winter (Experiment II) Irradiance on the Rate and Duration of Grain Filling.

The effect of increasing the temperature under (i) summer irradiance from (a) 18/13°C to 21/16°*C for cvs. Triple Dirk and Timgalen and (b) 21/16°*C to 30/25°C for cvs. Triple Dirk, Timgalen, WW15 and Late Mexico 120 and (ii) winter irradiance from (a) 15/10°C to 21/16°*C and (b) 21/16°*C to 30/25°C for cvs. Triple Dirk, Timgalen, WW15 and Late Mexico 120, on the rate and duration of grain filling for grains from the central spikelets are given in the Flow Charts below.

FLOW CHART (1)a: The effect of increasing the temperature under summer irradiance from 18/13°C to 21/16°*C.

TIMGALEN	CULTIVAR	TRIPLE DIRK
2.2 2.2	MEAN NUMBER OF GRAINS PER SPIKELET at 18/13°C at 21/16°*C	2.0 1.8
41 to 31 -25 ± 7%	AVERAGE DURATION (days)	40 to 34 -17 ± 4%
1.28 to 1.43 +11 ± 8%	AVERAGE GROWTH RATE (mg day^{-1})	1.37 to 1.58 +13 ± 6%
51 to 46 -10 ± 6%	AVERAGE FINAL WEIGHT PER GRAIN (mg)	55 to 53 -4 ± 3%
-13 ± 3% -14 ± 3% - 9 ± 5% -0.4 ± 8%	FINAL WEIGHTS CENTRAL SPIKELETS OF a grains b grains c grains d grains	-3 ± 4% -7 ± 5% +3 ± 8%

Tabulated data in Appendix C p 82. Absolute values in Table 1(a); % values in Table 2(a); Growth rates, Appendix D p 99; Durations, Appendix E p 104; Final Grain Weight, Appendix F p 108.

- decrease, + increase, n.s.d. no significant difference.

<u>FLOW CHART (1)b</u>: The effect of increasing the temperature under summer irradiance from 21/16°*C to 30/25°C

CULTIVAR	TIMGALEN	TRIPLE DIRK
MEAN NUMBER OF GRAINS PER SPIKELET at 21/16°*C	2.2	1.8
at 30/25°C	2.2	1.7
AVERAGE DURATION (days)	31 to 19 -37 ± 10%	34 to 20 -40 ± 7%
AVERAGE GROWTH RATE (mg. day^{-1})	1.43 to 1.77 + 19 ± 5%	1.58 to 1.79 +13 ± 6%
AVERAGE FINAL WEIGHT PER GRAIN (mg)	46 to 34 - 26 ± 5%	53 to 38 - 28 ± 2%
FINAL WEIGHTS CENTRAL SPIKELETS OF <u>a</u> grains	- 31 ± 3%	- 28 ± 4%
<u>b</u> grains	- 31 ± 5%	- 30 ± 4%
<u>c</u> grains	- 28 ± 5%	failed at 30/25°C
<u>d</u> grains	- 19 ± 2%	

Tabulated data in Appendix C p 84
Absolute values in Table 1 (b) p 84
% values in Table 2 (b) p 87
Growth rates, Appendix D p 99 ; Durations, Appendix E p 104 ;
Final Grain Weight, Appendix F p 108 .

FLOW CHART (1) b (cont): The effect of increasing the temperature under summer irradiance from 21/16°*C to 30/25°C

LATE MEXICO 120	CULTIVAR	WW15
2.6 2.4	MEAN NUMBER OF GRAINS PER SPIKELET at 21/16°*C at 30/25°C	2.6 2.5
33 to 21 - 39 ± 6%	AVERAGE DURATION (days)	35 to 20 - 42 ± 8%
1.35 to 1.49 + 10 ± 9%	AVERAGE GROWTH RATE ($mg. day^{-1}$)	1.28 to 1.52 +16 ± 9%
49 to 33 - 32 ± 3%	AVERAGE FINAL WEIGHT PER GRAIN (mg)	43 to 32 - 27 ± 4%
-32 ± 6%	FINAL WEIGHTS CENTRAL SPIKELETS OF a grains	-24 ± 8%
-34 ± 5%	b grains	-28 ± 7%
-33 ± 5%	c grains	-23 ± 8%

Tabulated data in Appendix C p 84 .

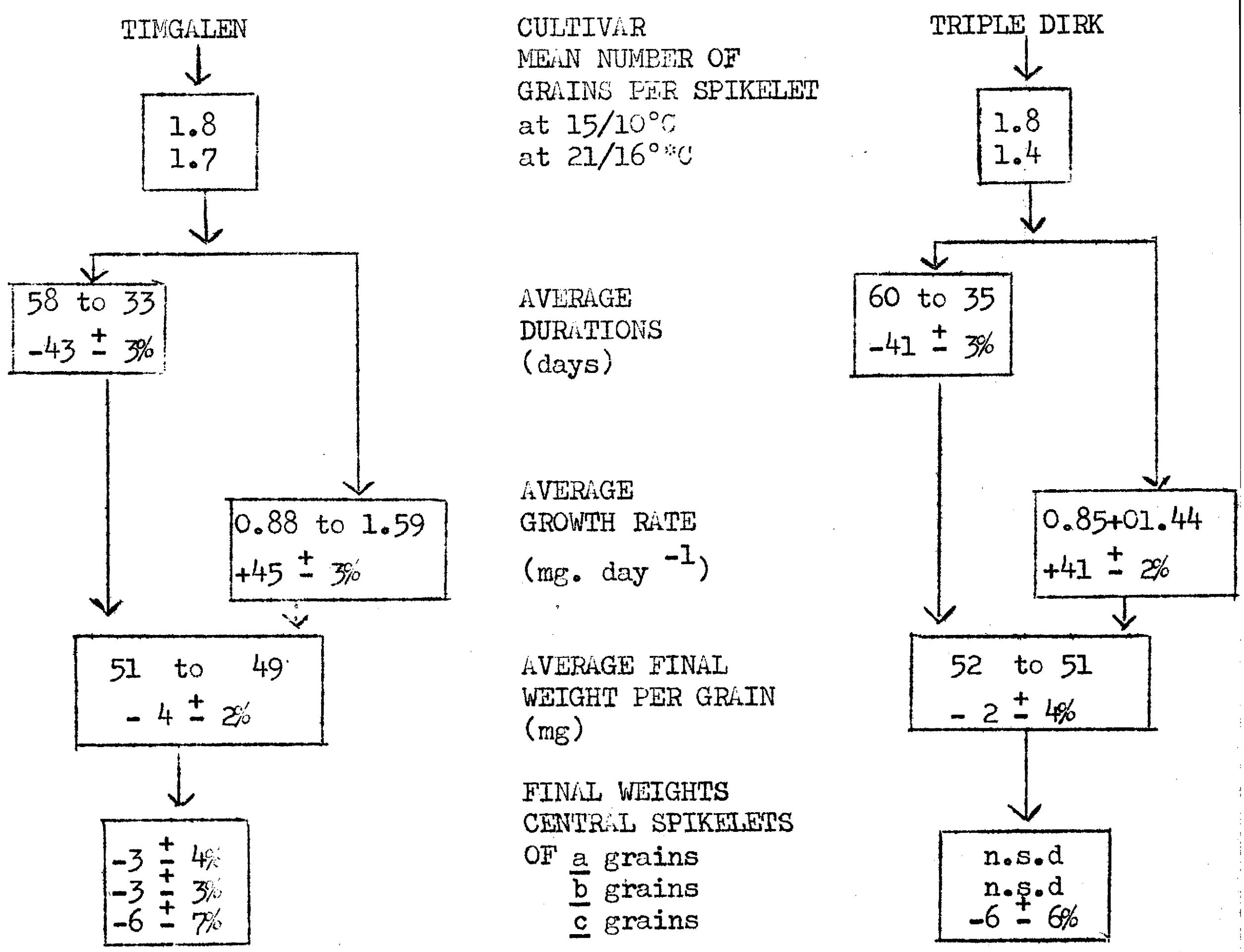
Absolute values in Table 1(b) p 84

% values in Table 2(b) p 87.

Growth Rates, Appendix D p 99 ; Durations, Appendix E p 104 ;

Final Grain Weight, Appendix F p 108 .

FLOW CHART (2) a: The effect of increasing the temperature under winter irradiance from 15/10°C to 21/16°*C.



Tabulated data in Appendix C p 89 .

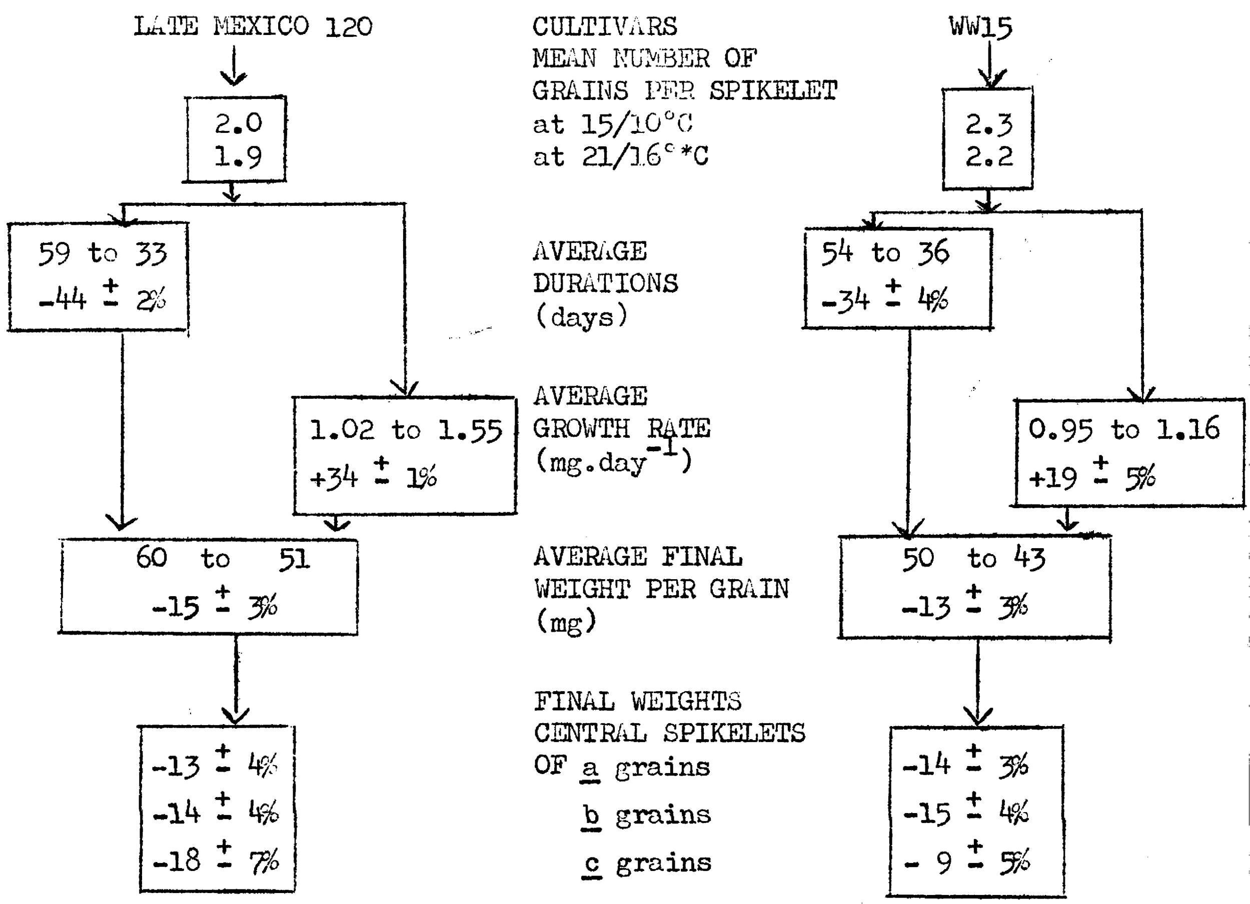
Absolute values in Table 3(a) p 89.

% values in Table 4(a) p 91.

Growth rates, Appendix D p101 ; Durations, Appendix E p 106 ;

Final Grain Weight, Appendix F p 110 .

FLOW CHART (2)a (continued): The effect of increasing the temperature under winter irradiance from 15/10°C to 21/16°*C.



Tabulated data in Appendix C p 89 .

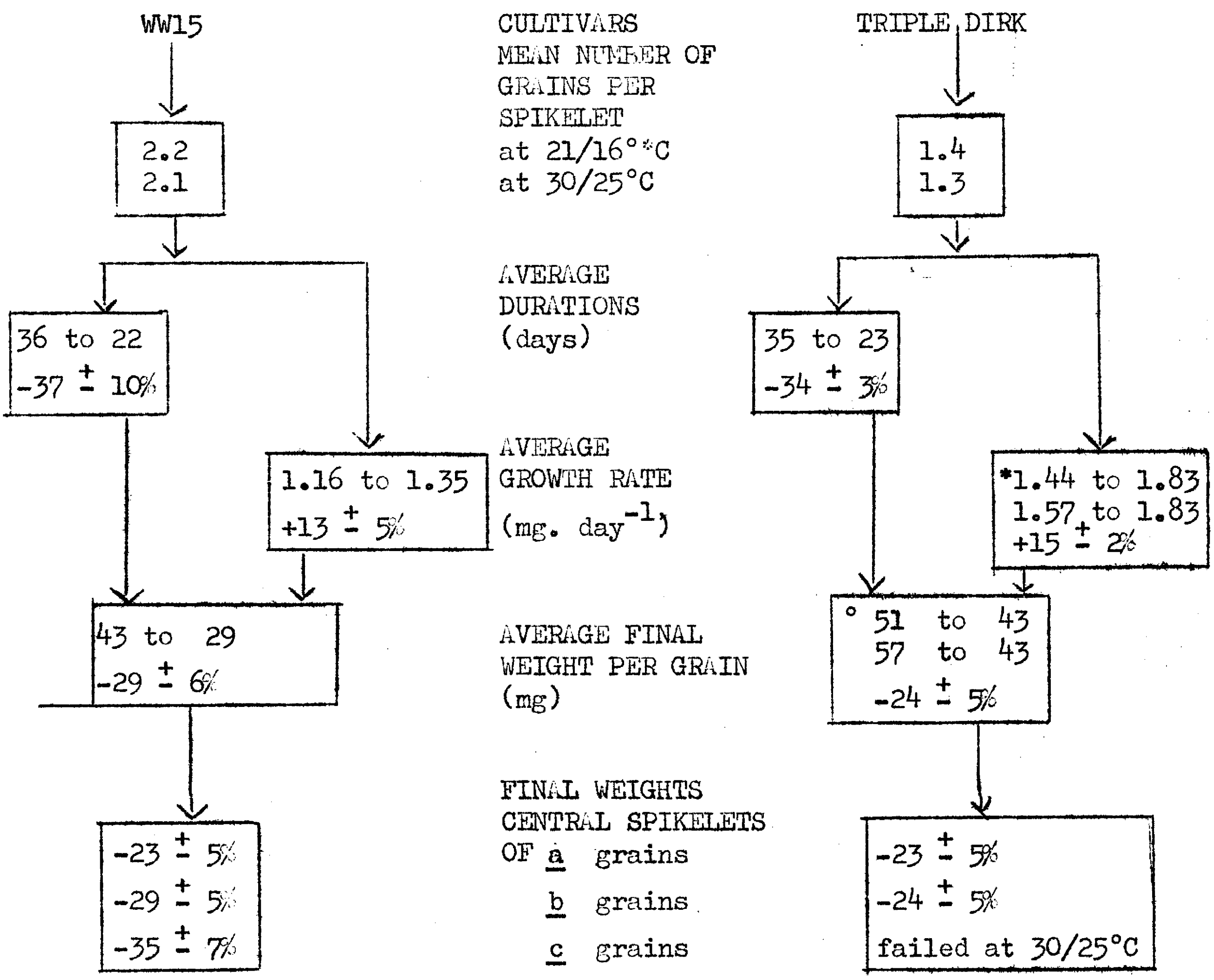
Absolute values in Table 3(a) p 89.

% Values in Table 4(a) p 91.

Growth rates, Appendix D p 101; Durations, Appendix E p 106 ;

Final Grain Weight Appendix F p 110 .

FLOW CHART (2)b: The effect of increasing the temperature under winter irradiance from 21/16°*C to 30/25°C.



Tabulated data in Appendix C p 90 .

Absolute values in Table 3(b) p 90.

% Values in Table 4(b) p 91.

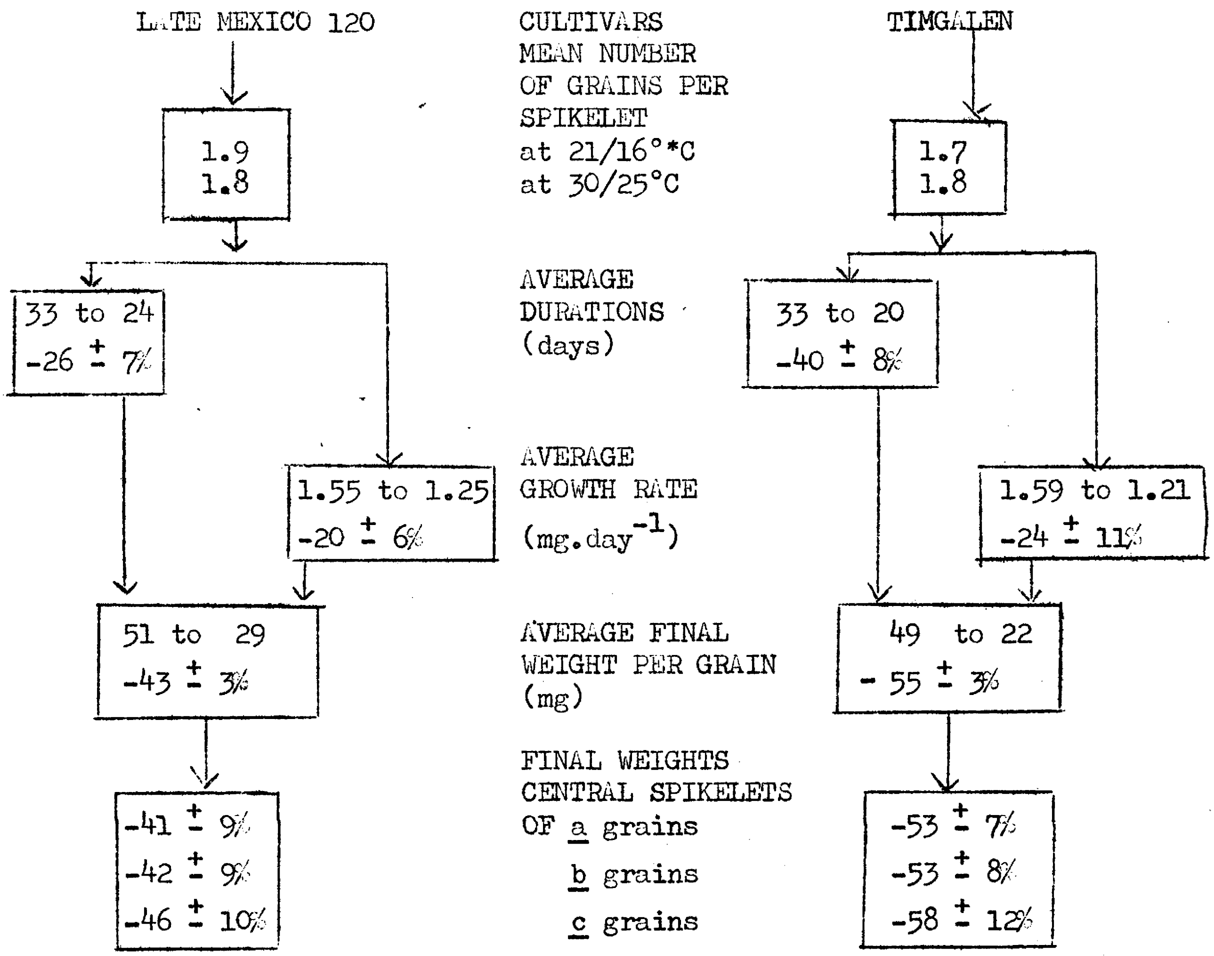
Growth rates, Appendix D p 101 ; Durations, Appendix E p 106 ;

Final Grain Weight Appendix F p 110 .

* 1.44 mg. day^{-1} is the average growth rate calculated over the a b and c grains at 21/16°*C, 1.57 mg. day^{-1} is the average calculated over the a and b grains only. At 30/25°C grain c failed to set and therefore 1.83 is the average growth rate calculated for the a and b grains.

° 51 mg average final weight calculated over a, b and c grains at 21/16°*C. 57mg average final weight calculated over a and b grains only.

FLOW CHART 2(b) (continued): The effect of increasing the temperature under winter irradiance from 21/16°*C to 30/25°C.



Tabulated data in Appendix C p 90 .

Absolute values in Table 3(b) p 90.

% values in Table 4(b) p 91.

Growth rates, Appendix D p 101 ; Durations, Appendix E p 106 ;

Final Grain Weight, Appendix F p 110 .

An increase in temperature generally results in a reduction in final dry weight and this is largely associated with a decrease in the duration of grain filling. The higher the temperature, the more severe was the reduction in duration. For example in experiment II at 15/10°C, 21/16°*C and 30/25°C, the duration of grain filling for all cultivars was 54 to 60 days, 33 to 36 days and 20 to 24 days respectively (Flow Charts (2) a and (2)b).

No consistent differences in duration were observed between the cultivars * nor did the marked difference in incident radiation between experiment I and II appear to affect the duration of grain filling (Fig. 4.1). For example at 21/16°*C the duration of grain filling for all cultivars was 31 to 35 days and 33 to 36 days in experiment I (summer irradiance) and II (winter irradiance) respectively (Flow Charts (1)a and (2)a, Fig. 4.1).

The growth rate increased as temperature was increased from 15/10°C to 21/16°*C (Flow Chart (2)a, Appendix C p 89 Tables 3(a) and 4(a)) and from 18/13°C to 21/16°*C (Flow Chart (1)a, Appendix C p 82 Tables 1(a) and 4(a)). Thus for example in Triple Dirk a temperature increase from 18/13°C to 21/16°*C resulted in an increased growth rate of 13 $\pm$ 6% (Flow Chart (1)a). Under summer irradiance of experiment I the rates were further increased in all cultivars by 10-19% as the temperature rose to 30/25°C (Flow Chart (1) b) but under the winter irradiance of experiment II growth rates only increased in Triple Dirk and WW15. They decreased in Timgalen and Late Mexico 120. (Flow Chart (2)b).

Final grain weight was not markedly lower at 21/16°*C when the temperature was increased from 18/12°C to 21/16°*C under summer irradiance and from 15/10°C to 21/16°*C under winter irradiance because increases in growth rate largely compensated for the reduction in duration. However the magnitude of compensation due to the increase in growth rate varied among the cultivars. For example when the

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* Cultivars used are summarized in Table 2.1. In Experiment I, at 18/13°C, WW15 had a marginally longer duration of grain filling than the other cultivars (Appendix E p 104).

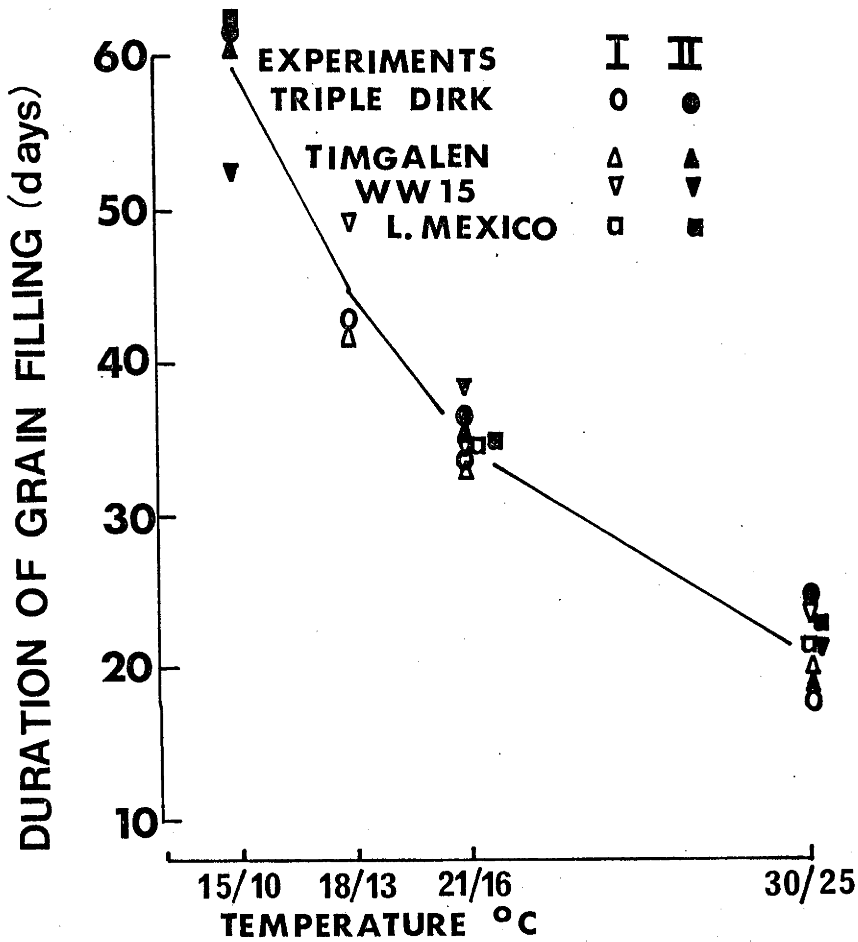


FIGURE 4.1 EXPERIMENTS I and II. The effect of temperature on the duration of grain filling for the floret a grain from the central spikelets. Solid symbols, grain filling in winter (Experiment II); Open symbols,grain filling in summer. Responses for the other central floret grains Appendix E p104.

temperature was increased under summer irradiance from 18/13°C to 21/16°*C final dry weight at 21/16°*C was lighter by 4 to 14% (Flow Chart (1)a, Appendix C p82 Table 2(b) for WW15). Similar to experiment I, in experiment II an increase in temperature for moderate temperature regimes, that is, 15/10°C to 21/16°C did not greatly reduce final grain weight, where reductions of 2 to 5% were observed (Flow Chart (2)a).

Final grain weight was reduced by 26 to 32% under summer irradiance and by 24 to 55% under winter irradinace when the temperature was increased from 21/16°*C to 30/25°C. The marked reduction in duration far outweighed the increase in growth rates. Moreover under winter irradiation growth rates also decreased in Timgalen and Late Mexico 120 consequently the latter two cultivars suffered a more severe reduction in final grain weight than Triple Dirk and WW15. (Flow Charts (1)b and (2)b).

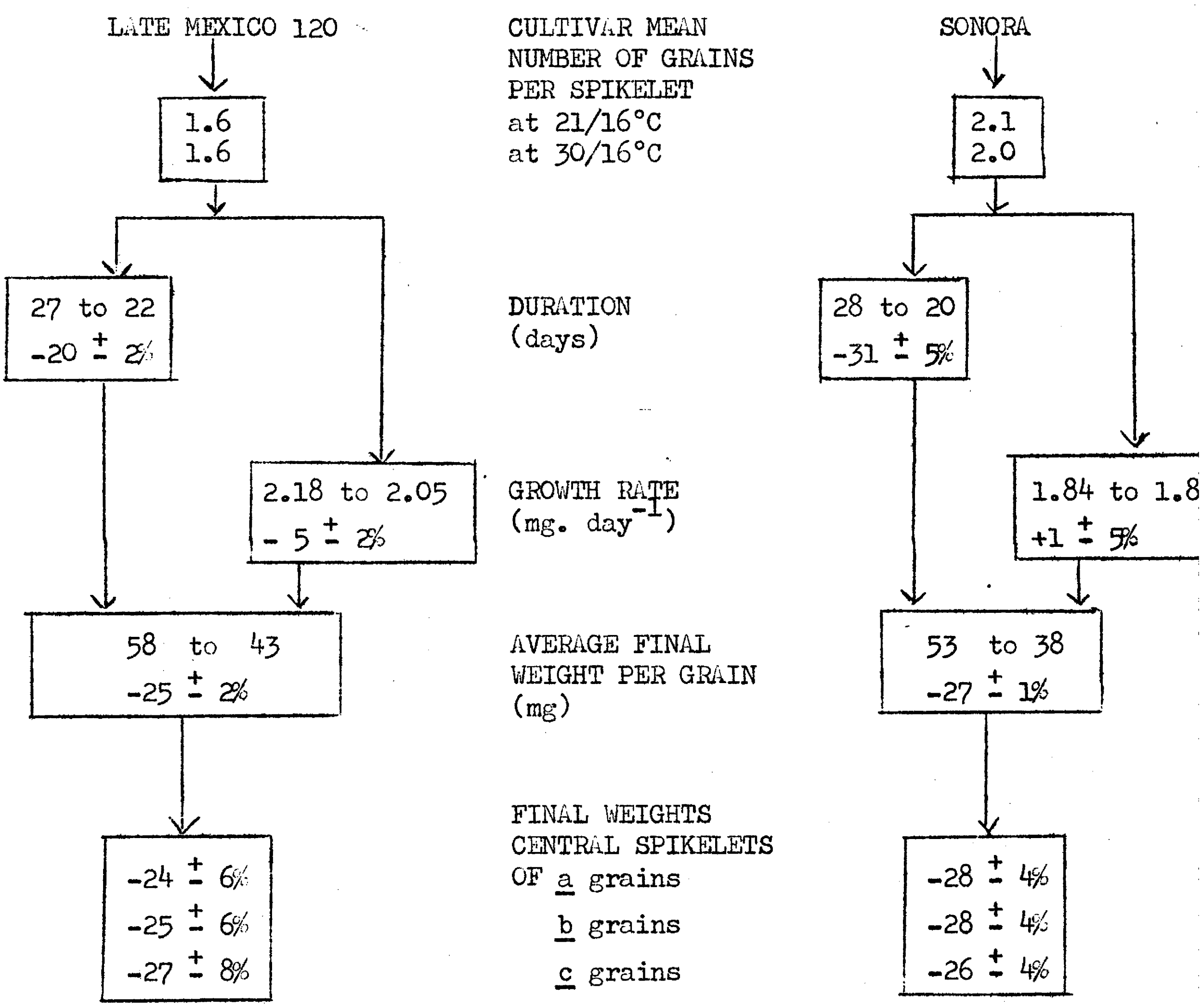
Therefore it appears that for temperatures below 21/16°*C under summer or winter irradiance, a decrease in the duration of grain filling may be compensated by an increase in growth rate but at temperatures above 21/16°*C the reduction in the duration of grain filling is the major component causing a reduction in yield. Furthermore high temperature (30/25°C) combined with low winter irradiance had the added adverse effect that growth rates were also reduced in some cultivars.

4.2.2 Experiment IV. The Effect of Day and Night Temperatures on the Rate and Duration of Grain Filling for cvs. Sonora and Late Mexico 120.

The effect of increasing the day temperature by 9°C, at a night temperature of (a) 16°C and (b) 25°C, on the rate and duration of grain filling are presented in Flow Charts 3(a) and 3(b) respectively.

Also the effect of increasing the night temperature by 9°C, at a day temperature of (a) 21°C and (b) 30°C, on the rate and duration of grain filling are presented in Flow Charts 4(a) and 4(b) respectively.

<u>Flow Chart 3(a):</u> The effect of an increase in day temperature from 21°C to 30°C at a night temperature of 16°C (ie. 21/16°C to 30/16°C).



Tabulated data in Appendix C p 95 .

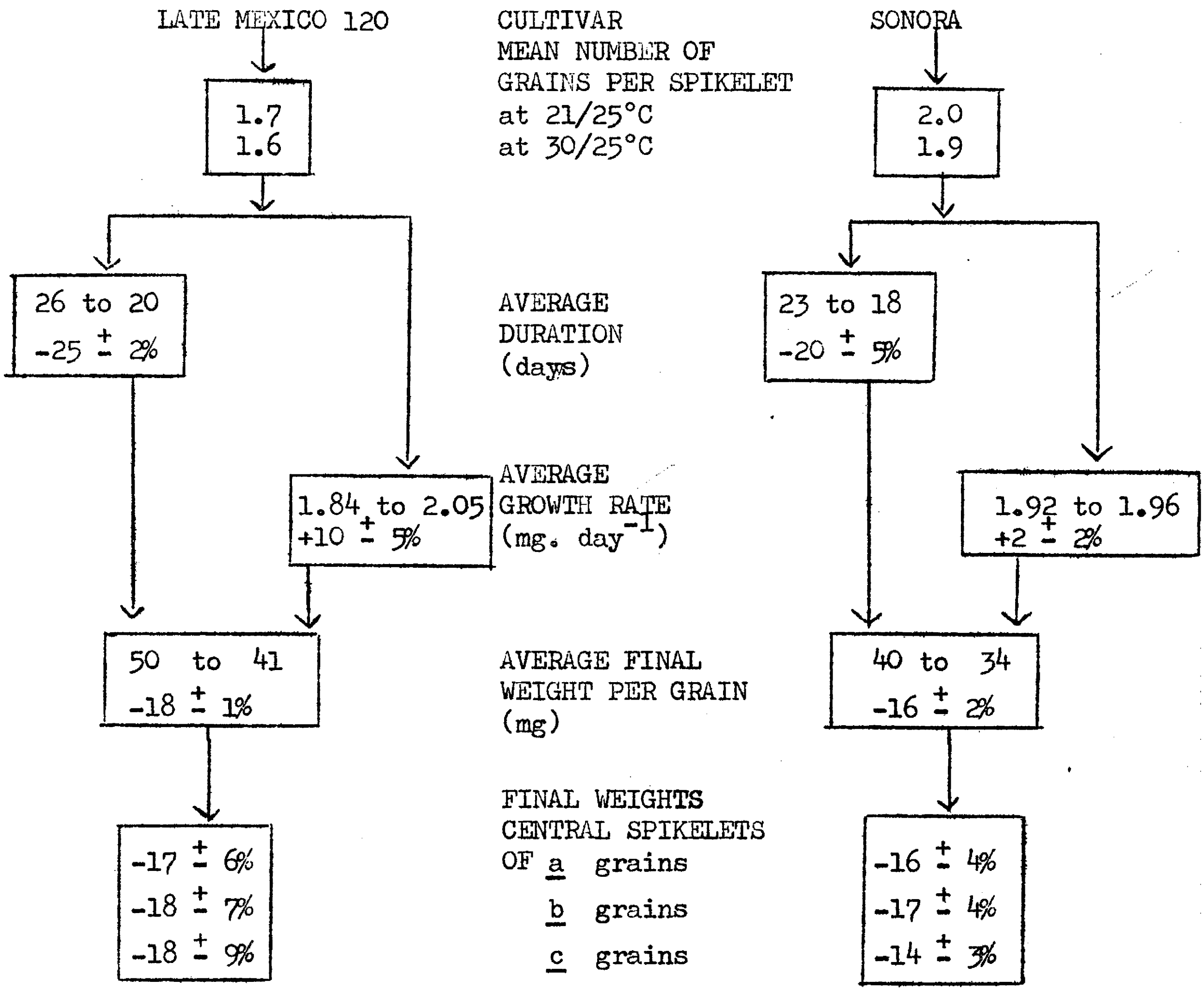
Absolute values in Table 7 b(i) p 95.

% Values in Table 8 b(i) p 97.

Growth rates, Appendix D p103; Durations, Appendix E. p 107 ;

Final Grain Weight, Appendix F p112 .

FLOW CHART 3(b): The effect of an increase in day temperature from 21°C to 30°C at a night temperature of 25°C (ie., 21/25°C to 30/25°C)



Tabulated data in Appendix C p 96 .

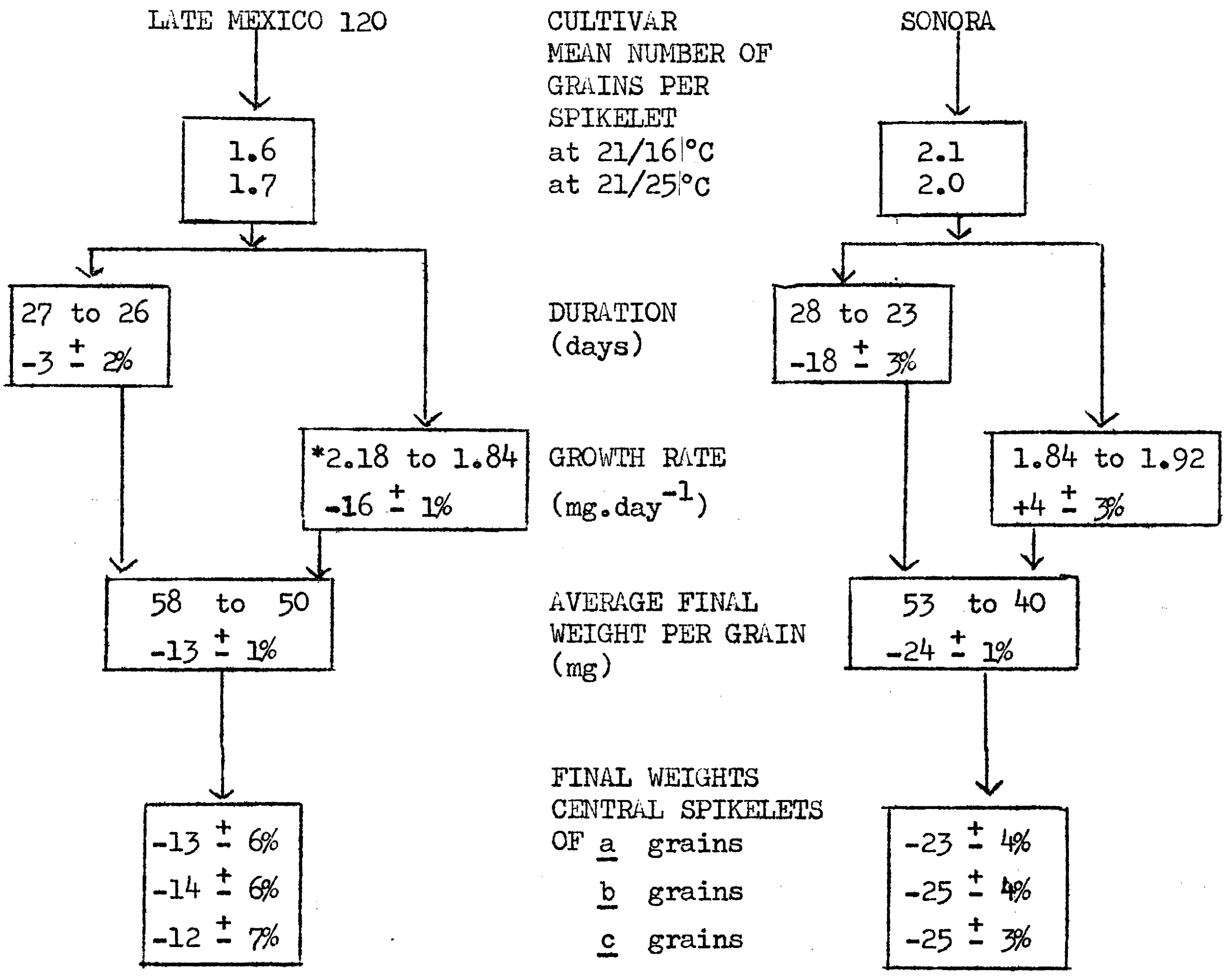
Absolute values in Table 7b(ii) p 96.

% Values in Table 8b(ii) p97.

Growth rates, Appendix D p 103; Durations, Appendix E 107 ;

Final Grain Weight, Appendix F p 112 .

FLOW CHART 4(a): The effect of an increase in night temperature from 16°C to 25°C at a day temperature of 21°C (ie, 21/16°C to 21/25°C)



Tabulated data in Appendix C p96 .

Absolute values in Table 7c(i) p 96.

% values in Table 8c(i) p 98.

Growth rates, Appendix D p103 ; Durations, Appendix E p107 ;

Final Grain Weight, Appendix F p112 .

*For Late Mexico 120, the decrease in final grain weight was largely due to a decrease in growth rate.

<u>FLOW CHART 4(b):</u> The effect of an increase in night temperature from 16°C to 25°C at a day temperature of 30°C (ie., 30/16°C to 30/25°C)

LATE MEXICO 120	CULTIVAR	SONORA
1.6 1.6	MEAN NUMBER OF GRAINS PER SPIKELET at 30/16°C at 30/25°C	2.0 1.9
22 to 20 -6 ± 3%	AVERAGE DURATION (days)	20 to 18 -6 ± 5%
2.05 to 2.05 n.s.d (%)	AVERAGE GROWTH RATE (mg. day^{-1})	1.86 to 1.96 +5 ± 2%
43 to 41 -4 ± 2%	AVERAGE FINAL WEIGHT PER GRAIN (mg)	38 to 34 -12 ± 2%
-5 ± 7%	FINAL WEIGHTS CENTRAL SPIKELETS OF <u>a</u> grains	-10 ± 4%
-6 ± 8%	<u>b</u> grains	-13 ± 4%
-2 ± 9%	<u>c</u> grains	-13 ± 4%

Tabulated data in Appendix C p 96 .

Absolute values in Table 7c(ii) p 96.

% values in Table 8c(ii) p 98.

Growth rates, Appendix D p 103; Durations, Appendix E p 107 ; Final Grain Weight, Appendix F p 112.

For both high day and high night temperatures final grain weight was less in both cultivars. For example when the day temperature was increased by 9°C (21/16°C to 30/16°C) final grain weight was reduced from 58 to 43mg (25%) and from 53 to 38mg (27%) in Late Mexico 120 and Sonora respectively (Flow Chart 3(a)). When the night temperature was increased by 9°C (21/16°C to 21/25°C) final grain weight was reduced from 58 to 50mg (13%) and from 53 to 40mg (24%) in Late Mexico 120 and Sonora respectively (Flow Chart 4(a)).

For both cultivars the reduction in final grain weight in response to increasing the day temperature was largely due to a decrease in the duration of grain filling, similar to that observed in experiments I and II (Flow Charts 3(a) and 3(b)). However for an increase in the night, 21/16°C to 21/25°C the major component causing the reduction in final grain weight differed in the two cultivars: for Sonora it was due to a decrease in the duration of grain filling, a similar response to that observed for increasing the day temperature while for Late Mexico 120 it was largely due to a decrease in the growth rate (Flow Chart 4(a)). This observation for Late Mexico 120 is surprising when considering that its duration component responded similarly to Sonora under the conditions of high day temperature (Flow Charts 3(a) and 3(b)) and for the night temperature increase of 30/16°C to 30/25°C, that is reduction in final grain weight was largely due to a decrease in the duration of grain filling. (Flow Chart 4(b)).

A high day temperature appears to have a more adverse effect on final grain weight than a high night temperature and the magnitude of this difference varied between the cultivars: it was very slight in Sonora but much more marked in Late Mexico 120. Furthermore the more adverse effect of a high day temperature appears to be largely due to a more severe reduction in the duration of grain filling. The more adverse effect of a high day than high night temperature is indicated by two alternative approaches:-

(1) When the day temperature was increased by 9°C (that is, 21/16°C to 30/16°C) this resulted in a 25 $\pm$ 2% and 27 $\pm$ 1% reduction in final grain weight in Late Mexico 120 and Sonora respectively (Flow Chart 3(a)). Whereas a 9°C increase in night temperature (that is, 21/16°C to 21/25°C) resulted in a 13% and 24% reduction in Late Mexico 120 and Sonora respectively (Flow Chart 4(a)). Moreover it would appear that the higher the day temperature the less effect an increase in night temperature has on the final grain weight. For example for, Late Mexico 120, when the night temperature was increased by 9°C for day temperatures of 21°C and 30°C final grain weight was reduced by 13% and 4% respectively (Flow Charts 4(a) and 4(b)).

(2) The 30/16°C treatment and the 21/25°C treatment both received the same total heat sum per day* but they differed in day and night temperatures. The former treatment (that is, 30/16°C) had a higher day temperature whereas the latter treatment (21/25°C) had a higher night temperature.

Final grain weight was less at 30/16°C than at 21/25°C and this appears to be largely due to the fact that the duration of grain filling was more adversely affected at 30/16°C (Table 4.1). For example for Late Mexico 120 the floret a grain weighed approximately 45mg and 52mg at 30/16°C and 21/25°C respectively and the duration of the floret a grain was approximately 23 days and 27 days at 30/16°C and 21/25°C respectively. (Table 4.1 ~~Figure 4.2~~)

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* Recall that within each treatment day and night temperatures were imposed for 12h respectively (Table 2.1).

Table 4.1 Experiment IV. The effect of (i) a high day temperature, 30/16°C, and (ii) a high night temperature, 21/25°C, on the rate and duration of grain filling and final grain weight.

r - growth rate (mg. day^{-1}); d - duration of grain filling (days); w - final grain weight (mg $\pm$ S.E.$\bar{X}$.)

Floret Position / Cultivar, Temperature		Floret a	Floret b	Floret c
Late Mexico 120 30/16°C	r	2.096±0.156	2.170±0.149	1.911±0.096
	d	22.5 ±2.4	21.2 ±2.4	20.8 ±3.0
	w	44.8 ±1.3	46.2 ±1.6	38.3 ±1.7
21/25°C	r	1.855±0.177	1.971±0.135	1.698±0.223
	d	26.9 ±2.4	25.9 ±2.4	25.9 ±3.3
	w	51.5 ±1.2	53.5 ±1.4	45.9 ±1.8
Sonora 30/16°C	r	1.815±0.146	1.890±0.224	1.886±0.124
	d	19.5 ±1.7	20.5 ±2.0	18.7 ±1.5
	w	38.3 ±0.8	40.6 ±0.7	36.4 ±0.9
21/25°C	r	1.858±0.097	1.971±0.290	1.926±0.041
	d	24.1 ±1.4	23.4 ±1.9	21.7 ±1.7
	w	40.8 ±0.9	42.6 ±0.9	37.1 ±0.6

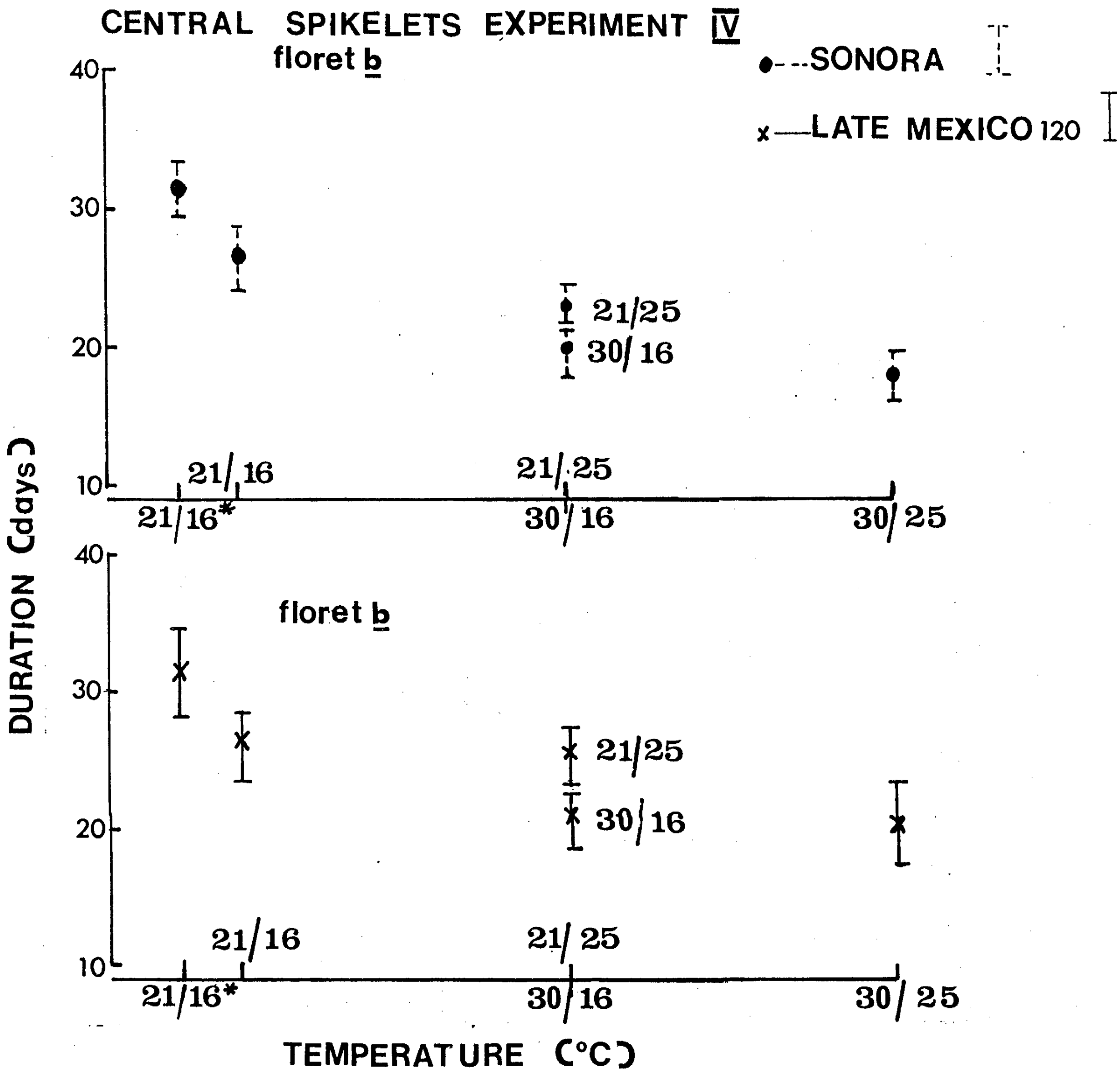
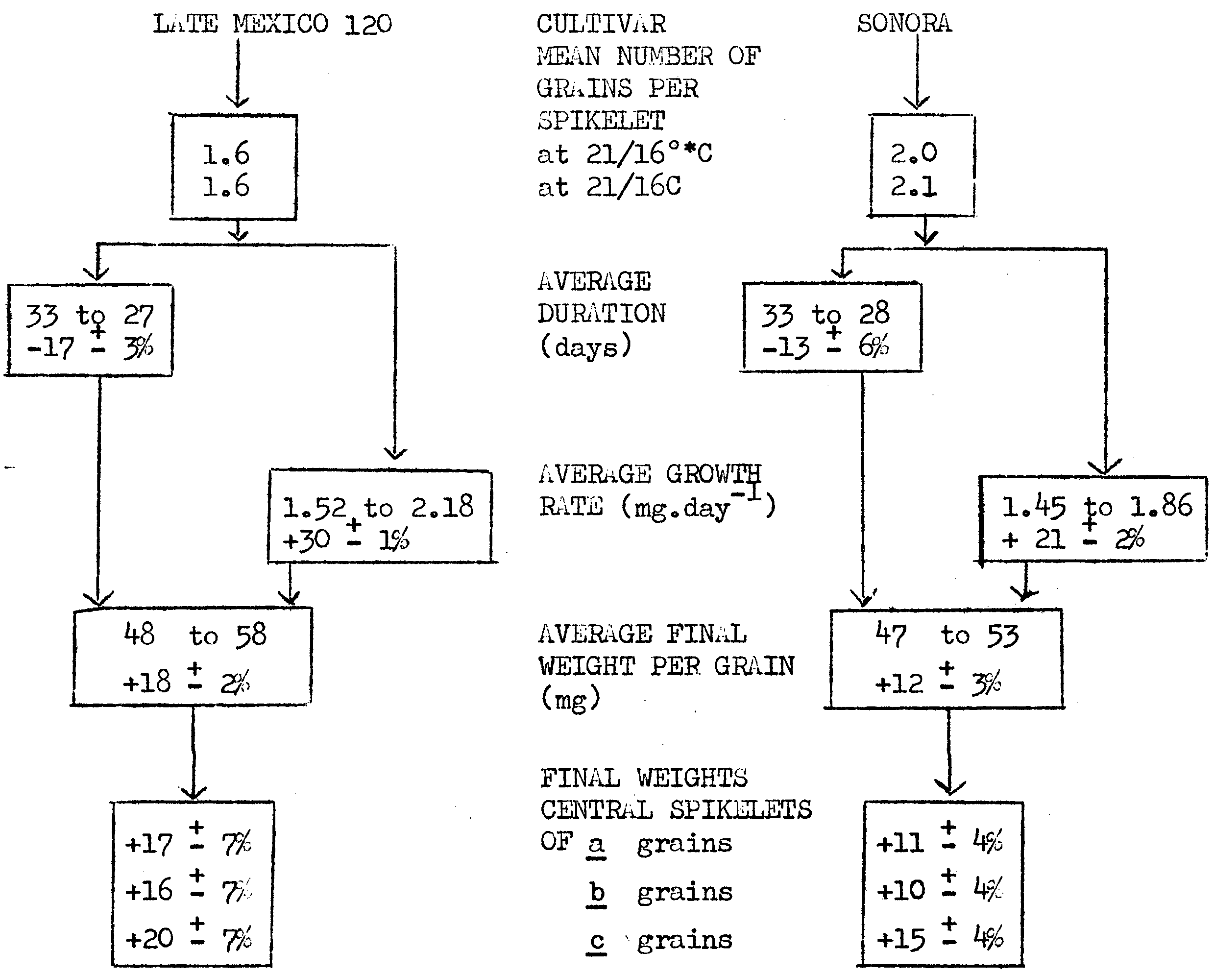


FIGURE 4.2 EXPERIMENT IV. The effect of day and night temperatures on the duration of grain filling for the floret b grain from the central spikelets. Responses for the other central floret grains Appendix E p 107.

4.2.3 Experiment IV. The Effect of Extending the Day Temperature by Four Hours during the Photoperiod on the Rate and Duration of Grain Filling for cvs. Sonora and Late Mexico 120.

When the day temperature at 21°C was extended during the photoperiod by four hours, from eight to twelve hours final grain weight increased in Late Mexico and Sonora but the magnitude of the increase varied between them. Thus final grain weight increased by 18 $\pm$ 2% and 12 $\pm$ 3% in Late Mexico 120 and Sonora respectively (Flow Chart 5). For both cultivars the heavier final grain weight was due to an increase in growth rate it being faster in Late Mexico 120 than Sonora, that is, the growth rate increased by 30 $\pm$ 1% and 21 $\pm$ 2% in Late Mexico and Sonora respectively (Flow Chart 5). However the increase in growth rate was accompanied by a decrease in duration by 17 $\pm$ 3% and 13 $\pm$ 6% in Late Mexico and Sonora (Flow Chart 5). Nevertheless the increase in growth rate outweighed the decrease in duration and thus final grain weight was heavier at the extended day temperature (Appendix F p112).

FLOW CHART 5: Experiment IV. The effect of extending the day temperatures by four hours during the photoperiod (ie., to compare the 21/16°*C treatment with the 21/16°C treatment. (Table 2.1)



Tabulated data in Appendix C p 95 .

Absolute values in Table 7(a) p 95.

% values in Table 8(a) p 97.

Growth rates Appendix D p 103 ; Durations, Appendix E p 107 ;

Final Grain Weight, Appendix F p 112 .

4.3 EXPERIMENT III. THE EFFECT OF LIGHT INTENSITY AT 21/16°C ON THE RATE AND DURATION OF GRAIN FILLING FOR INDIVIDUAL GRAINS FROM THE CENTRAL SPIKELETS OF CVS. SONORA AND TRIPLE DIRK.

There are marked differences between cultivars in their grain growth rates and in the extent to which these are influenced by light intensity and temperature interactions (Experiments I and II) and by light intensity (Experiment III)* after anthesis.

Comparisons of the results of experiments I and II in which grain filling occurred under high summer and low winter irradiance respectively suggested that irradiance had little effect at any temperature on grain growth rates in Triple Dirk and at 21/16°*C for Timgalen and Late Mexico 120 and that under low winter irradiance grain growth rates were slower at both 21/16°*C and 30/25°C in WW15 and at 30/25°C in Timgalen and Late Mexico 120 (Figure 4.3)

In experiment III, at 21/16°C, grain growth rate in Triple Dirk, the cultivar which set fewer grains per spikelet and readily aborted its outer floret grains (c) at the two lower light intensities (1.31×10^6 J m^{-2}day and 2.52×10^6 J m^{-2}day (400-700nm), was only slightly affected by light intensity over a six fold range (48,420 to 8,070 lux), in conformity with the results of experiments I and II (Fig. 4.4). Whereas in Sonora the cultivar which set more grains per spikelet and did not readily abort its outer floret grains (d) at the lowest light intensities, the growth rate per grain was greatly affected by light intensity particularly in the more distal florets (Flow Charts 6 and 7).

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*The results for the 34,432 lux treatment (5.92×10^6 J $m^{-2}$$day^{-1}$ 400-700nm) were 'abnormal' and the reasons for this are not clear. Although the results for this treatment will be given they will not be referred to.

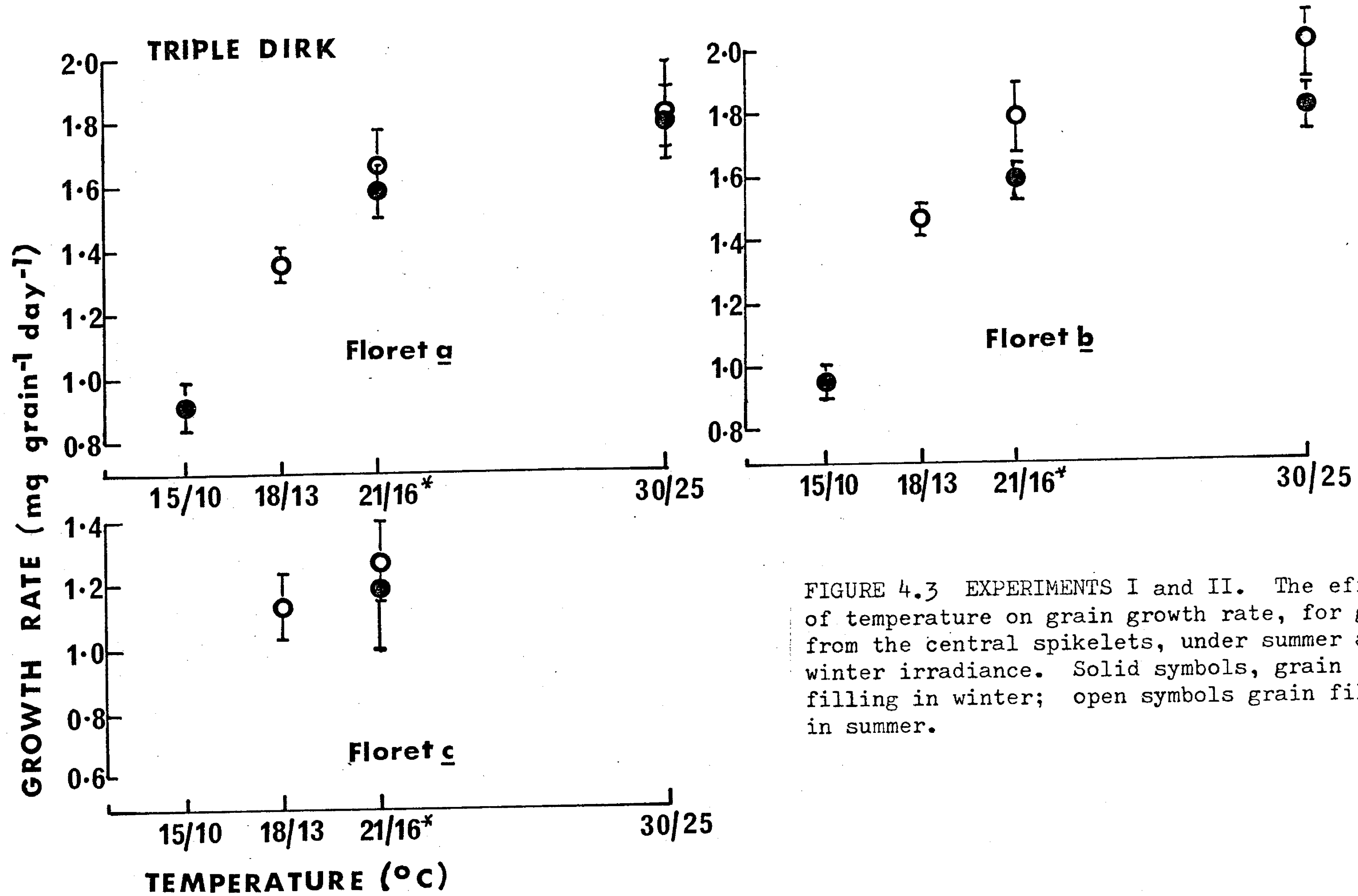
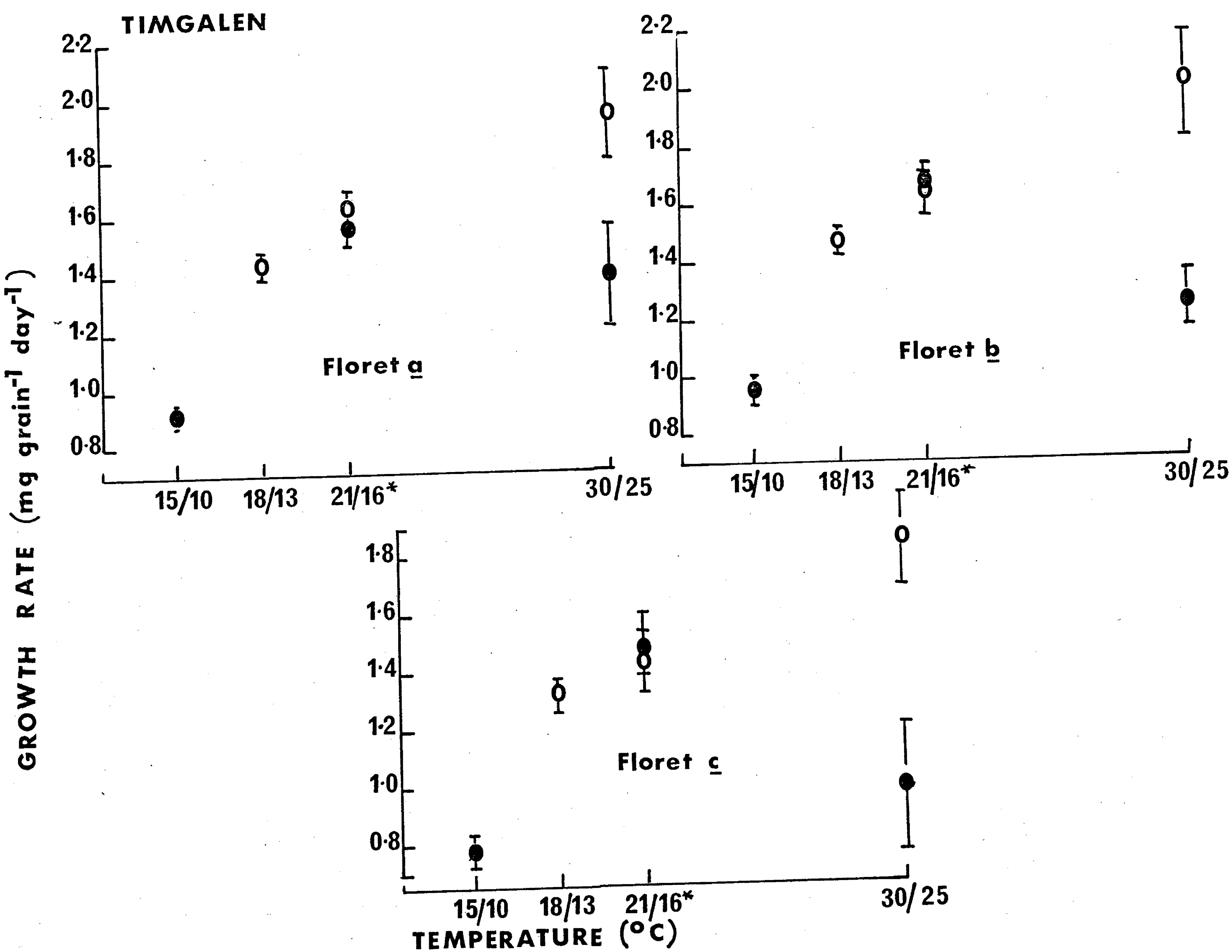
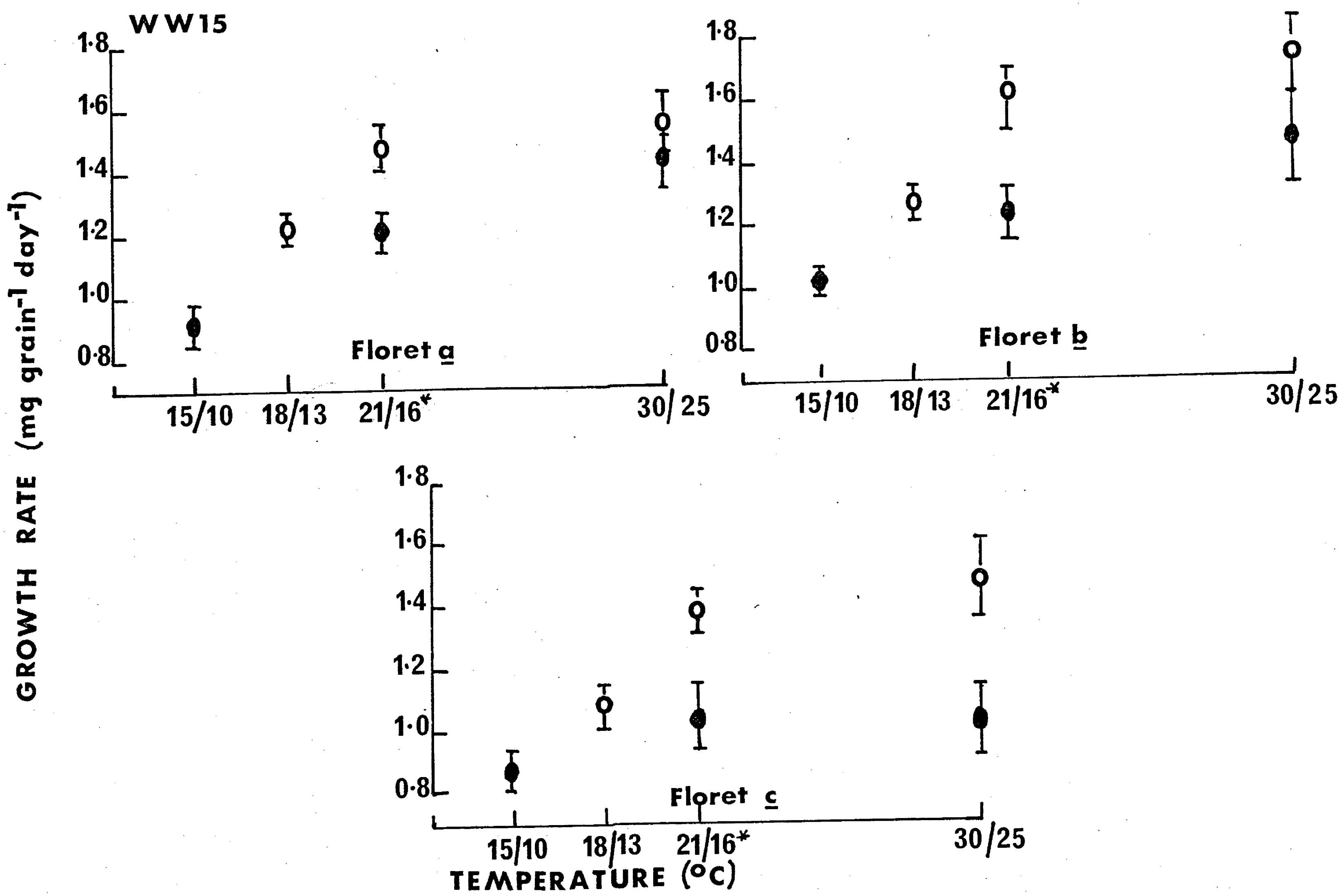


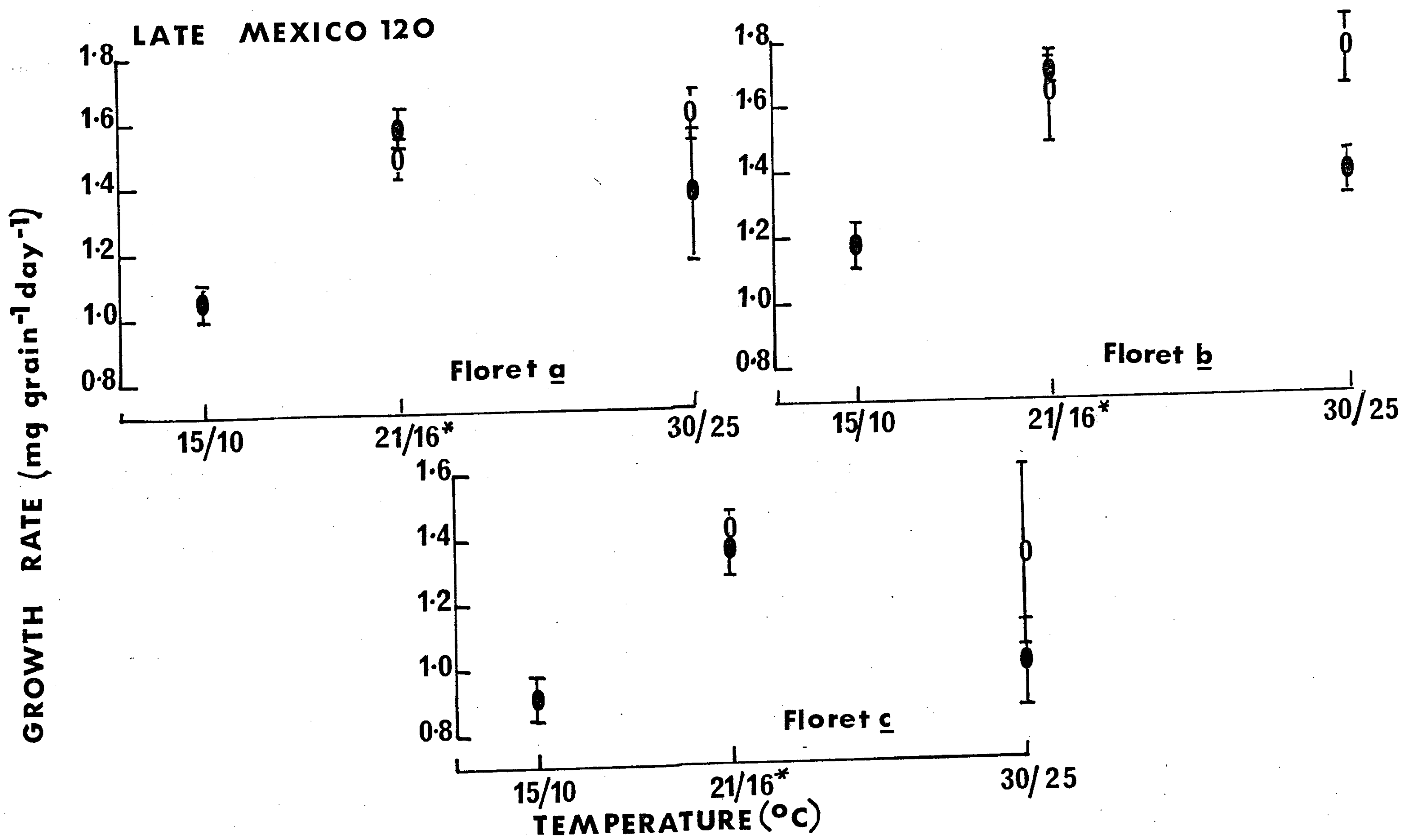
FIGURE 4.3 EXPERIMENTS I and II. The effect of temperature on grain growth rate, for grains from the central spikelets, under summer and winter irradiance. Solid symbols, grain filling in winter; open symbols grain filling in summer.



TIMGALEN
GROWTH RATE (mg grain-1 day-1)
Floret a
Floret b
Floret c
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
15/10
18/13
21/16*
30/25
TEMPERATURE (°C)



WW15
GROWTH RATE (mg grain-1 day-1)
Floret a
Floret b
Floret c
15/10
18/13
21/16*
30/25
TEMPERATURE (°C)



LATE MEXICO 120
GROWTH RATE (mg grain^{-1} day^{-1})
1·8
1·6
1·4
1·2
1·0
0·8
Floret a
15/10
21/16*
30/25
Floret b
Floret c
TEMPERATURE (°C)

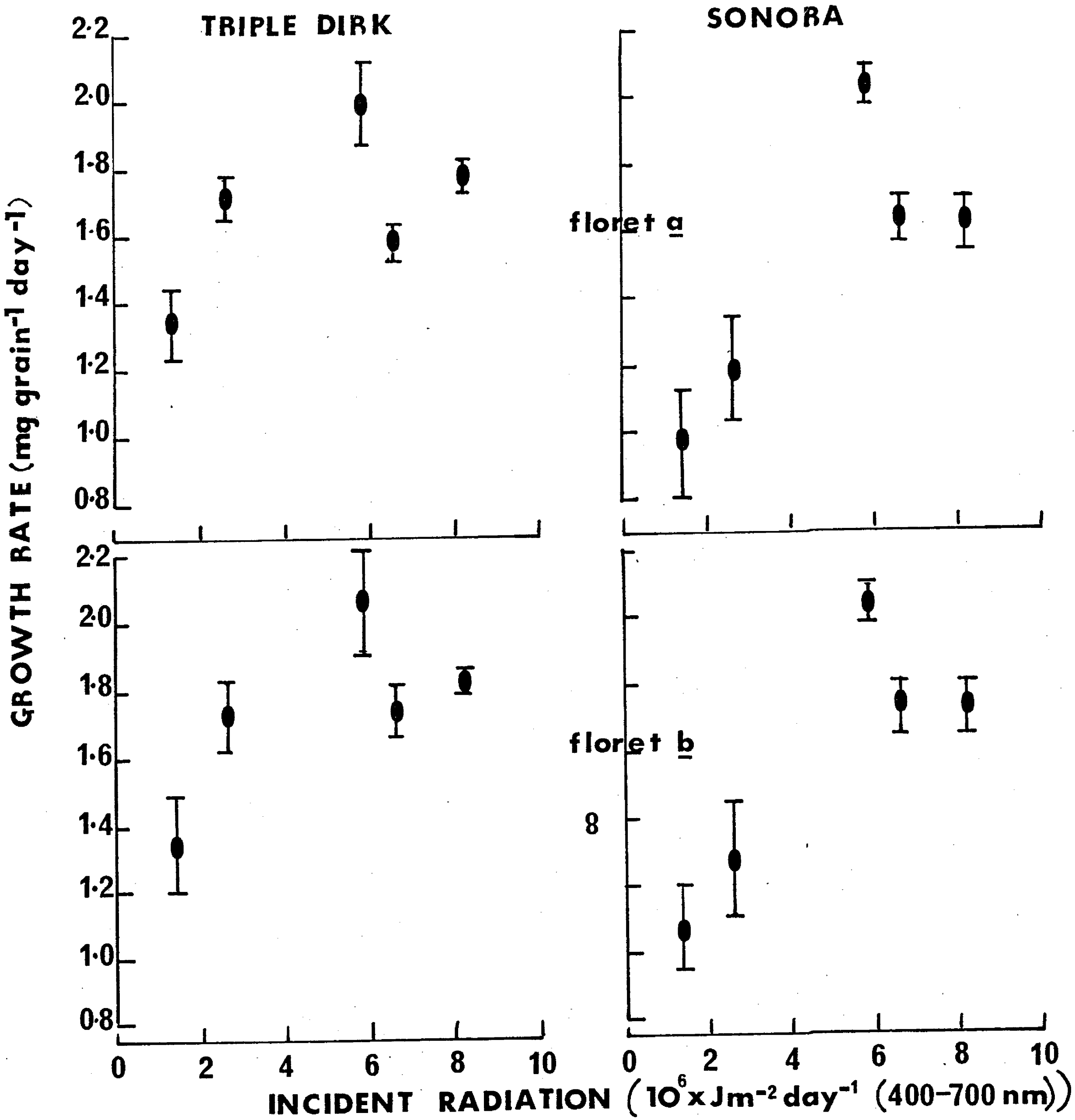
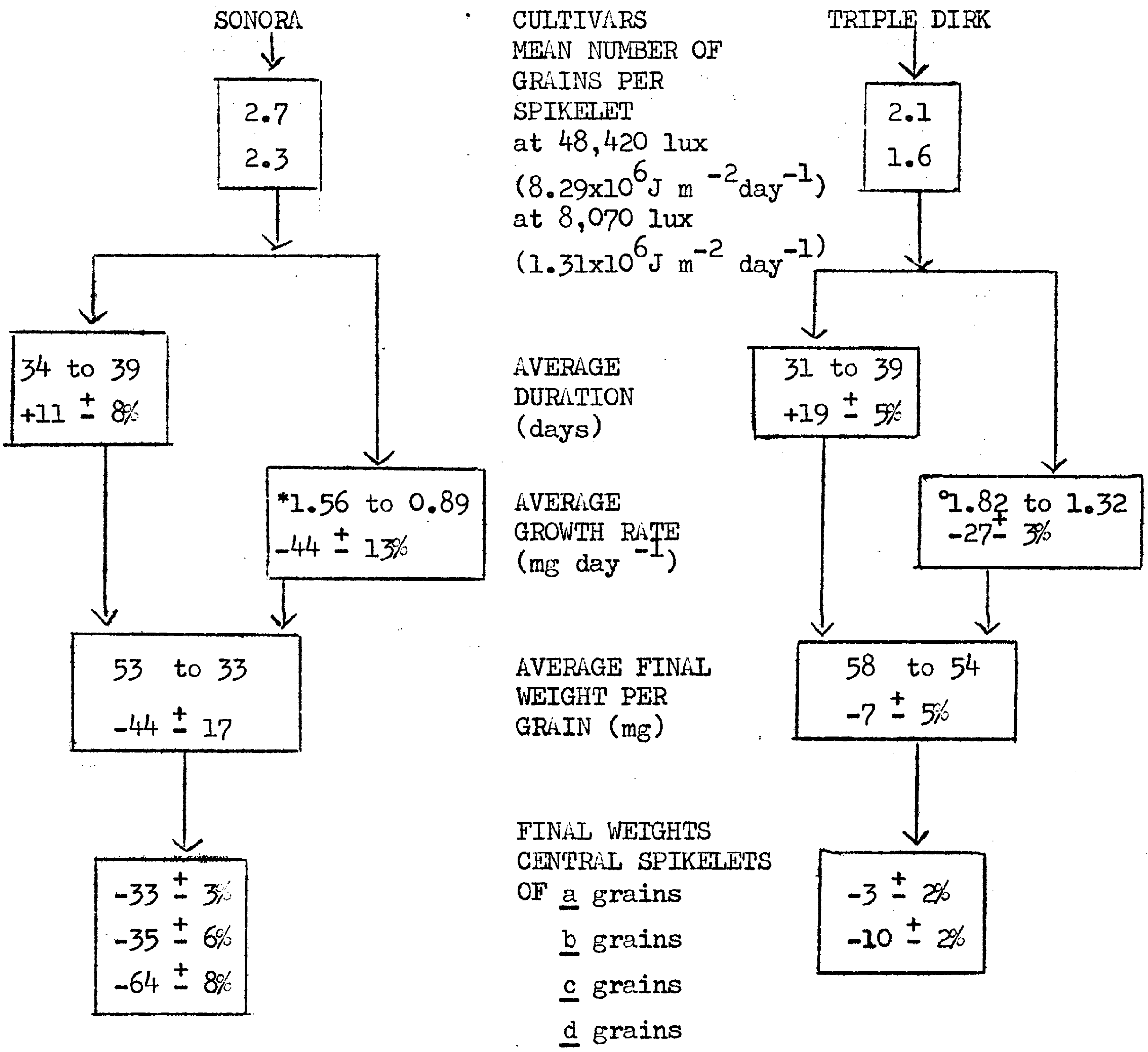


FIGURE 4.4 EXPERIMENT III. At 21/16°C, the effect of light intensity on grain growth rate for the floret a and b grains from the central spikelets.
Note, in both cultivars grain growth rates were 'abnormally' high at 5.92 x 10^6 J. m.$^{-2}$ day $^{-1}$ (400 - 700nm) and the reasons for this are not clear.
Responses for the other grains from the central spikelets, Appendix D P102 ·

Lower final dry grain weight due to low light intensity was largely due to the decrease in growth rate. The lower the light intensity, the more severely was the growth rate affected. Thus at the two lowest light intensities, 16,140 lux and 8,070 lux, growth rates were decreased by 26 $\pm$ 6% and 44 $\pm$ 13% in Sonora and by 5 $\pm$ 2% and 7 $\pm$ 5% in Triple Dirk (Flow Charts 6 and 7).

The duration of grain filling was not influenced by the marked difference in incident radiation between experiments I and II (Fig. 4.1). Indeed light intensity ranging from 6.7 to 13.2 x 10^6 J m^{-2} day $^{-1}$ (400-700 nm), did not appear to influence the duration. (Figure 4.5) This conclusion is reinforced by the results of experiment III where light intensity was systematically varied at 21/16°C. It had no pronounced effect on the duration of grain filling in either of the cultivars studied, although at the lowest light intensity, 8,070 lux (ie., 1.3 x 10^6 J m $^{-2}$ day $^{-1}$ (400 - 700nm)) there was a slight increase in the duration of grain filling in both (Fig. 4.6)

FLOW CHART 6 Experiment III The effect of reducing the light intensity at 21/16°C from 48,420 lux to 8,070 lux (ie. 8.29×10^6 to 1.31×10^6 J m^{-2} day^{-1} (400-700nm)) on the rate and duration of grain filling for cvs. Sonora and Triple Dirk.



Tabulated data in Appendix C p 93.

Absolute values in Table 5(a) p 93.

% values in Table 6(a) p 94.

Growth rates, Appendix D p 103 Durations, Appendix E p 107 ;

Final Grain Weight, Appendix F p 111.

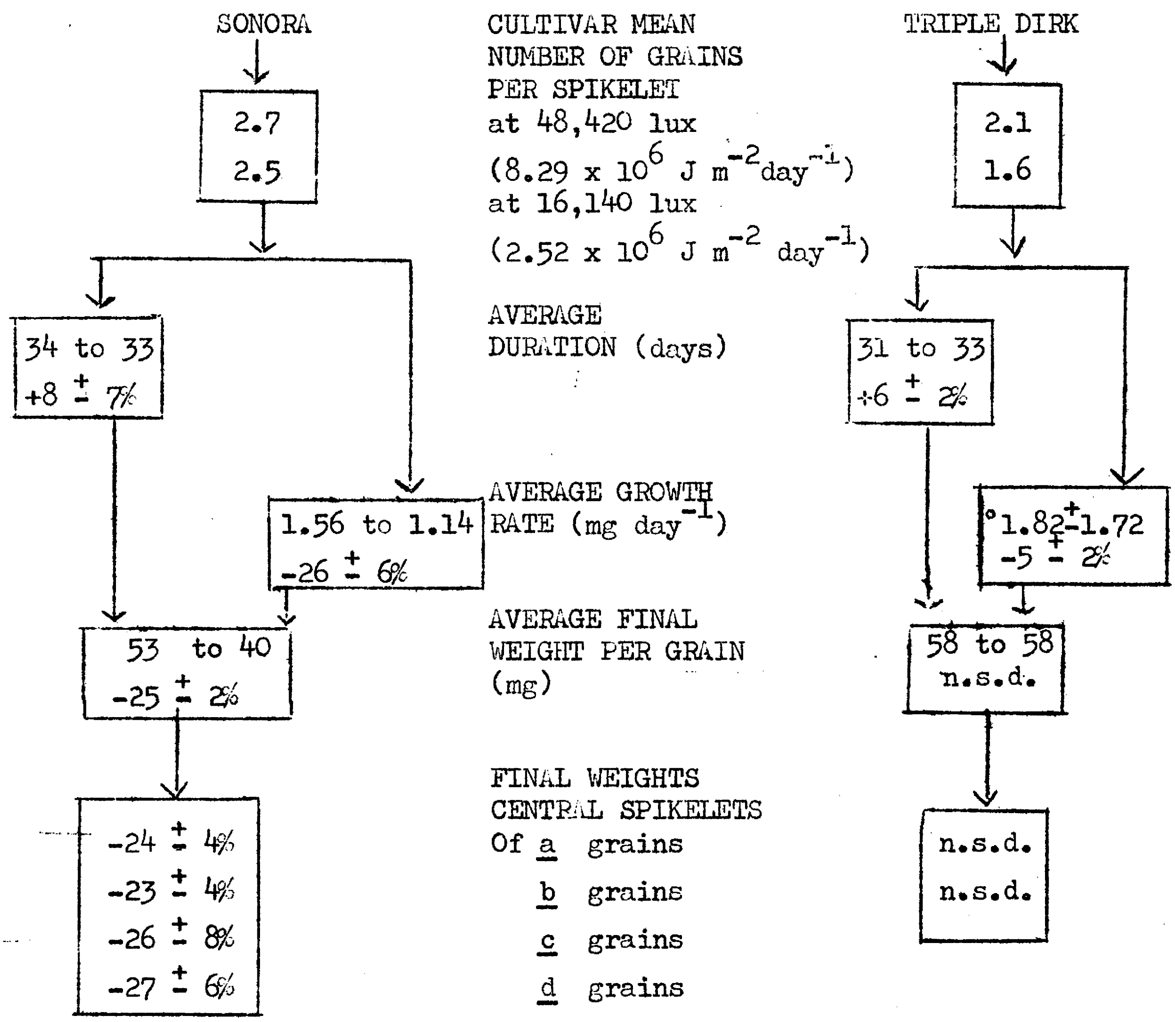
* At 8,070 lux growth was not linear in the outer floret grains, but for consistency a 'growth rate' for the c and d grains was determined:

P.T.O

a rate of growth for two consecutive harvests was calculated, this was repeated for all harvests during filling and then the values obtained were averaged. The average growth rate of 0.89 mg. day $^{-1}$ at 8,070 lux is an average growth rate calculated over the a, b, c, and d grains.

° averaged over the a and b grains only as c grains failed at 8,070 lux.

FLOW CHART 7 EXPERIMENT III The effect of reducing the light intensity at 21/16°C from 48,420 lux to 16,140 lux (ie., 8.29×10^6 to 2.52×10^6 J m^{-2} day^{-1} (400-700 nm)) on the rate and duration of grain filling for cvs. Sonora and Triple Dirk.



Tabulated data in Appendix C p. 93.

Absolute values in Table 5(a) p 93.

% values in Table 6(a) p 94.

Growth rates, Appendix D p 102; Durations, Appendix E p 107;

Final Grain Weight, Appendix F p 111;

° averaged over a and b grains only as c grain failed to set at 8,070 lux.

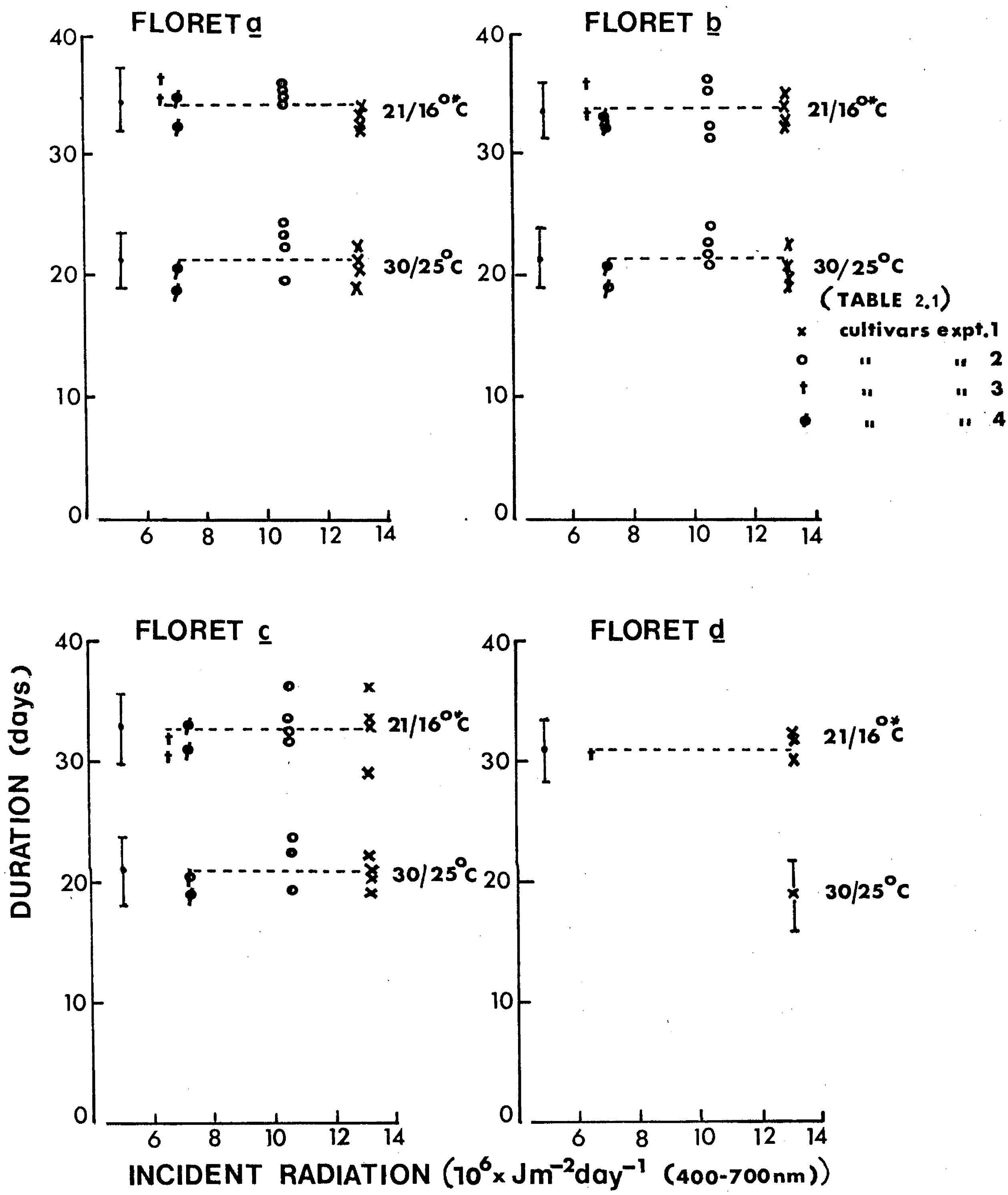


FIGURE 4.5 EXPERIMENTS I,II,III and IV. The effect of light intensity (ranging from 6.7 to 13.6 x 10^6 J m^{-1} day^{-1} (400-700nm), on the duration of grain filling for all cultivars in Experiments I, II, III and IV at 21/16°*C and for all cultivars in Experiments I, II and IV at 30/25°C. The dotted line indicates the mean duration of grain filling for grains in each floret position. The grains were situated in the central spikelets.

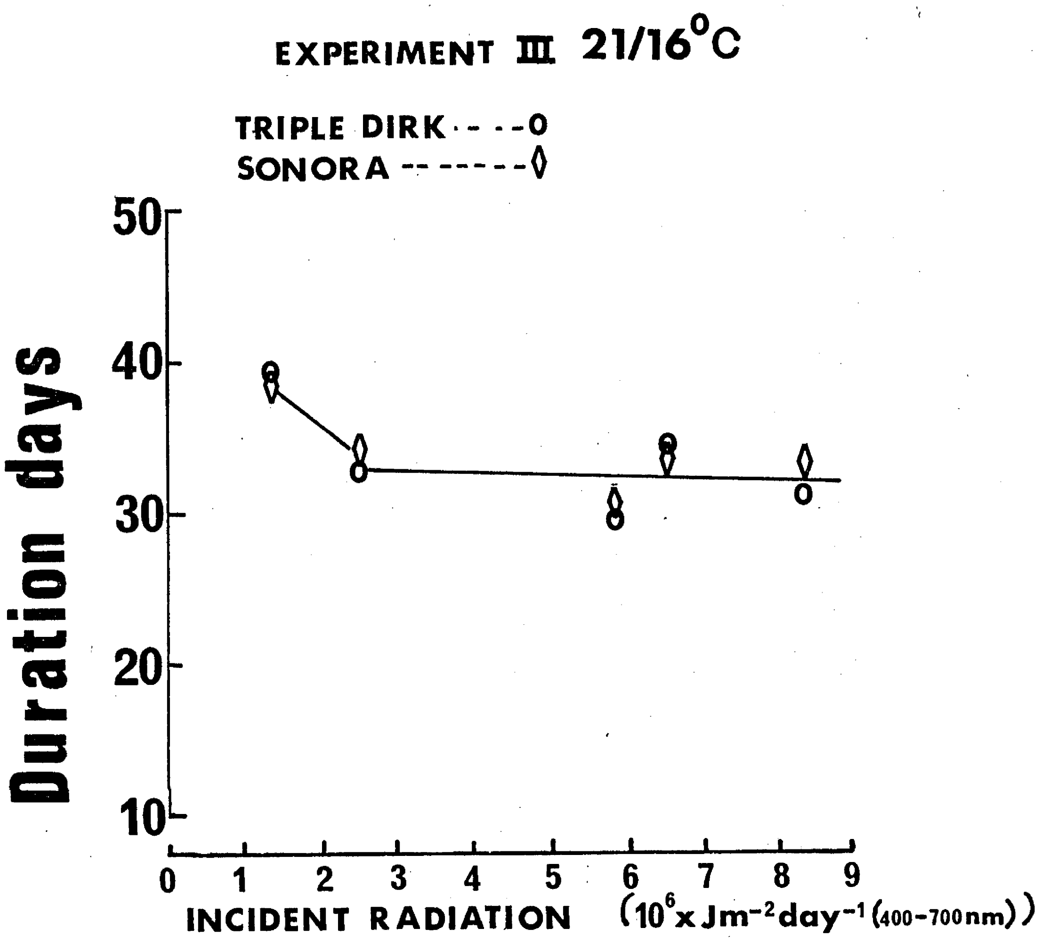


FIGURE 4.6 EXPERIMENT III. At 21/16°C, the effect of incident radiation on the duration of grain filling for the floret a grain from the central spikelets. Errors Appendix E p 107.

4.4 CULTIVAR

The cultivars used in these experiments differed substantially in the numbers of spikelets per ear and in grains per spikelet under given conditions (Table 3.1 a to d). However, as indicated in the introduction (Section 4.1.3) under a given condition no consistent differences in the duration of grain filling, for grains from the central spikelets were evident between the cultivars (Figs. 4.1, 4.2 and 4.6), except for the high night temperature treatment, 21/25°C,(Experiment IV.). For the latter treatment Late Mexico 120 had a slight, but consistently longer duration of grain filling (by three days) than Sonora (Fig. 4.6, Table 4.1).

On the other hand, there were marked differences between cultivars in their grain growth rates and in the way these were influenced by environmental conditions after anthesis. The way grain growth rates were influenced by environmental conditions in different cultivars has been presented in Section 4.2 and 4.3. Briefly, the results suggest that grain growth rate in Triple Dirk was not greatly influenced by a twofold range in incident radiation (Fig. 4.3). Similarly at 21/16°C grain growth rates in Timgalen and Late Mexico 120 did not appear to be greatly influenced by incident radiation but at 30/25°C growth rates for the latter two cultivars were considerably slower under winter irradiation (Fig. 4.3). For WW15 grain growth rate was consistently slower at all temperatures under winter irradiance (Fig. 4.3). The controlled light intensity treatment results (Experiment III) indicate that grain growth rate in Triple Dirk was only slightly influenced by light intensity over a sixfold range (Fig. 4.4) and this is in conformity with the results of experiments I and II. On the other hand, in Sonora grain growth rate was greatly affected by light intensity (Fig. 4.4) and in this respect the response of Sonora resembled that of WW15 in experiments I and II.

Environmental conditions after anthesis also influence grain set. High temperature reduced it slightly and low light intensity to a considerable degree, particularly in Triple Dirk (Table 3.1 a-d). Such adjustment of grain number in Triple Dirk according to the conditions at anthesis may have the consequence that light intensity had far less effect on growth rate per grain.

The effect of temperature on grain growth rate, illustrated in Flow Charts 1 and 2, was generally similar (in as much that grain growth rates increased) for all cultivars except that 30/25°C was above optimal for Timgalen and Late Mexico 12O under the low light conditions of experiment II (Flow Chart 2b).

The response to an increase in night temperature (21/16°C to 21/25°C) varied between Late Mexico 12O and Sonora. Final grain weight was less at 21/25°C in Late Mexico 12O largely because of a slower growth rate whereas in Sonora the reduction was largely due to a decrease in the duration of grain filling (Flow Chart 4a). Moreover a high day temperature (30/16°C) appeared to have only a slightly more adverse effect on final grain weight than a high night temperature (21/25°C) for Sonora (of 4 ± 2%) whereas in Late Mexico 120 a high day temperature resulted in a more marked reduction in final grain weight than a high night temperature (of 14 ± 2%) (Table 4.1).

Thus the way grain growth rates were influenced by environmental conditions after anthesis differed between the cultivars. Also under a given condition there were marked differences between the cultivars (Fig. 4.7). For example in experiment I, at all temperature treatments for all floret positions* grain growth rate in Timgalen and Triple Dirk, which set fewer grains per spikelet were

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* This was not the case in Triple Dirk for the florets grain from the central spikelet (Figure 4.7 ExperimentI)

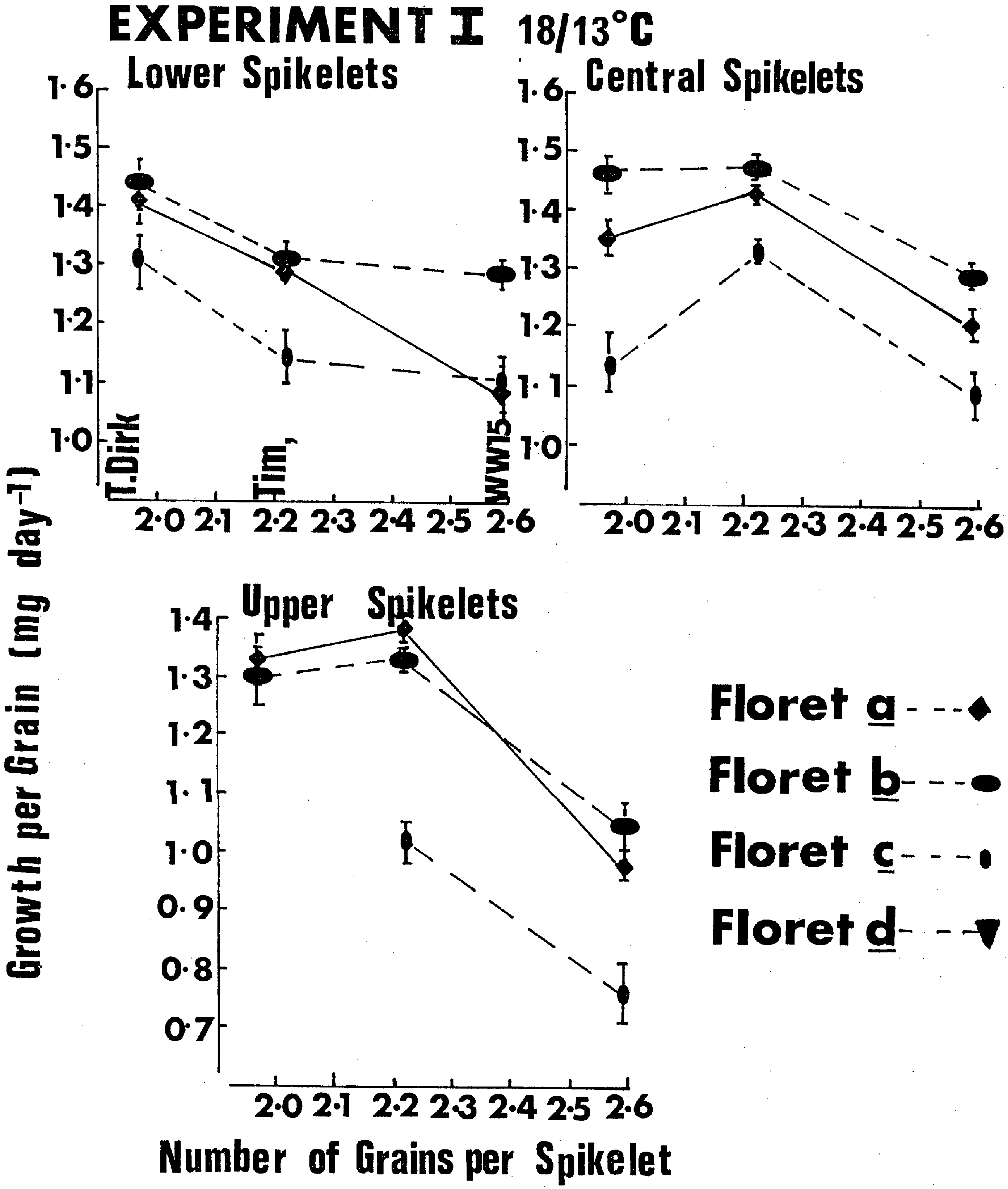
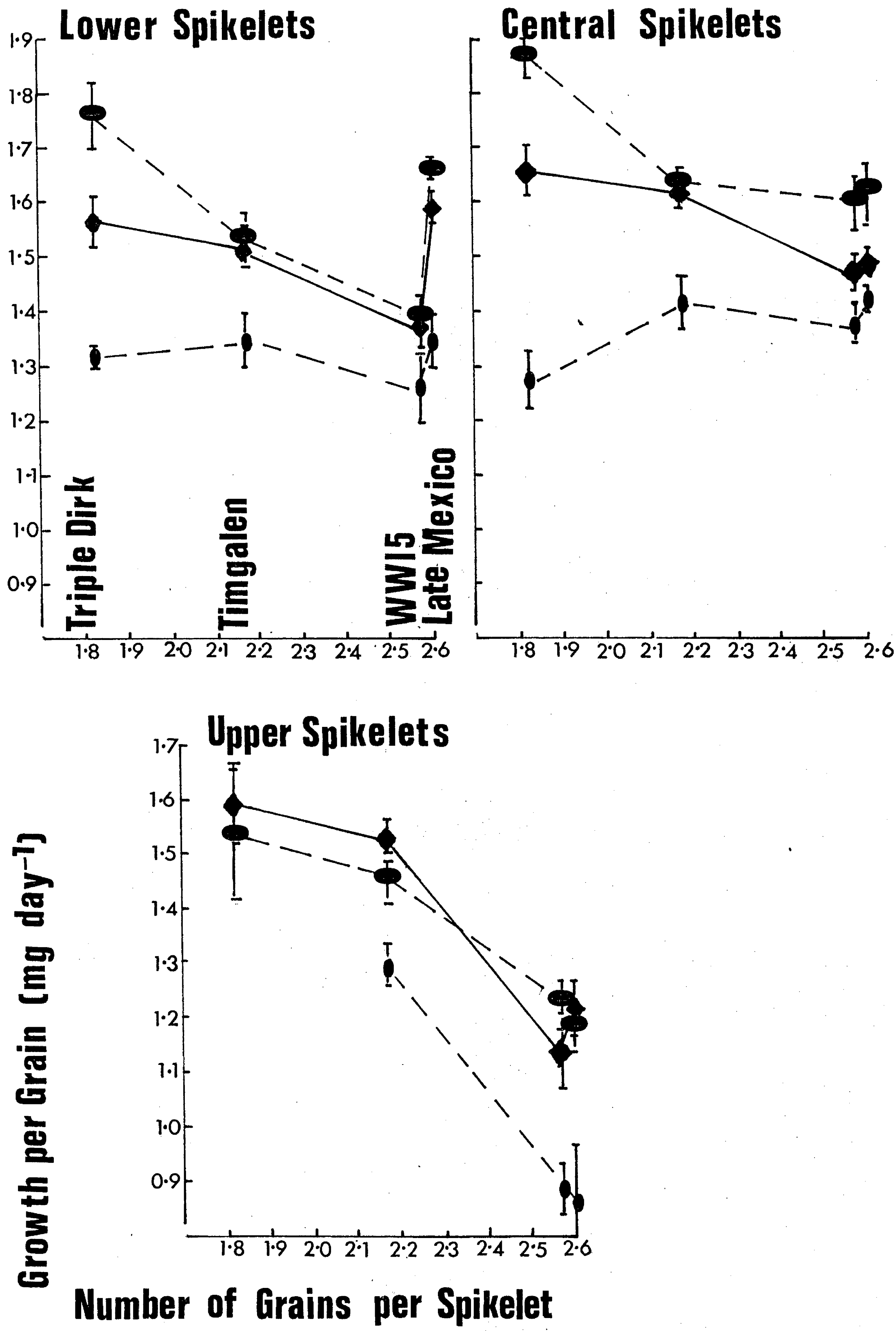
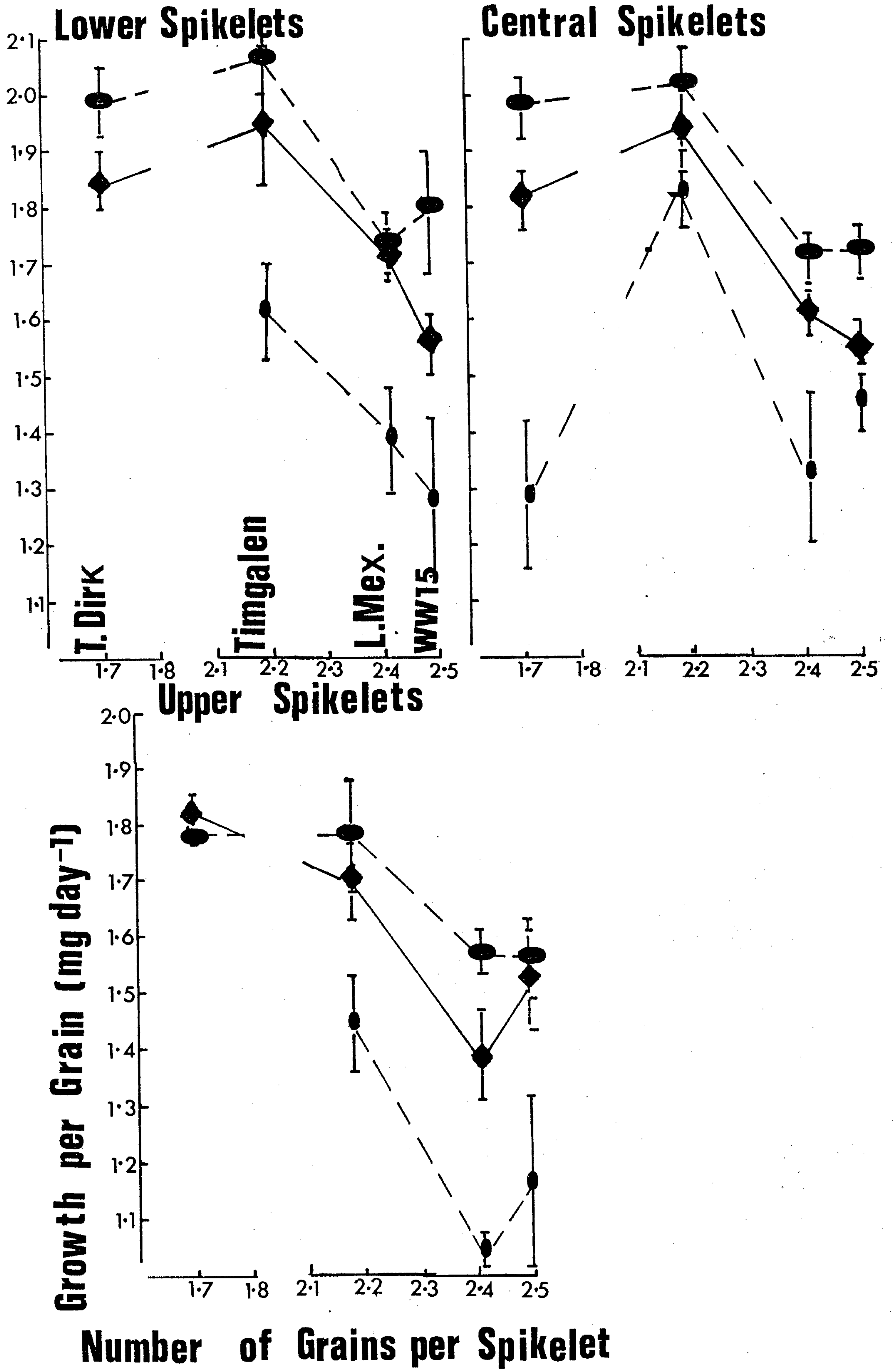


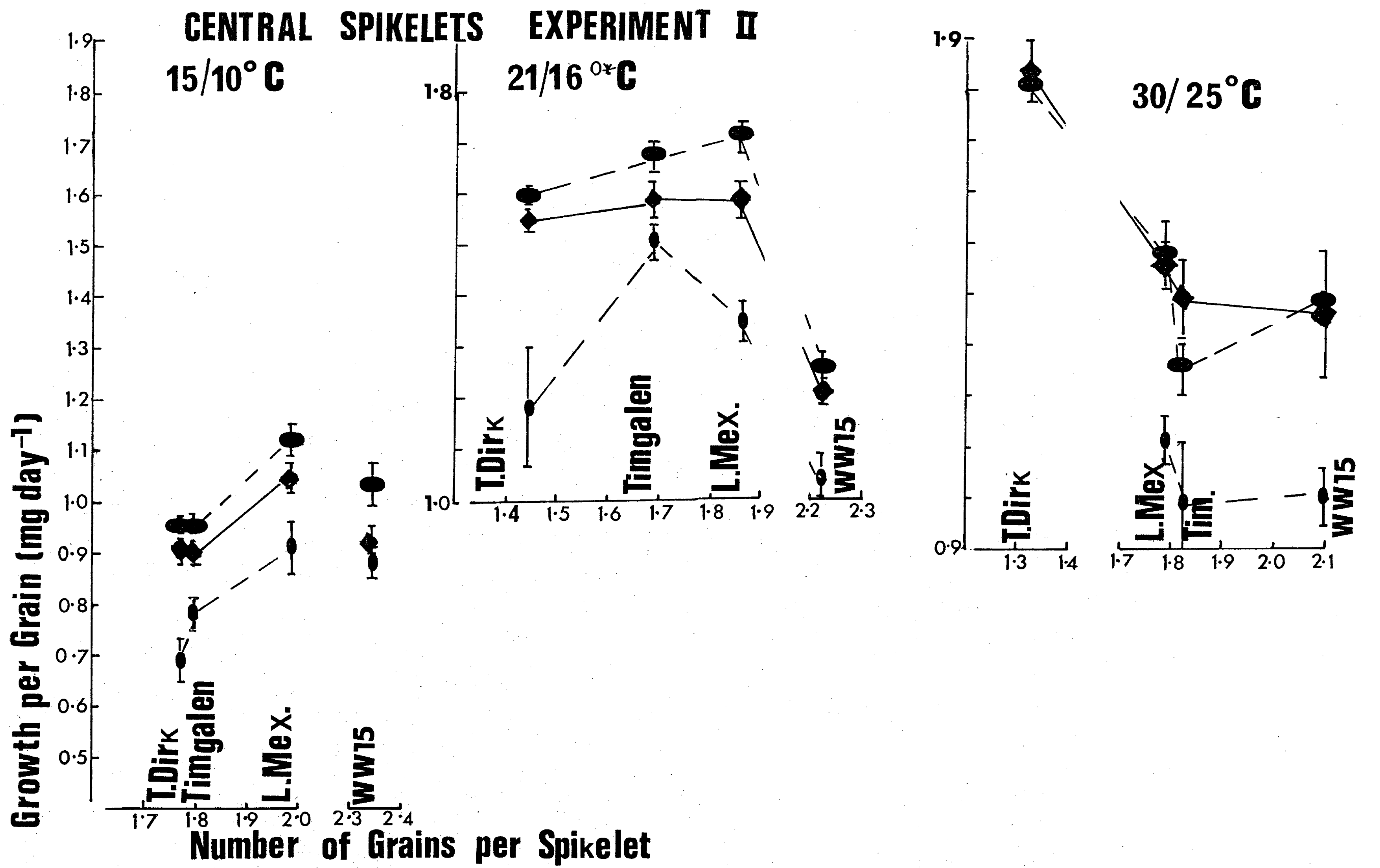
FIGURE 4.7 EXPERIMENTS I, II, IV and III. The relation between grain growth rate and the average number of grains per spikelet for grains from the upper, central and lower spikelets in Experiment I and for grains from the central spikelets only in Experiments II, IV and III.

EXPERIMENT I 21/16°C

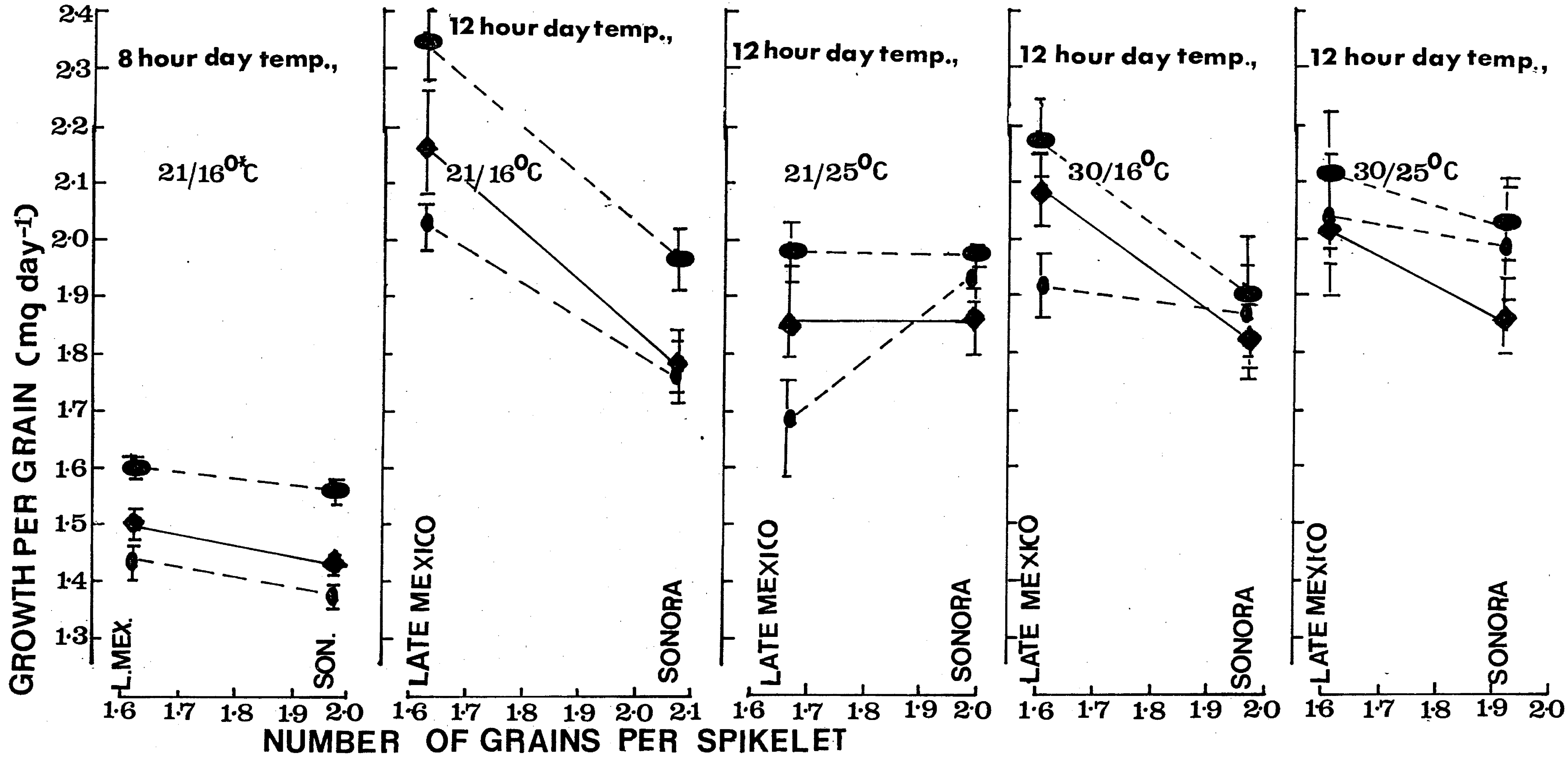


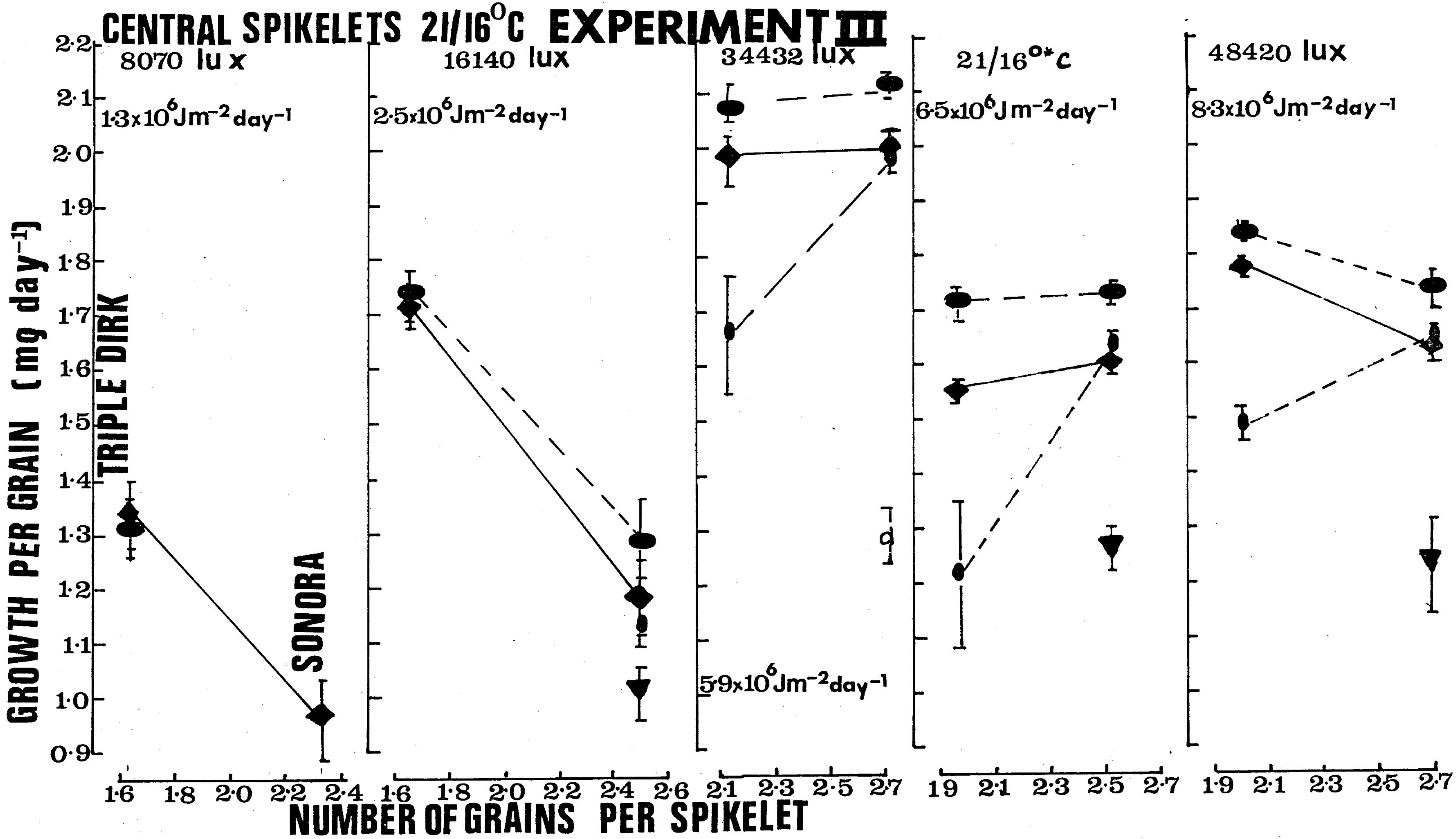
EXPERIMENT I 30/25°C




CENTRAL SPIKELETS EXPERIMENT II
15/10° C
21/16 °C
30/25°C
Growth per Grain (mg day⁻¹)
Number of Grains per Spikelet
T.Dirk
Timgalen
L.Mex.
WW15
Tim.
1·9
1·8
1·7
1·6
1·5
1·4
1·3
1·2
1·1
1·0
0·9
0·8
0·7
0·6
0·5
2·0
2·2
2·3
2·4
2·1

EXPERIMENT IV. CENTRAL SPIKELETS





CENTRAL SPIKELETS 21/16°C EXPERIMENT III
8070 lux
1·3x10⁶Jm⁻²day⁻¹
16140 lux
2·5x10⁶Jm⁻²day⁻¹
34432 lux
5·9x10⁶Jm⁻²day⁻¹
21/16°*c
6·5x10⁶Jm⁻²day⁻¹
48420 lux
8·3x10⁶Jm⁻²day⁻¹
TRIPLE DIRK
SONORA
d
GROWTH PER GRAIN (mg day⁻¹)
NUMBER OF GRAINS PER SPIKELET

consistently faster than in WW15, which set more grains per spikelet (Fig. 4.7 Experiment I). This may suggest that cultivars which set more grains per spikelet have a slower grain growth rate. However while the above statement was observed to hold in may cases (especially under the stress treatments, that is, 30/25°C in Experiments I and II, at 8,070 lux and 16,140 lux Experiment III and at 30/16°C and 30/25°C in Experiment IV Fig. 4.7) clearly there were a number of situations where grain number per spikelet had relatively little effect on grain growth rate (Fig. 4.7 Experiment IV basal a and b grains at 21/25°C) and in fact under some treatments there was a positive relation between the number of grains per spikelet and grain growth rate (Fig. 4.7 Experiment II at 15/10°C compare Triple Dirk and Timgalen to Late Mexico 120).

4.5 GROWTH RATE PER EAR. EXPERIMENTS I to IV.

Cultivar, day and night temperature, light intensity and extension of the day temperature during the photoperiod all influenced the rate of grain growth of ears. The cultivars differed substantially in grain number and in the average number of grains set per spikelet at a given environmental condition and these differences had a marked effect on growth rates of ears. Also environmental conditions after anthesis influenced grain set in some cultivars. High temperature reduced it slightly in Triple Dirk, Late Mexico 120 and WW15 but not in Timgalen in neither experiment (Table 3.1 a and b). Low light intensity reduced grain set to a considerable degree in Triple Dirk and to a lesser extent in Sonora (Table 3.1c). This in turn also influences the growth rate of ears.

Differences among the cultivars in the rate of growth of ears were much greater than those of individual grains because of substantial differences in the number of grains per ear. In experiment I, for example, grain number of ears at 21/16°*C ranged from 25.6 for Triple Dirk through 31.6 and 46.5 for Timgalen and WW15 respectively to 69.3 for Late Mexico 120. In both experiments I and II and in fact for all cultivars in each experiment at 21/16°*C growth rates of ears tended to increase in proportion to grain number, as differences between cultivars in growth rates of individual grains were much smaller than those in grain number (Fig. 4.8, 4.9). However ear grain number is not the only factor which accounts for different growth rates of ears among the cultivars and this was more apparent under stress conditions. For example at 30/25°C in experiment II growth per ear was considerably lower in Timgalen than in Triple Dirk yet Timgalen set more grains per ear (Table 4.2). In experiment II a similar but less extreme trend was observed between Late Mexico 120 and WW15 (Table 4.2). Furthermore in experiment IV grain number per ear was similar in Late Mexico and Sonora (28-30) however in most treatments growth of ears was faster in Late Mexico 120 (Table 4.2).

Figure 4.10 shows the close relationship between the photosynthetic rate of the flag leaves and the rate of grain growth of ears in the various light intensity treatments apart from the anomolous values at 34,432 lux in experiment III. The faster growth rates in Sonora compared with Triple Dirk reflect the higher grain number of an ear in the former cultivar. Among the light intensity treatments of experiment III final grain yield was closely related to the rate of grain growth of ears (Fig. 4.11). Differences between the cultivars and light intensity treatments in the duration of grain filling were far less important in determining yield than differences in rate of growth of ears as influenced by the number of

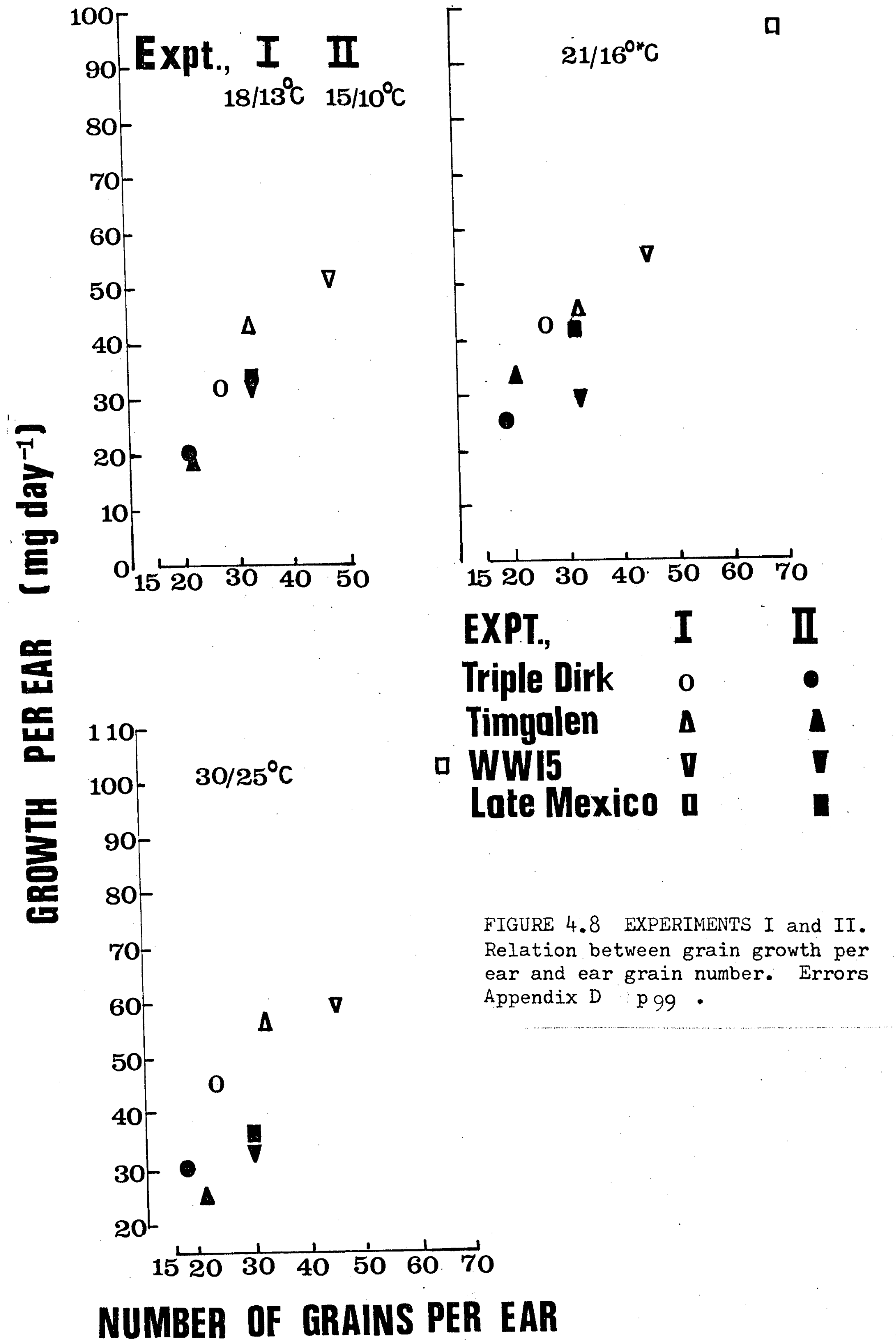


FIGURE 4.8 EXPERIMENTS I and II. Relation between grain growth per ear and ear grain number. Errors Appendix D p 99 .

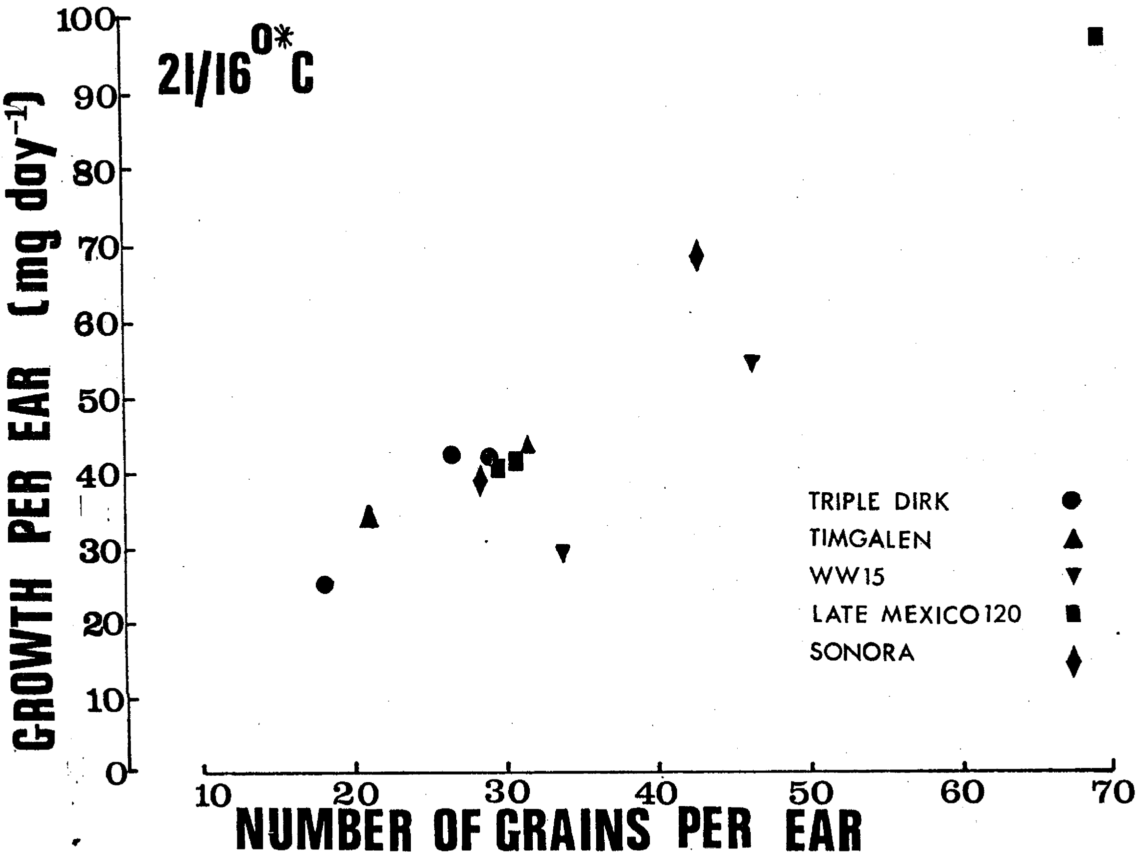


FIGURE 4.9 EXPERIMENTS I, II, III and IV. At 21/16°*C the relation between grain growth per ear and grain number.

TABLE 4.2 EXPERIMENTS I, II, III and IV. Ear grain number, the rate and duration of grain filling per ear and final yield per ear.

EXPERIMENT I

Temperature Treatment	Cultivar	Duration (days)	Growth Rate (mg day^{-1})	Ear Grain Number	Yield per ear (mg) $\pm$ 2 x S.E.$\bar{X}$
18/13°C	Triple Dirk	43.7 $\pm$ 3.7	32.7	26.6	1548.9 $\pm$ 53.9
	Timgalen	41.0 $\pm$ 4.0	43.9	31.9	1860.2 $\pm$ 75.7
	WW15	53.8 $\pm$ 3.6	51.3	46.5	2793.5 $\pm$ 62.3
21/16°*C	Triple Dirk	32.3 $\pm$ 4.7	43.3	25.7	1430.9 $\pm$ 72.5
	Timgalen	36.7 $\pm$ 4.0	44.7	31.6	1683.8 $\pm$ 69.4
	WW15	36.5 $\pm$ 3.0	55.2	46.5	2518.2 $\pm$ 53.6
	Late Mexico 120	35.0 $\pm$ 4.0	97.7	69.3	3406.2 $\pm$136.1
30/25°C	Triple Dirk	20.0 $\pm$ 1.0	45.7	22.7	912.1 $\pm$ 17.3
	Timgalen	19.0 $\pm$ 1.7	57.2	31.8	1111.7 $\pm$ 39.4
	WW15	22.0 $\pm$ 3.5	59.4	44.8	1463.7 $\pm$ 63.6
	Late Mexico 120	21.7 $\pm$ 2.0	103.5	64.3	2237.9 $\pm$ 69.7

TABLE (4.2 cont)

EXPERIMENT II

Temperature Treatment	Cultivar	Duration (days)	Growth Rate (mg day^{-1})	Ear Grain Number	Yield per ear (mg) $\pm$ 2 x S.E.$\overline{X}$
15/10°C	Triple Dirk	61.3 $\pm$ 3.5	20.9	20.9	1367.2 $\pm$ 84.1
	Timgalen	57.7 $\pm$ 1.6	18.9	22.0	1065.0 $\pm$ 89.6
	WW15	57.5 $\pm$ 5.8	32.9	33.5	1834.3 $\pm$ 71.0
	Late Mexico 120	59.0 $\pm$ 8.5	32.9	32.3	2015.2 $\pm$ 93.7
21/16°*C	Triple Dirk	33.5 $\pm$ 3.0	25.5	18.1	980.3 $\pm$ 50.9
	Timgalen	32.8 $\pm$ 1.5	33.7	21.1	1111.1 $\pm$ 69.2
	WW15	40.5 $\pm$ 6.6	31.8	33.6	1606.9 $\pm$ 61.3
	Late Mexico 120	35.4 $\pm$ 4.0	42.7	30.8	1547.5 $\pm$ 69.2
30/25°C	Triple Dirk	25.4 $\pm$ 2.8	30.8	17.4	672.8 $\pm$ 46.1
	Timgalen	19.8 $\pm$ 1.5	24.1	21.4	437.3 $\pm$ 16.9
	WW15	26.5 $\pm$ 3.9	33.7	30.6	1077.3 $\pm$ 37.9
	Late Mexico 120	24.3 $\pm$ 2.5	36.0	28.8	801.8 $\pm$ 15.4

TABLE (4.2 cont.) EXPERIMENT III

Light Intensity Treatment	Cultivar	Duration (days)	Growth Rate (mg. day^{-1})	Ear Grain Number	Yield per ear (mg $\pm$ 2 x S.E.$\overline{X}$
21/16°*C	Triple Dirk	36.5 $\pm$ 2.2	42.3	29.1	1777.7 $\pm$ 45.5
8070 lux		38.9 $\pm$ 5.3	28.0	24.5	1202.3 $\pm$ 66.1
16140 lux		32.2 $\pm$ 2.8	40.2	24.7	1381.2 $\pm$ 50.3
34432 lux		35.5 $\pm$ 4.5	59.3	31.2	2017.1 $\pm$ 52.8
		33.3 $\pm$ 3.5	42.7	30.6	1614.4 $\pm$ 78.1
21/16°*C	Sonora	33.5 $\pm$ 3.0	69.7	42.7	2189.3 $\pm$ 80.7
8070 lux		36.0 $\pm$ 4.3	37.7	39.7	1217.6 $\pm$ 56.2
16140 lux		35.8 $\pm$ 3.8	43.1	42.8	1729.5 $\pm$ 67.6
34432 lux		31.5 $\pm$ 3.5	79.3	46.1	2609.5 $\pm$ 77.3
48420 lux		33.3 $\pm$ 3.2	66.3	45.9	2312.9 $\pm$ 78.5

TABLE (4.2 cont.) EXPERIMENT IV

Temperature Treatments	Cultivar	Duration (days)	Growth Rate (mg day^{-1})	Ear Grain Number	Yield per ear (mg $\pm$ 2 x S.E.$\overline{X}$
21/16°*C	Sonora	32.5 $\pm$ 4.1	39.6	28.5	1300.9 $\pm$ 49.0
21/16°C		27.4 $\pm$ 3.4	52.3	30.0	1516.7 $\pm$ 71.0
21/25°C		22.7 $\pm$ 3.0	53.4	28.9	1153.6 $\pm$ 57.3
30/16°C		20.5 $\pm$ 3.0	55.6	28.8	1118.6 $\pm$ 51.5
30/25°C		19.2 $\pm$ 2.7	51.3	28.9	998.9 $\pm$ 44.6
21/16°C	Late Mexico 120	34.6 $\pm$ 5.0	40.8	29.2	1404.5 $\pm$ 75.9
21/16°C		26.6 $\pm$ 4.4	62.7	29.4	1656.6 $\pm$ 83.7
21/25°C		28.9 $\pm$ 5.4	48.5	30.3	1418.0 $\pm$ 87.5
30/16°C		20.2 $\pm$ 3.9	65.0	29.0	1124.0 $\pm$ 82.2
30/25°C		20.2 $\pm$ 2.7	62.3	29.0	1166.1 $\pm$ 66.5

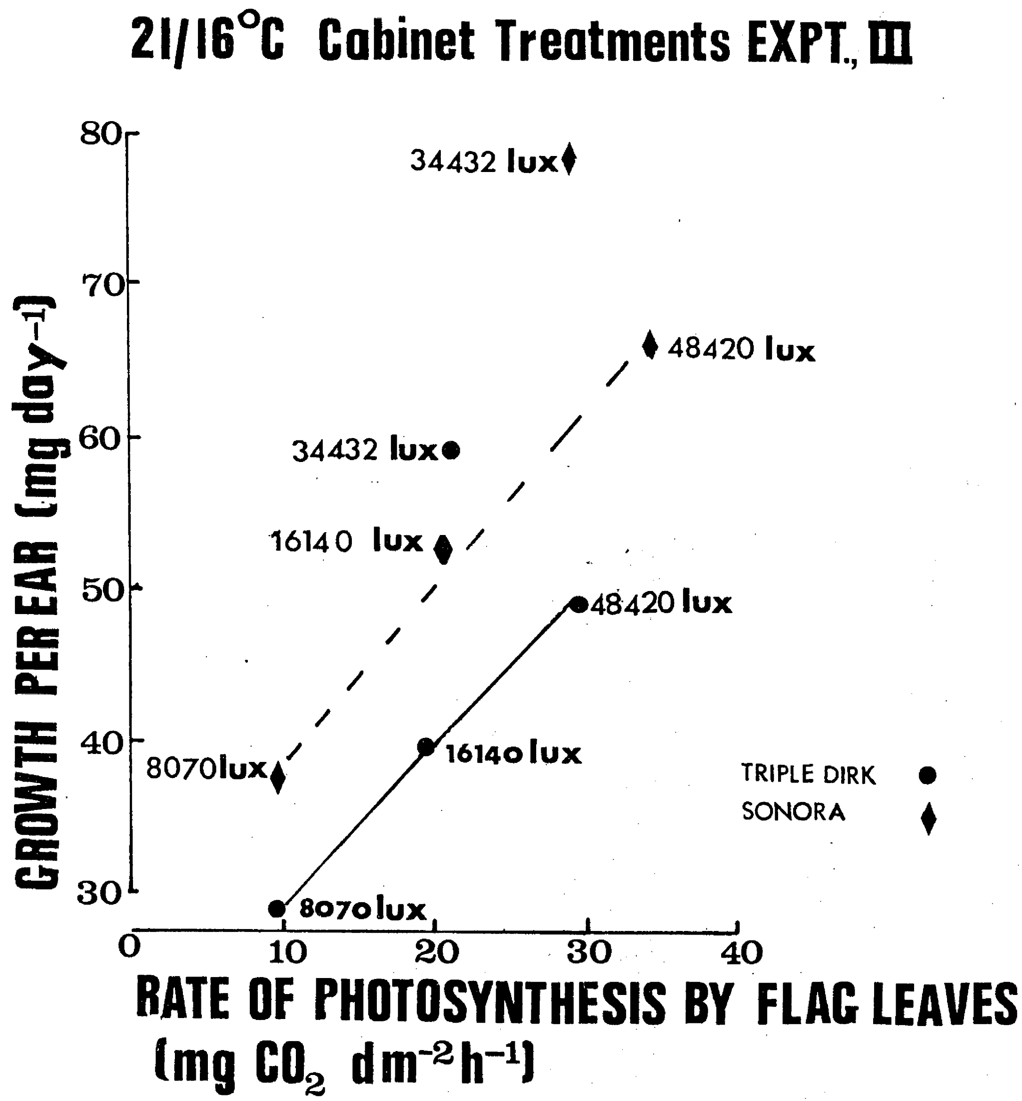


FIGURE 4.10 EXPERIMENT III. The relation between the photosynthetic rate of flag leaves and the rate of grain growth per ear.

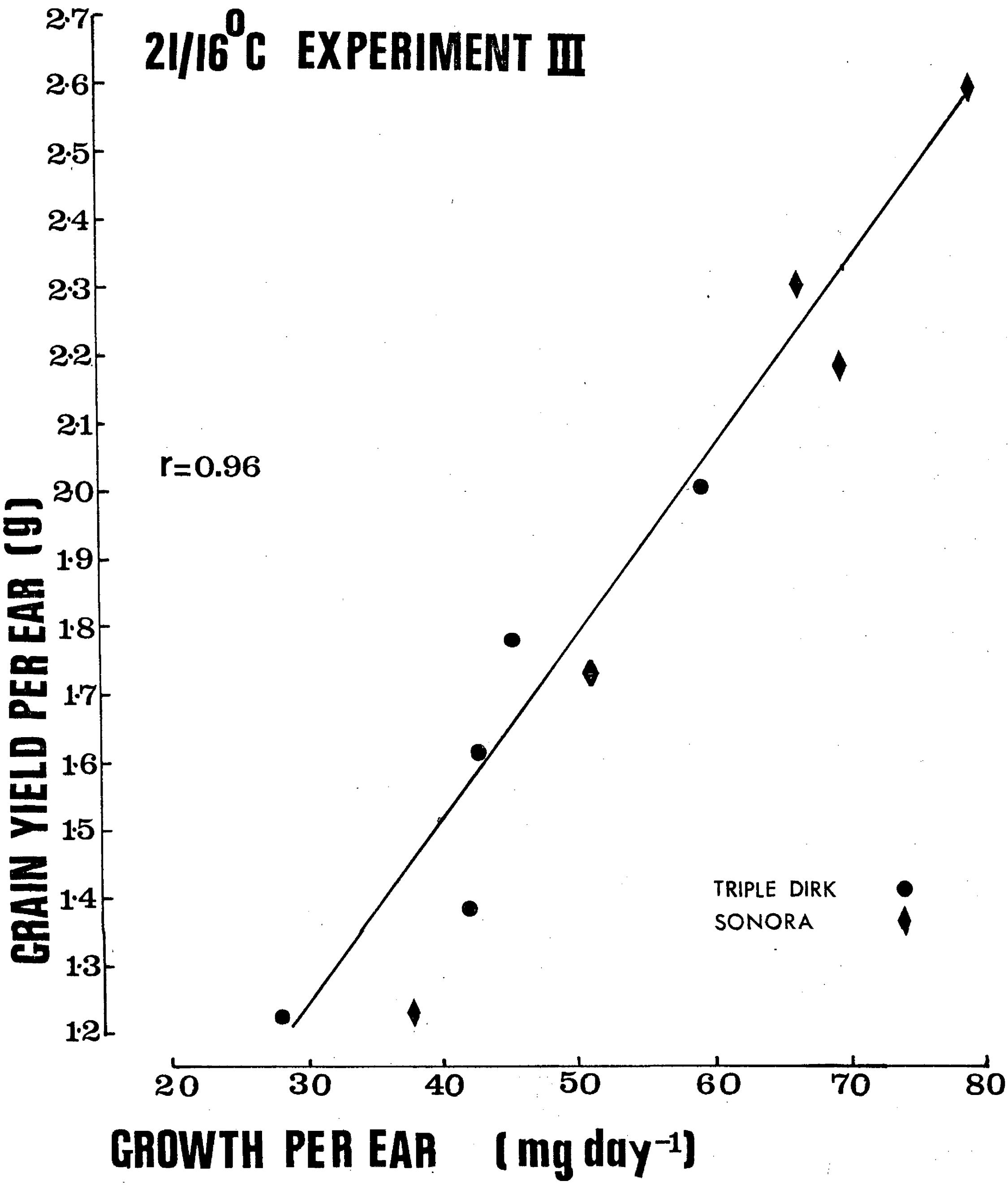


FIGURE 4.11 EXPERIMENT III. The relation between the rate of grain growth per ear and final ear weight (per ear). r is the correlation coefficient.

grains set on the one hand and by the photosynthetic rate as influenced by light intensity on the other.

The pronounced effects of high day and high night temperature are illustrated in Figure 4.12. Both high day or high night temperature resulted in a lower final yield per ear and this was largely due to a decrease in the duration of grain filling except for Late Mexico 120 where the increase in night temperature (21/16°C to 21/25°C Experiment IV) resulted in a lower final weight per ear largely due to a slower growth rate at 21/25°C. (Table 4.2) For Late Mexico 120 (Experiment IV) a high day temperature (30/16°C) had a more adverse effect than a high night temperature (21/25°C) on final yield per ear. This was not very pronounced in Sonora (Fig. 4.12, Experiment IV).

A treatment response for grains on a <u>per ear</u> basis was similar to that observed for individual grains from the central spikelets. However this did not necessarily imply that all grains within an ear responded uniformly to a treatment. In fact, in some cultivars, small but nonetheless significant differences were observed in the extent that individual grains responded to a treatment and this aspect is considered in more detail in Section 4.6 below.

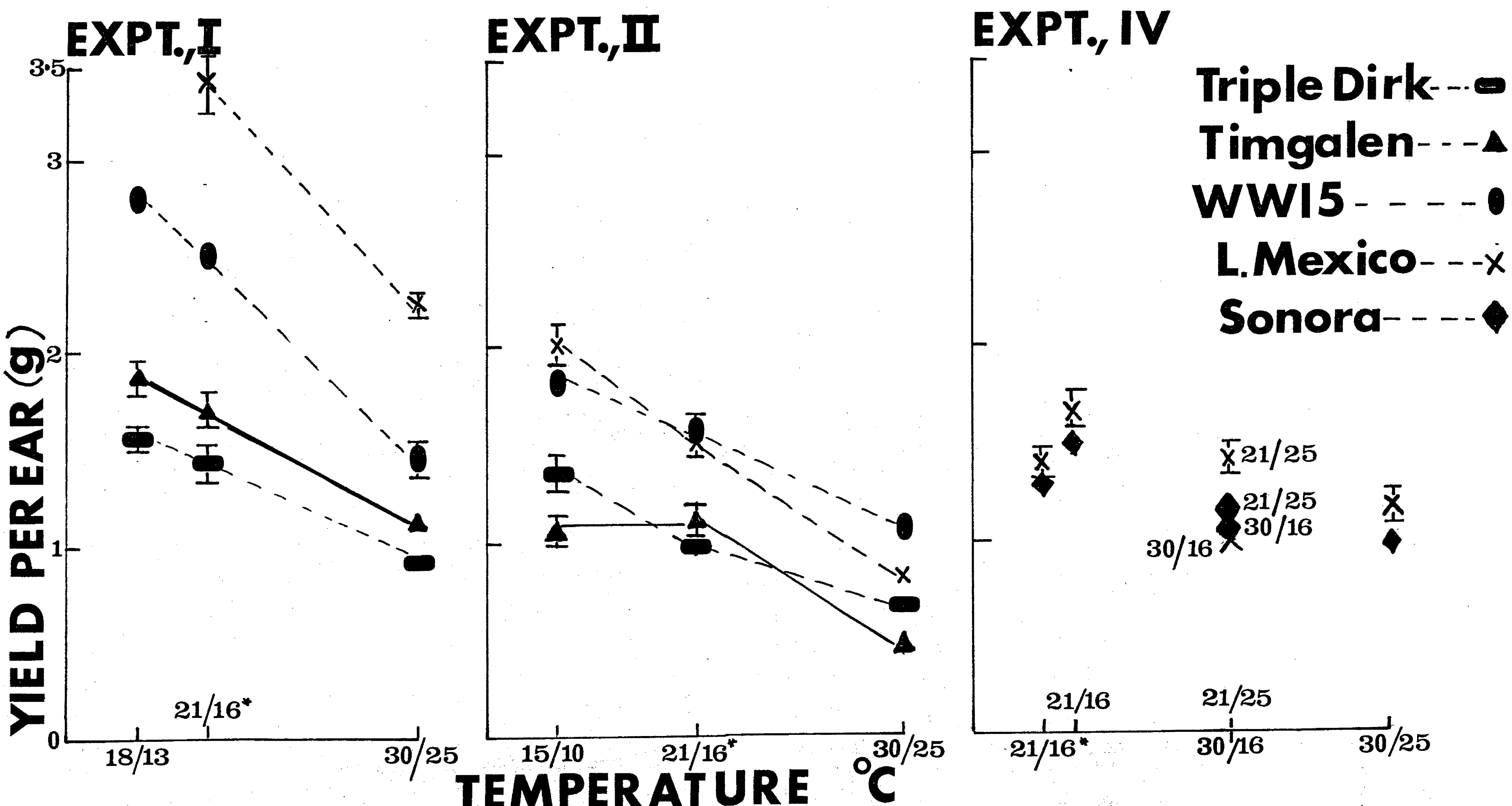


FIGURE 4.12 EXPERIMENTS I, II and IV. The effect of temperature on final ear weight (per ear). Where errors bars are not visible, they fall within the range of the symbol used. Final dry weight of ears Appendix F p 108 Experiment I, p 110 Experiment II and p 112 Experiment IV.

4.6 EXPERIMENTS I, II AND III THE EFFECT OF TEMPERATURE, LIGHT INTENSITY AND CULTIVAR ON THE RATE AND DURATION OF GRAIN FILLING FOR INDIVIDUAL GRAINS SITUATED AT DIFFERENT POSITIONS* WITHIN AN EAR.

4.6.1 Introduction

That final dry weight of individual grains varies markedly with their position within an ear, a difference associated with either the rate or duration of grain filling or both, is well known (Ra 70) and the results from experiments I, II, III and IV generally agree with the previous observations. It is not intended to present this aspect in detail but only in passing in order to indicate the effect of a treatment on individual grains situated at different positions within an ear.

For the grain positions* examined, all the grains responded similarly to a treatment. For example at 30/25°C under summer irradiance (Experiment I, Section 4.2.1) a shorter duration for outweighed the increase in growth rate and consequently final grain weight was lower for all grains at 30/25°C. However the effect of a treatment was not uniform in all grains and the extent of the response varied with position of the grain within the ear. Moreover which grain positions were more adversely affected appeared to be

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* Recall that under summer irradiance (Experiment I) the temperature treatment effects were recorded for individual grains from the lower central and upper spikelets, whereas in experiment II (temperature treatments under winter irradiance) and in experiment III (light intensity treatments) the treatments were recorded for individual grains in the central spikelets only (Table 2.2).

influenced by the type of stress applied and also varied between the cultivars. Thus for Timgalen under summer irradiance at 30/25°C (Experiment I) the basal a and b grains from the central spikelets where more adversely affected than the outer floret grains, largely because their durations were more adversely affected. On the other hand at 21/16°*C low light intensity (Experiment III) had less effect on the basal grains from the central spikelets and was most marked in the outermost florets, largely because the growth rates were more adversely affected in the outer floret grains.

Temperature treatment effects on individual grains under summer (Experiment I) and winter irradiance (Experiment II) will only be inferred for Timgalen as at the higher temperatures in both expt.I and II the other cultivars aborted some of their outer floret grains. Similarly light intensity treatment effects (Experiment III) will be inferred only for Sonora as Triple Dirk readily aborted its outer floret grains at the two lowest light intensities (Tables 3.1). Nevertheless the results are presented for each cultivar as there are many common aspects of responses between them.

4.6.2 Experiment I Temperature Treatment Effects Under Summer Irradiance Within Spikelets:

At the lower temperature of 18/13°C within the central and lower spikelets grain b was generally marginally heavier than grain a and both were considerably heavier than c and d and c was heavier than d.

Grain b was marginally heavier than grain a largely because it grew faster than a by 2 to at most 10%. However the a and b grains (basal floret grains) not only grew up to 38% faster than the outermost floret grains but they also had longer durations of filling of generally six to ten days (up to 18% longer). For example for Timgalen at 18/13°C, the final dry weight of the a grain from the central spikelets was 48 ± 5% heavier than the d grain. This was largely because grain a had a faster growth rate of 27 ± 19% and a longer duration of grain filling of 18 ± 13% than grain d (Table 4.3).

At 30/25°C final grain weight was less in all grains but not all were equally affected. Final grain weight remained heavier in the basal than outer floret grains, however generally the magnitude of difference between them was reduced. This was largely due to the fact that, especially in the central and upper spikelets the basal a and b grains were more seriously affected than the outer ones. For example, for Timgalen, when the temperature was increased from 18/13°C to 30/25°C final grain weight of grains from the central spikelets were reduced by 24.67 ± 1.30mg, 25.31 ± 2.0mg, 17.41 ± 1.87mg and 5.84 ± 2.12mg (ie., 41 ± 3%, 41 ± 4%, 34 ± 5% and 19 ± 8%) in the a, b, c and d florets respectively (Appendix C p 84 Tables 1(b), 1(c), 2(b), 2(c)).

The basal grains were more adversely affected largely because their durations were more adversely affected. Thus for Timgalen when the temperature was increased from 18/13°C to 30/25°C for grains from the central spikelets the duration of grain filling was reduced by 22, 24, 19 and 13 days (ie., 57 ± 6%, 57 ± 9%, 50 ± 11% and 44 ± 10%) in the a, b, c and d florets respectively (Appendix C p 85 Tables 1(c) and 2(c)).

At the higher temperature of 30/25°C growth rates were greater in all grains, in fact they generally increased more in the basal than the outer floret grains* but as indicated above, these faster

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*For Timgalen, when the temperature was increased from 18/13°C to 30/25°C growth rates increased by 0.50,0.54,0.51 and 0.23 mg day^{-1} in the a, b, c and d floret positions respectively for grains from the central spikelets (Appendix C p85 Table 1(c)).

TABLE 4.3 EXPERIMENTS I, II and III. The rate and duration of grain filling and the final dry weight of individual grains situated at different positions within an ear. r - growth rate (mg. day^{-1}); d- duration of grain filling (days); w - final dry weight (mg $\pm$ S.E.$\bar{X}$)

EXPERIMENT I (summer irradiance) 18/13°C

Cultivar	Spikelet Position \ Floret Position		Floret a	Floret b	Floret c	Floret d
Triple Dirk	Lower	r	1.405 ± 0.068	1.431 ± 0.077	1.307 ± 0.086	
		d	42.0 ± 3.4	41.7 ± 0.7	38.0 ± 2.0	
		w	57.7 ± 1.3	61.0 ± 2.0	45.1 ± 2.2	
	Central	r	1.355 ± 0.056	1.464 ± 0.059	1.142 ± 0.096	
		d	41.7 ± 3.7	40.6 ± 2.0	40.0 ± 3.0	
		w	57.8 ± 1.1	62.9 ± 1.8	45.5 ± 2.1	
	Upper	r	1.333 ± 0.080	1.297 ± 0.098		
		d	38.0 ± 3.0	37.6 ± 3.4		
		w	54.8 ± 1.4	54.6 ± 4.0		
Timgalen	Lower	r	1.300 ± 0.032	1.309 ± 0.049	1.139 ± 0.083	
		d	43.4 ± 2.7	44.4 ± 3.7	43.0 ± 1.0	
		w	54.8 ± 1.6	55.9 ± 2.3	47.5 ± 0.4	
	Central	r	1.437 ± 0.035	1.470 ± 0.033	1.329 ± 0.044	1.045 ± 0.178
		d	40.7 ± 1.3	42.3 ± 1.7	38.3 ± 2.3	33.3 ± 3.3
		w	60.9 ± 0.90	61.9 ± 0.9	51.0 ± 0.9	31.4 ± 1.1
	Upper	r	1.388 ± 0.067	1.348 ± 0.047	1.019 ± 0.071	
		d	43.0 ± 1.4	43.7 ± 2.4	36.6 ± 2.7	
		w	57.1 ± 0.7	56.1 ± 1.2	34.9 ± 1.1	

TABLE 4.3 EXPERIMENT I (summer irradiance) 18/13°C continued

Cultivar	Spikelet Position \ Floret Position		Floret _a_	Floret _b_	Floret _c_	Floret _d_
WW15	Lower	r	1.088 ± 0.078	1.278 ± 0.038	1.102 ± 0.102	
		d	51.5 ± 3.0	46.5 ± 2.5	47.5 ± 2.6	
		w	56.5 ± 0.8	59.1 ± 1.0	52.9 ± 0.7	
	Central	r	1.213 ± 0.046	1.288 ± 0.038	1.099 ± 0.069	0.746 ± 0.256
		d	46.9 ± 3.2	47.9 ± 4.0	44.0 ± 2.0	42.6 ± 3.5
		w	57.4 ± 1.6	60.0 ± 2.0	50.0 ± 1.3	32.9 ± 1.1
	Upper	r	0.981 ± 0.052	1.036 ± 0.086	0.759 ± 0.108	
		d	48.0 ± 2.0	46.0 ± 3.0	45.5 ± 3.2	
		w	49.0 ± 1.1	47.8 ± 1.2	33.9 ± 1.4	

EXPERIMENT I (summer irradiance) 30/25°C

Cultivar	Spikelet Position	Floret Position	Floret a	Floret b	Floret c	Floret d
Triple Dirk	Lower	r	1.850 ± 0.101	1.982 ± 0.116		
		d	21.0 ± 1.0	20.7 ± 1.7		
		w	42.8 ± 0.8	42.1 ± 1.4		
	Central	r	1.821 ± 0.133	1.982 ± 0.122		
		d	20.3 ± 1.3	21.3 ± 1.0		
		w	41.2 ± 0.9	40.8 ± 0.8		
	Upper	r	1.823 ± 0.073	1.794 ± 0.028		
		d	18.3 ± 0.7	19.6 ± 2.0		
		w	39.6 ± 2.0	39.7 ± 1.6		
Timgalen	Lower	r	1.956 ± 0.262	2.079 ± 0.087	1.624 ± 0.177	
		d	17.6 ± 3.0	16.9 ± 3.0	19.7 ± 3.7	
		w	35.4 ± 0.9	35.7 ± 1.8	33.5 ± 1.7	
	Central	r	1.938 ± 0.146	2.006 ± 0.166	1.839 ± 0.147	1.276 ± 0.230
		d	18.7 ± 1.7	18.3 ± 2.7	19.0 ± 3.0	18.7 ± 2.0
		w	36.2 ± 0.4	36.6 ± 1.1	33.5 ± 0.9	25.4 ± 1.1
	Upper	r	1.704 ± 0.141	1.793 ± 0.186	1.454 ± 0.172	
		d	20.7 ± 2.0	19.6 ± 1.4	19.3 ± 1.7	
		w	35.1 ± 0.6	35.5 ± 1.0	28.7 ± 1.2	

EXPERIMENT I (summer irradiance) 30/25°C continued

Cultivar	Spikelet Position \ Floret Position		Floret a	Floret b	Floret c	Floret c
WW15	Lower	r	1.566 ± 0.105	1.843 ± 0.232	1.275 ± 0.315	
		d	22.3 ± 3.1	19.9 ± 2.1	20.5 ± 2.8	
		w	34.6 ± 1.3	36.7 ± 1.2	28.0 ± 1.2	
	Central	r	1.549 ± 0.094	1.739 ± 0.114	1.464 ± 0.117	
		d	23.0 ± 3.3	22.7 ± 3.2	21.0 ± 3.3	
		w	37.1 ± 1.8	37.5 ± 1.8	32.4 ± 1.8	
	Upper	r	1.533 ± 0.165	1.554 ± 0.122	1.167 ± 0.300	
		d	19.9 ± 2.2	19.0 ± 2.2	14.5 ± 2.0	
		w	31.8 ± 1.2	30.4 ± 1.0	20.7 ± 1.2	
Late Mexico 120	Lower	r	1.717 ± 0.117	1.730 ± 0.131	1.396 ± 0.188	
		d	21.7 ± 2.4	20.3 ± 2.4	22.0 ± 2.7	
		w	37.4 ± 1.5	37.4 ± 1.2	32.1 ± 1.3	
	Central	r	1.613 ± 0.081	1.706 ± 0.095	1.333 ± 0.270	0.728 ± 0.346
		d	21.7 ± 2.3	19.3 ± 2.0	22.3 ± 2.3	27.3 ± 5.6
		w	37.1 ± 1.3	36.0 ± 1.2	32.0 ± 1.0	23.9 ± 6.3
	Upper	r	1.385 ± 0.168	1.574 ± 0.081	1.040 ± 0.036	
		d	22.0 ± 2.7	18.6 ± 2.0	20.7 ± 2.7	
		w	35.1 ± 0.9	34.5 ± 1.4	24.8 ± 1.6	

EXPERIMENT II (winter irradiance) 15/10°C For grains from the central spikelets.

Cultivar		Floret a	Floret b	Floret c
Triple Dirk	r	0.908 ± 0.070	0.958 ± 0.05	0.697 ± 0.10
	d	61.7 ± 3.2	58.9 ± 2.4	58.5 ± 5.5
	w	56.5 ± 1.1	58.1 ± 0.7	40.2 ± 1.4
Timgalen	r	0.901 ± 0.031	0.957 ± 0.042	0.782 ± 0.056
	d	59.3 ± 2.8	57.7 ± 2.4	56.1 ± 5.9
	w	54.6 ± 0.7	55.1 ± 0.6	43.9 ± 1.6
WW15	r	0.919 ± 0.081	1.034 ± 0.040	0.885 ± 0.05
	d	55.3 ± 4.4	55.3 ± 2.4	52.2 ± 4.0
	w	50.3 ± 0.7	55.0 ± 0.8	43.9 ± 1.1
Late Mexico 120	r	1.048 ± 0.053	1.109 ± 0.067	0.901 ± 0.083
	d	62.8 ± 3.2	58.5 ± 3.2	56.5 ± 6.7
	w	62.4 ± 0.9	64.5 ± 1.0	51.7 ± 1.7

EXPERIMENT II (winter irradiance) 30/25°C For grains from the central spikelets.

Cultivar		Floret a	Floret b	Floret c
Triple Dirk	r	1.839 ± 0.118	1.823 ± 0.068	
	d	24.2 ± 2.0	23.4 ± 2.4	
	w	43.5 ± 1.0	43.1 ± 1.3	
Timgalen	r	1.394 ± 0.169	1.248 ± 0.108	0.994 ± 0.233
	d	18.6 ± 2.4	21.5 ± 4.1	19.1 ± 3.4
	w	24.9 ± 1.2	25.0 ± 1.5	17.2 ± 1.4
WW15	r	1.459 ± 0.097	1.467 ± 0.142	1.127 ± 0.107
	d	23.0 ± 2.4	21.7 ± 1.7	22.7 ± 3.0
	w	30.2 ± 1.0	31.7 ± 1.0	25.9 ± 1.0
Late Mexico 120	r	1.367 ± 0.240	1.379 ± 0.045	1.003 ± 0.129
	d	23.4 ± 5.1	23.1 ± 5.4	24.1 ± 5.3
	w	32.1 ± 2.0	32.4 ± 2.0	23.1 ± 1.5

For the 21/16°°C treatment in both experiments I and II

Growth rates Appendix D p 101.
Duration Appendix E p 106.
Final grain weight Appendix F p 110.

EXPERIMENT III Light intensity treatments at 21/16°*C of 48,420 lux, 16,140 lux and 8070 lux respectively for grains from the central spikelets.

Light Intensity, Cultivar / Floret Position		Fl.a	Fl.b	Fl.c	Fl.d
Triple Dirk 48,420 lux	r	1.789 ± 0.018	1.845 ± 0.013	1.490 ± 0.063	
	d	32.0 ± 1.8	31.5 ± 1.9	28.0 ± 3.0	
	w	57.5 ± 0.6	58.5 ± 1.3	41.1 ± 1.4	
16,140 lux	r	1.710 ± 0.063	1.726 ± 0.103		
	d	33.5 ± 2.7	32.5 ± 2.0		
	w	58.2 ± 3.0	58.3 ± 1.2		
8070 lux	r	1.340 ± 0.112	1.304 ± 0.138		
	d	39.5 ± 4.8	38.0 ± 4.1		
	w	55.6 ± 2.3	52.6 ± 1.9		
Sonora 48,420 lux	r	1.634 ± 0.077	1.739 ± 0.078	1.658 ± 0.104	1.224 ± 0.157
	d	34.0 ± 2.8	35.0 ± 2.5	28.4 ± 2.2	27.5 ± 3.1
	w	58.4 ± 1.0	61.4 ± 1.5	52.4 ± 1.05	38.9 ± 1.2
16,140 lux	r	1.187 ± 0.140	1.274 ± 0.164	1.105 ± 0.096	1.010 ± 0.115
	d	34.5 ± 2.5	33.5 ± 2.5	33.2 ± 5.4	33.1 ± 3.8
	w	44.6 ± 0.9	47.4 ± 0.8	38.7 ± 2.2	28.6 ± 0.9
8070 lux	r	0.967 ± 0.159			
	d	38.3 ± 3.1	38.0 ± 2.5	40.5 ± 0.7	
	w	39.2 ± 1.1	39.7 ± 1.5	19.1 ± 2.6	

Light intensity treatments for the 21/16°*C glasshouse treatment and 34432 lux treatment respectively

Growth rates Appendix D p 103 ; Duration Appendix E p 107 ; Final grain weight Appendix F p 111.

growth rates of the basal grains were accompanied by more severe reductions in their duration and consequently their final grain weight was more adversely affected (Fig. 4.13).

Between Spikelets:

At the lower temperature of 18/13°C grains in the central spikelets were generally the heaviest (within an ear) and they were considerably heavier than the upper spikelet grains: this difference was more marked when progressing from the inner to outer floret grains. Thus for example at 18/13°C for Timgalen the final dry weight of grains a, b, and c, respectively was 4, 6 and 16 mg heavier in the central than upper spikelets (Table 4.3).

Grains in the central spikelets were heavier than those in the upper spikelets largely because they had faster growth rates and generally (depending on cultivar Table 4.3) they had a slightly longer duration of filling of 2 to 5 days (4 to 10%). For example at 18/13°C for Timgalen grains a, b and c respectively had faster growth rates of 3%, 8% and 23% in the central than upper spikelets. (Table 4.3)

At 30/25°C, overall the reductions in final grain weight of individual grains varied less with spikelet position than within spikelets. Nevertheless minor differences were observed: thus the basal a and b grains from the central and upper spikelets tended to be more adversely affected than the lower spikelet a and b grains. For example, for Timgalen, when the temperature was increased from 18/13°C to 30/25°C final grain weight of the a grain was reduced by 22, 25 and 19mg in the upper, central and lower spikelets respectively (Appendix C p85Table 1(c)). This was largely due to the fact that at 30/25°C growth rates decreased more in the upper

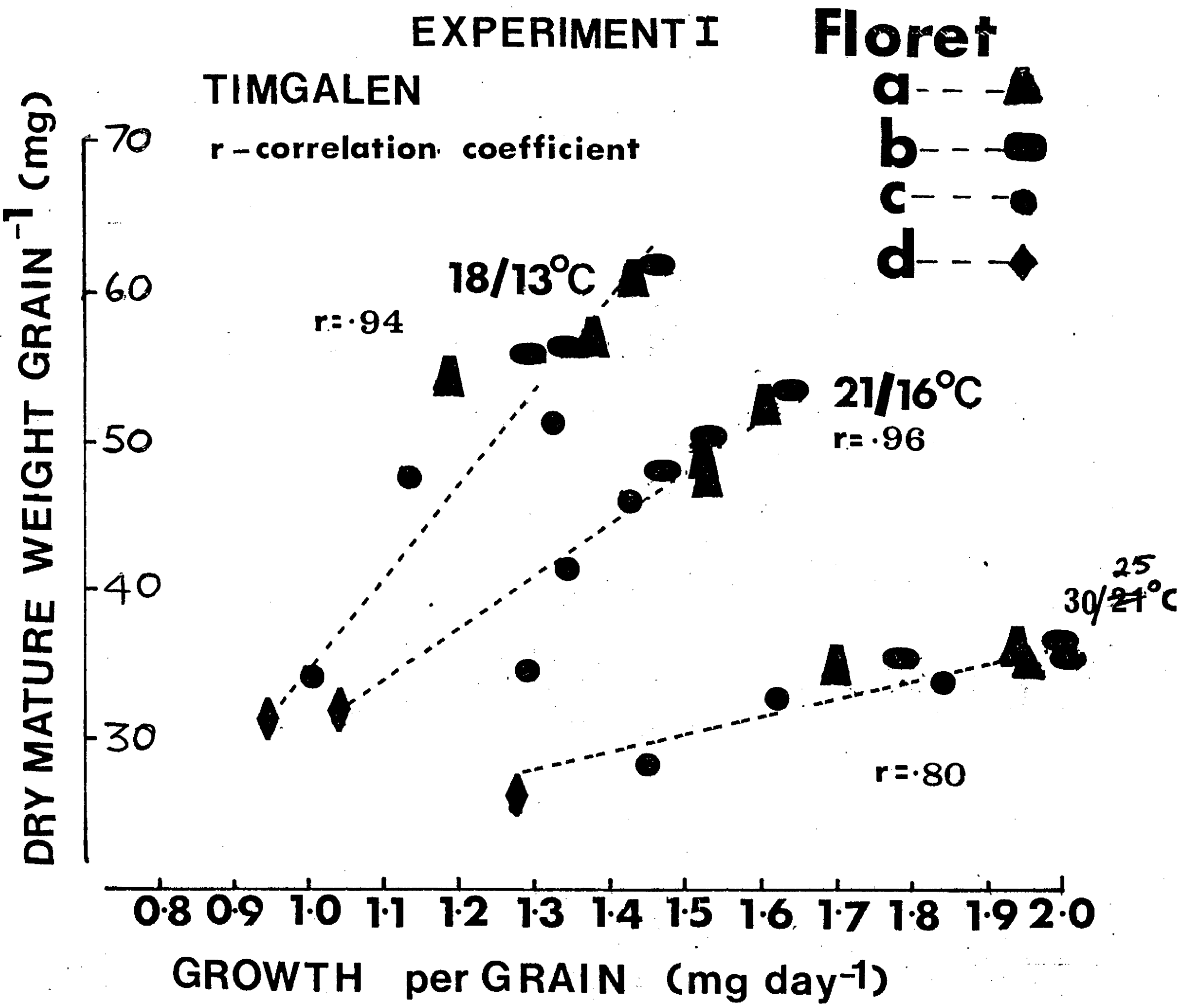

FIGURE 4.13 EXPERIMENT I. Grain growth rate per grain versus final weight per grain at 18/13°C, 21/16°*C and 30/25°C for cv. Timgalen. For each temperature, grain growth rates were plotted for individual grains from the upper central and lower spikelets. Growth rate Appendix D p 99 ; Final grain weight Appendix F p 108.

than central and least in the lower spikelets (Appendix C p 85 Tables 1(c), 2(c)).

4.6.3 Experiment II Temperature Treatment Effects Under Winter Irradiance

Within The Central Spikelets:

At the lower temperatures of 15/10°C, the responses under winter irradiance were similair to those under summer irradiance in as much, that

(i) generally growth rates of grains ranked b>a>c: b had a faster growth rate than a by 2 to 11% and both grew faster than grain c by 10-27% (Table 4.3).

(ii) grains a and b had marginally longer durations than c and consequently final dry weight of grain b was marginally heavier than grain a and both were heavier than grain c. Thus for example at 15/10°C for Timgalen grain a, b, and c had final grain weights of 54.56, 55.10 and 43.92 mg respectively (Table 4.3).

However unlike the results of experiment I at 30/25°C final grain weight was more adversely affected in the outer than basal floret grains. This was largely because the growth rates of the former were more adversely affected under winter irradiance (Flow Chart 2(b), Table 4.3) and this is supported by the results of experiment III.

4.6.4 Experiment III. Light Intensity Treatment Effects

Within the Central Spikelets

At the lower light intensities final grain weight was less in all grains but differences were more marked when progressing from the basal to outer floret grains. Thus at 8,070 lux final grain weight in Sonora was reduced by approximately 19, 22 and 33mg (ie. 33%, 35% and 64%) in the a, b and c grains respectively (% values Flow Chart 6, absolute values Table 4.3). This trend was also observed in Sonora at 16,140 lux but the reductions were not as severe (Flow Chart 7, Table 4.3).

Final grain weight was more adversely affected in the outer floret grains, largely because their growth rates were more adversely affected. In fact for Sonora at 8070 lux growth rates in the outer floret grains were no longer linear. However a 'growth rate'* was calculated for the b and c grains and it was found that the growth rates were reduced by approximately 41%, 45% and 50% in the a b and c grains respectively.

In conclusion two points are emphazised:-

(i) That the effect of a temperature treatment was not uniform in all grains from the central spikelets in cv. Timgalen clearly does not imply that all cultivars respond in this manner. In fact for the temperature treatments in experiment IV, the extent of a response to a temperature treatment was generally uniform for all grains from the central spikelets in cvs. Late Mexico 120 and Sonora respectively. (Flow Charts 4a and 4b)

(ii) That low light intensity has less effect on the final dry weight of basal than outermost floret grains for grains from the central spikelets was generally observed in all the cultivars examined but the extent of the response varied with cultivar (Flow Charts 2b, 6 and 7).

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* footnote in Flow Chart 6. Clearly these values are only approximations.

4.7 INITIAL LAG IN GRAIN GROWTH

Earlier experiments by Rawson and Evens (Ra71) suggested that cultivars which set more grains per spikelet appeared to display a longer initial lag between anthesis and the inception of linear grain growth per ear. This could be due to more distal floret grains being delayed relative to lower grains in the initiation of their growth. Consequently, comparisons were made among the cultivars on the basis of individual grain positions. In experiments I and II no consistent differences between cultivars in the length of the initial lag period were evident at the two higher temperatures, but at 15/10°C the lag was consistently longer in the two cultivars setting more grains per spikelet for first floret (a) grains, for example the lag was seven days in WW15 and Late Mexico 120 but was only four days in Triple Dirk and Timgalen. (Appendix B p 79)

CHAPTER 5

CESSATION OF GRAIN FILLING

5.1 INTRODUCTION

What determines the duration of grain filling and why it is so much shorter at higher temperatures or marginally longer at very low light intensities is not clear.

The results to be presented suggest that, at least, at the lower temperatures grain filling was limited by processes other than the supply of assimilates (Section 5.2). This supports the proposition put forward by Jenner and Rathjen (Je 72 a,b), that is, that the processes transporting carbohydrate on the final stages of its passage to the grain imposes the major limitation on grain filling. Whatever the nature of this bottleneck, the grain-water relation results (Section 5.3) suggest that water movement into the grain may be blocked at maturity.

From studies on mobilization of nitrogen from leaves (Ma 73) it is likely that amino acids and amides may move in conjunction with the carbohydrates. The results in Section 5.4 indicate a close association between the movement of carbohydrate and nitrogen and phosphorus into the developing grain. However no relationship could be discerned between absolute nitrogen and phosphorus contents (mgN/grain, mgP/grain) of grains and duration of growth.

5.2 SENESCENCE AND PHOTOSYNTHESIS

Ear, flag leaf and penultimate leaves were rated for greenness in experiments I-IV. It was subsequently shown by Dr. I.F. Wardlaw that on the main culm plants of experiment III such greenness ratings correlated well with measured rates of photosynthesis, although the exact relationship varied between the ear and leaves and between different leaf positions (Fig. 5.1).

In all cultivars at all temperatures ears lost their greenness more rapidly than did the flag leaves. Typical responses to temperature and light intensity are illustrated for Triple Dirk in experiment II, and for Sonora in experiment III respectively in Figure 5.2. The difference was most marked at the lower temperatures, where the flag leaves remained green and presumably active in photosynthesis for at least several weeks after grain growth in the main ear had ceased. Thus lack of assimiliates is unlikely to have caused cessation of grain growth at the lower temperatures and this conclusion is supported by the observation that stem dry weight tended to increase in these plants towards the end of grain growth. (Fig. 5.3) At. 30/25°C however the flag leaves rapidly lost their greenness as grain growth ceased nevertheless stem dry weights in plants tended to rise in experiment I but this was not so obvious in experiment IV for Sonora at 21/25°C, 30/16°C and 30/25°C. (Fig. 5.3)

Photosynthetic rates of the ear and the top three leaves were measured every few days throughout the latter part of grain filling at 8,070 and 48,420 lux in experiment III by Dr. Wardlaw. Although he found the rates fell towards the end of grain growth nevertheless 48 days after anthesis in Sonora by which time grain growth had ceased and ear photosynthesis and respiration were negligible, the <u>in situ</u> rates of flag leaf photosynthesis were about 12 and 5mg CO_2 $dm^{-2}h^{-1}$ in the 48,420 and 8,070 lux cabinets respectively. Termination of grain filling under these conditions was clearly not due to lack of assimilates.

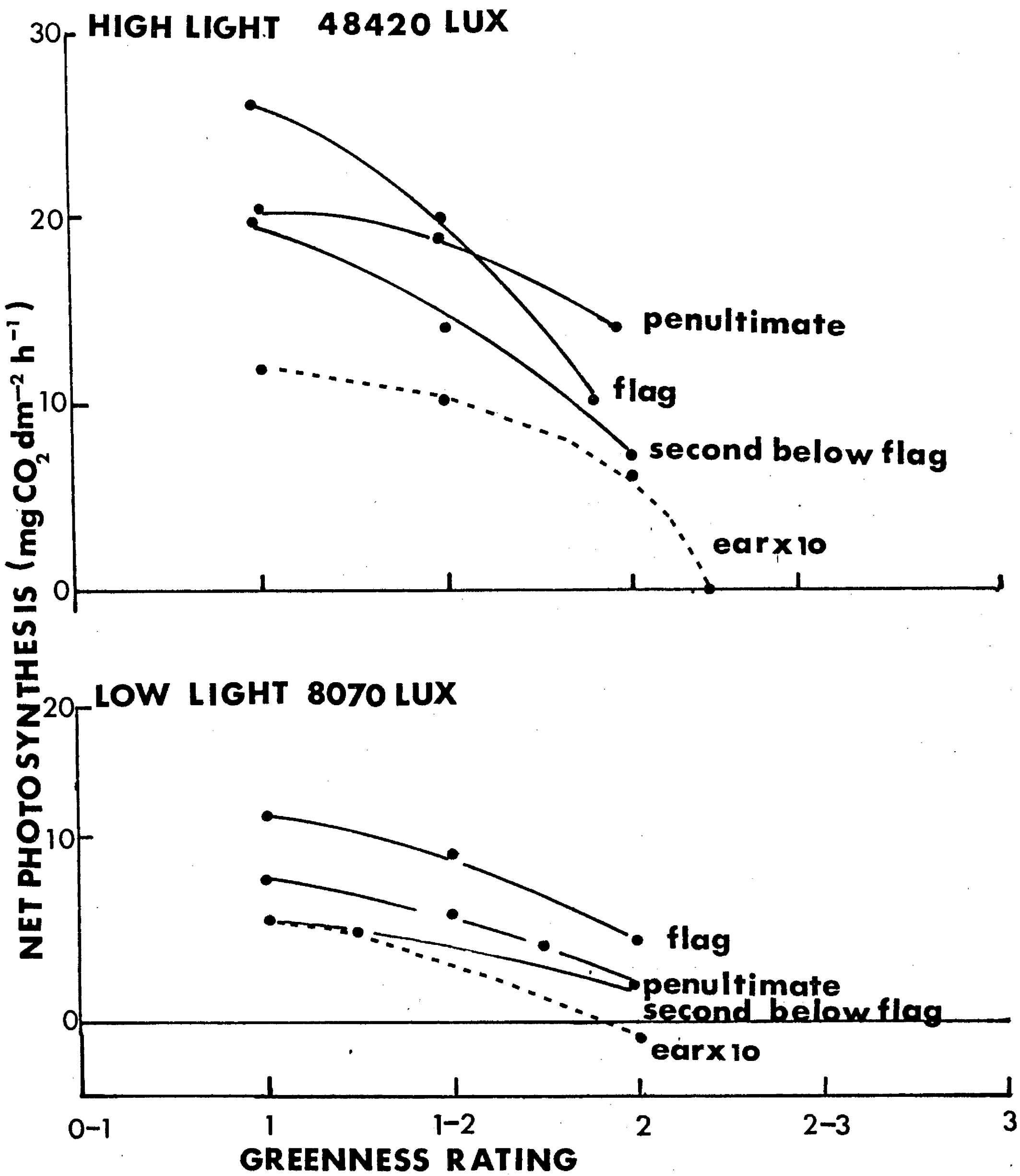


Figure 5.1 Comparison of greenness ratings and photosynthesis for the ear, flag, penultimate and lower leaf blades under high and low light intensity cabinet treatments at 21/16°C. Experiment III.

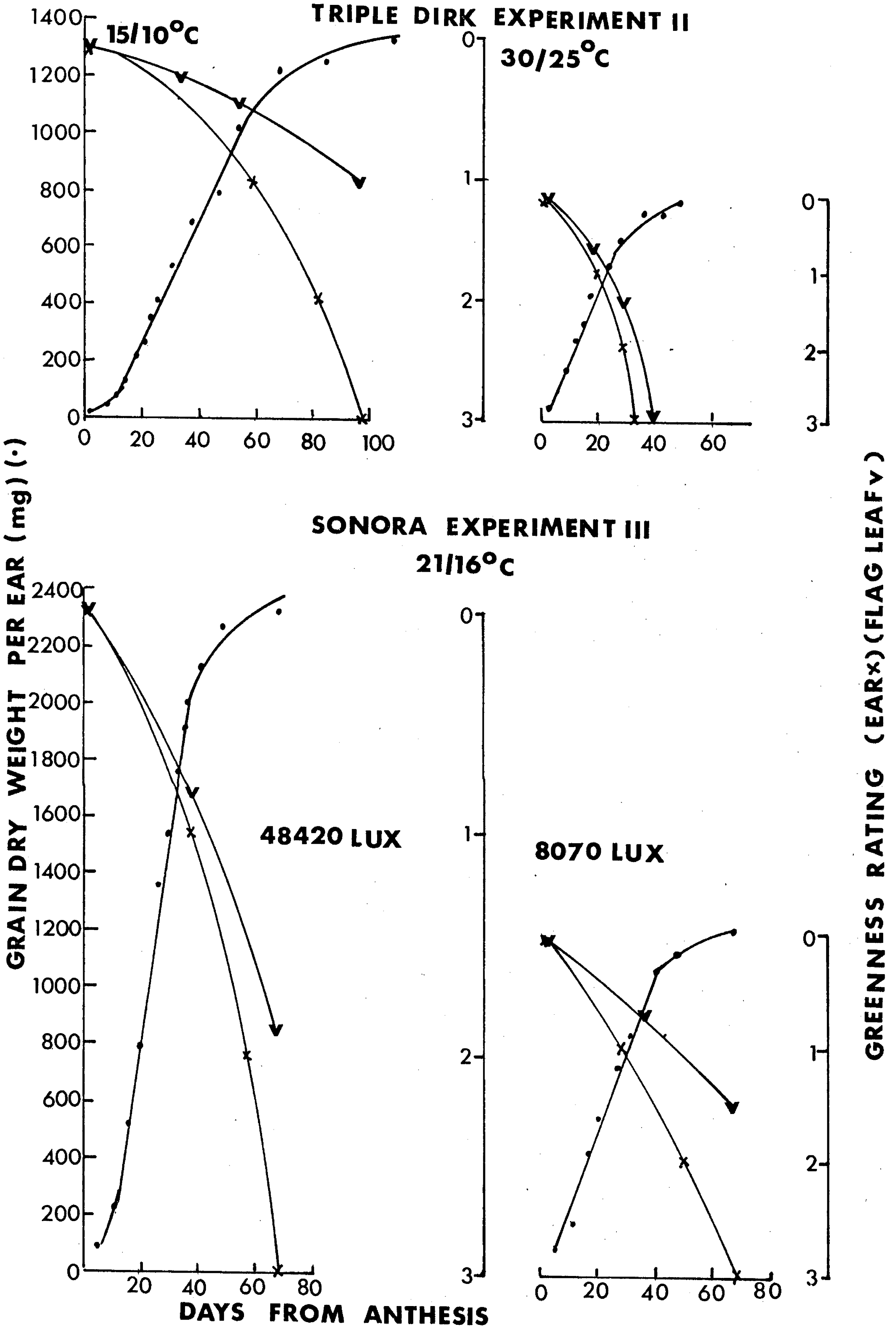


Figure 5.2 Experiment II and III. Loss of greeness in the flag leaf (v) and ear (x) at 15/10°C and 30/25°C in Triple Dirk in experiment II and for Sonora under 48420 lux and 8070 lux at 21/16°C in experiment III.

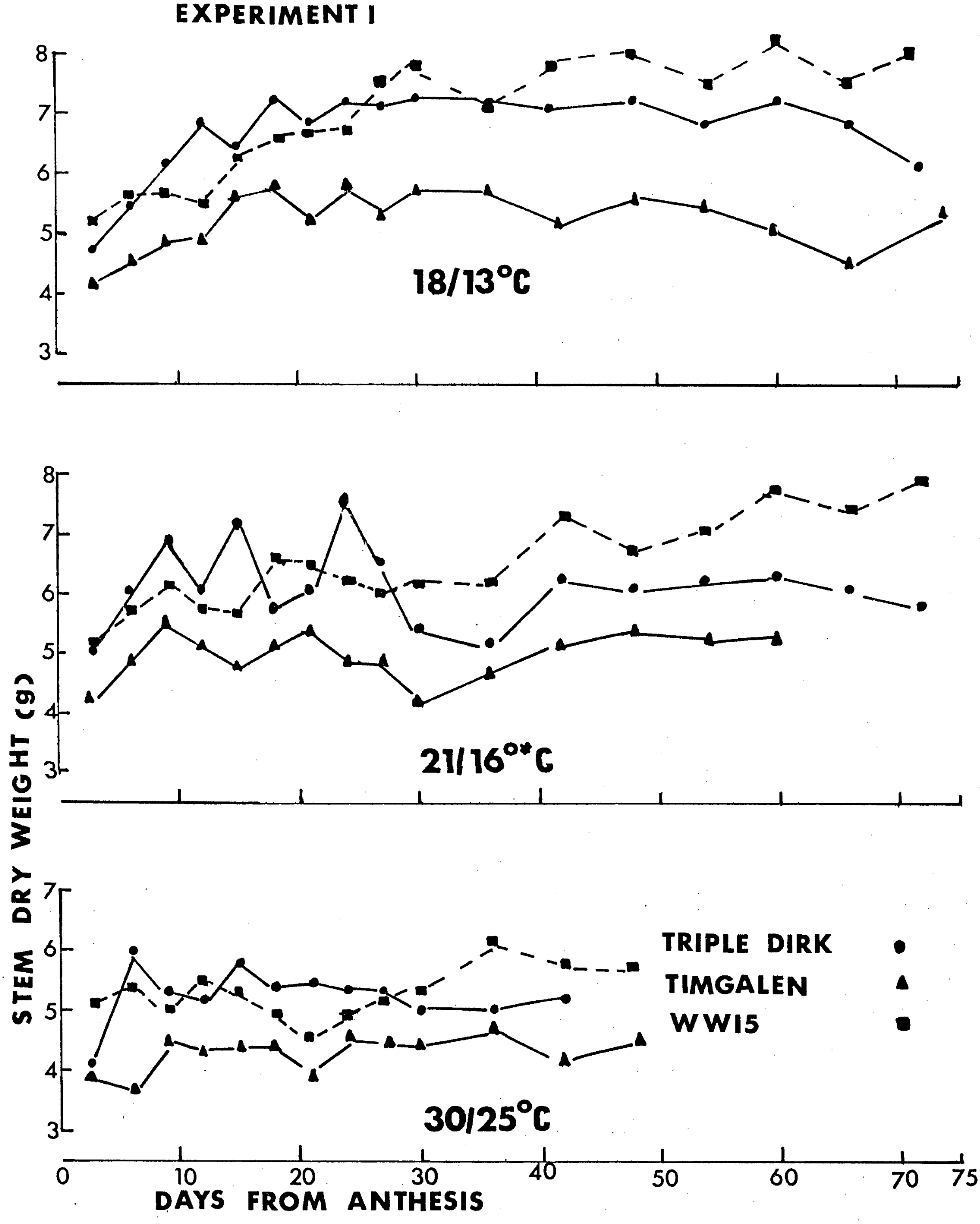
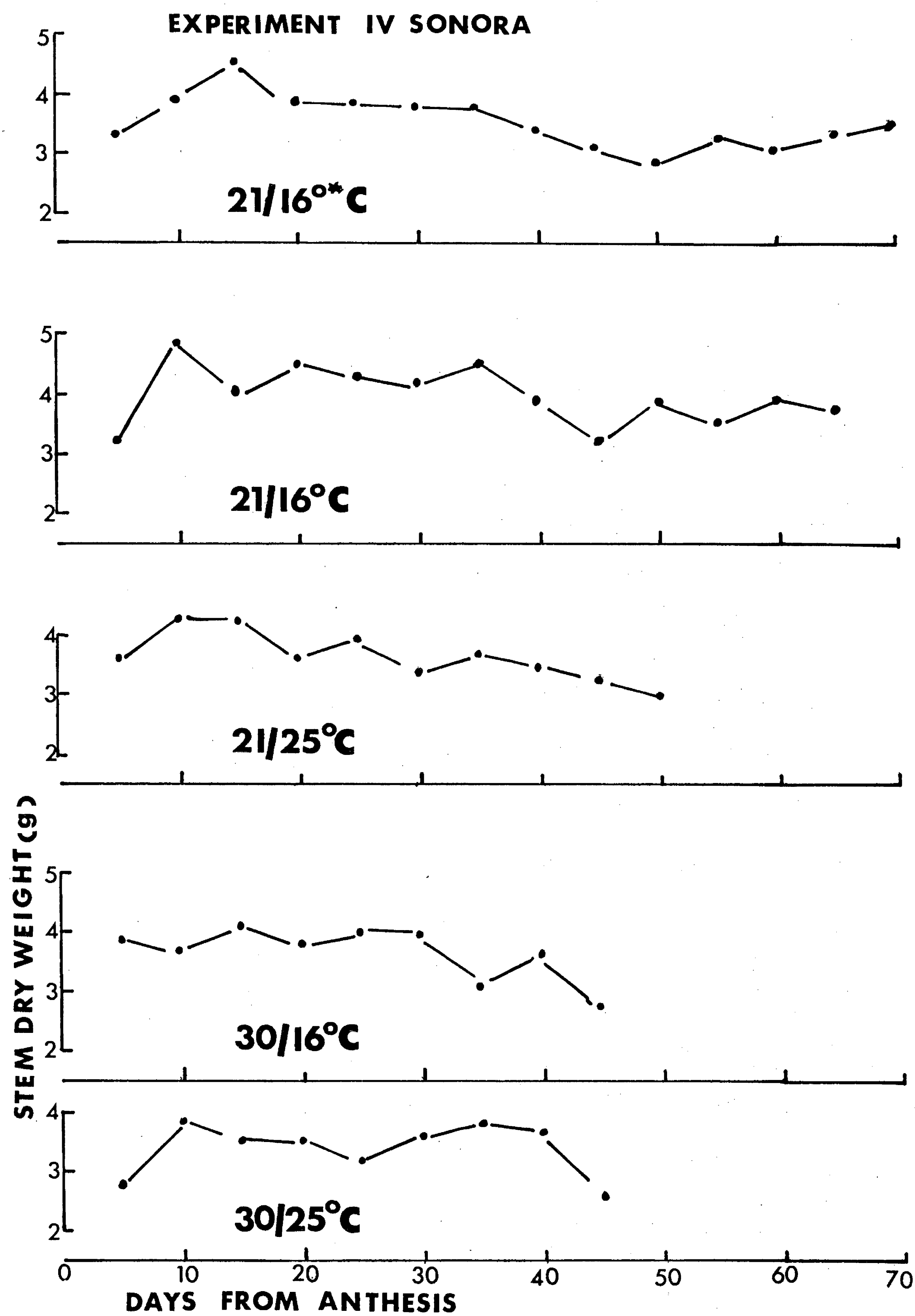


Figure 5.3 Experiments I and IV. Changes in the dry weight of the main culm stems during grain filling at 18/13°C, 21/16°*C and 30/25°C in Triple Dirk, Timgalen and WW15 in experiment I. In experiment IV in Sonora changes in the dry weight of the main culm stems during grain filling at 21/16°*C, 21/16°C, 21/25°C, 30/16°C and 30/25°C are given.


EXPERIMENT IV SONORA
21/16°*C
21/16°C
21/25°C
30/16°C
30/25°C
STEM DRY WEIGHT (g)
DAYS FROM ANTHESIS
0
10
20
30
40
50
60
70
2
3
4
5

5.3 VOLUME, WATER AND CALCIUM CONTENT OF GRAINS.

The water content of the floret a grain of the central spikelets, for Triple Dirk at 21/16°*C in experiment III, followed a course of three distinct phases during grain growth, as can be seen from Figure 5.4 . In phase I the water content increased at a fairly constant rate of approximately 2.8 mg/day till 18 days after anthesis. In phase II the net water content of the grains did not alter, the water content being 42.26 $\pm$ 0.40 mg from day 18 to 46. In phase III there was a sharp drop in the water content of the grains where from day 46 to 70 it dropped to 8.77 $\pm$ 0.28 mg, during the same period the volume of grains dropped from 82.9 x 10^{-3} to 50.6 x 10^{-3} c.c.

At the beginning of phase III there is a coincidence of events in that the dry weight and calcium content of the grain stop increasing just as the water content drops. The latter may be due to an increase in permeability to water of the grain coat as the grain approaches maturity or to water being "blocked" from entering the grain.

The calcium uptake was used as a guide to water uptake through the exylem by the grain. If calcium and water uptake are related (Mi 69) then the results suggest that at the beginning of phase III water movement is blocked from entering the grain. Also, Zee (unpublished) has obtained evidence for lipid deposition along the furrow, which could be expected to block water movement into the grain at maturity.

5.4 NITROGEN AND PHOSPHORUS CONTENT IN GRAINS.

Within each temperature treatment for floret a and c grains of the central spikelets, the nitrogen and phosphorus content of grains (mgN/grain, mgP/grain) in each cultivar closely followed the

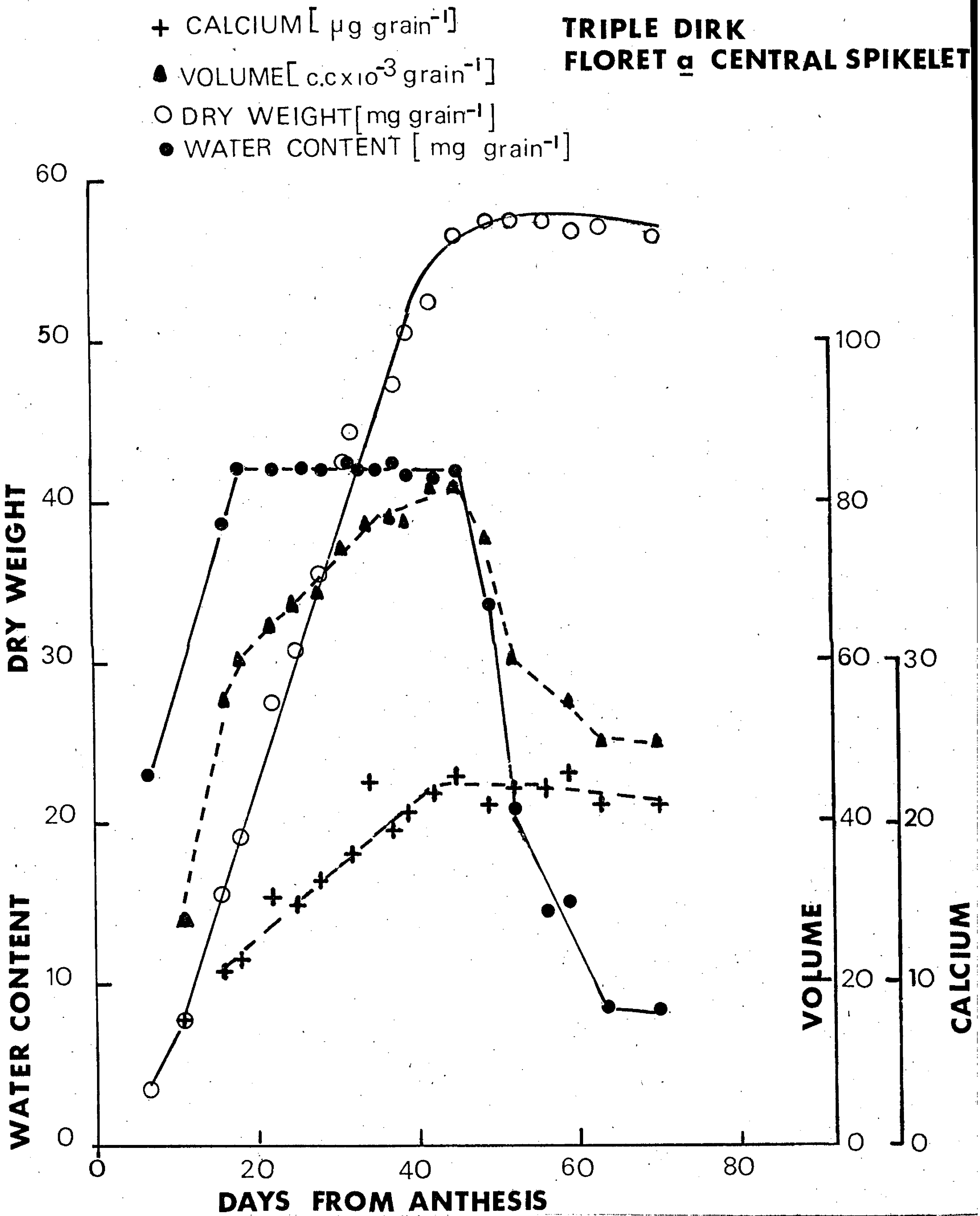


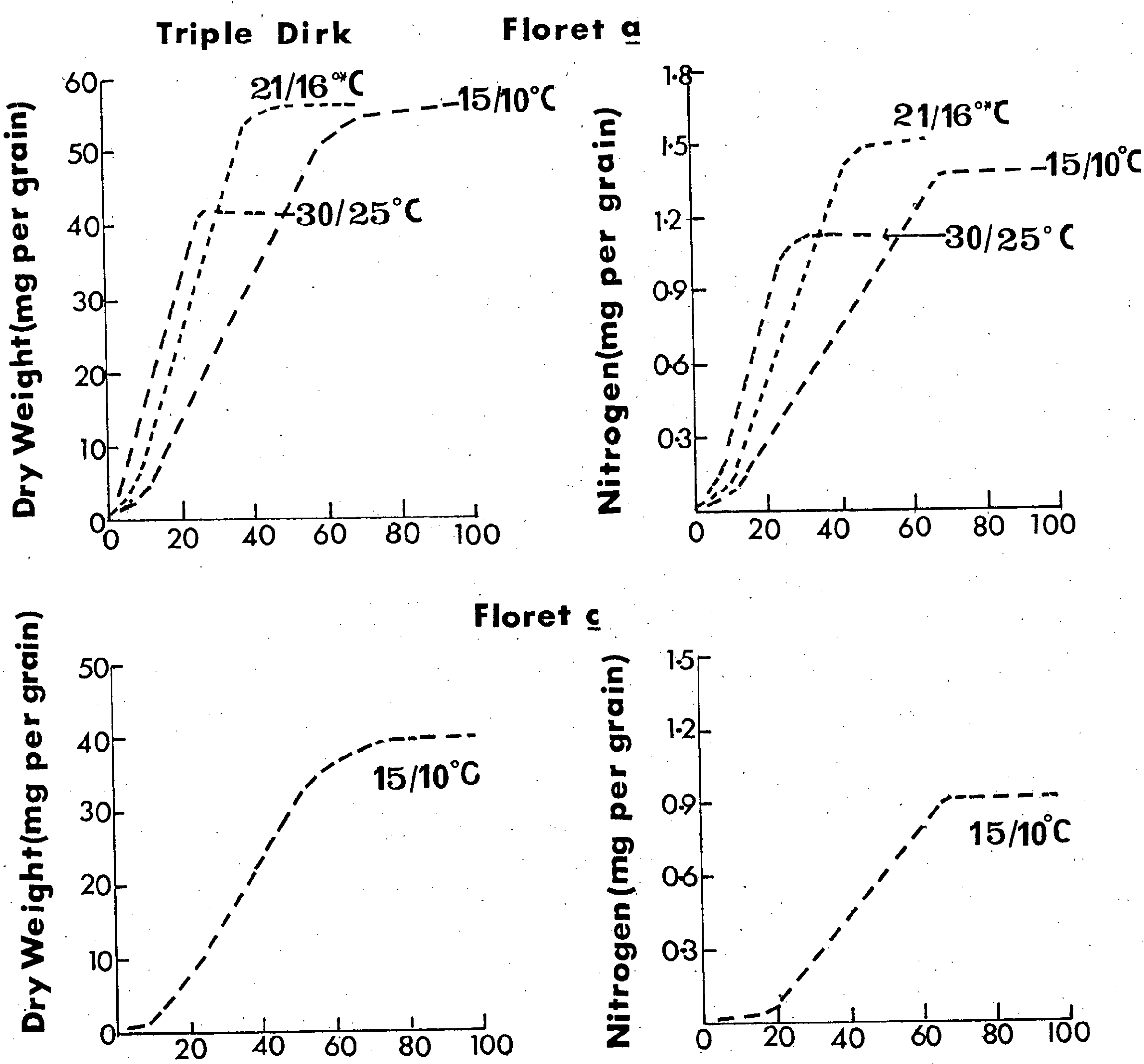
Figure 5.4 Experiment III. Water content, fresh volume, dry weight and calcium content of the floret a grains from the central spikelets in Triple Dirk at 21/16°*C.

patterns of their respective dry weight accumulation curves. As can be seen in Figure 5.5, both nitrogen and phosphorus accumulation displayed a linear phase of approximately the same duration as their respective dry weight accumulation curves and ceased when growth per grain ceased.

From Figure 5.6 percent nitrogen and phosphorus of grain increased in all cultivars at all temperatures during grain filling. However and especially at the lower temperatures of 15/10°C and 21/16°*C, generally from day zero (anthesis) to about day 10 percent nitrogen and phosphorus decreased and then steadily increased. Thus for example for Timgalen at 21/16°*C %N of grains fell from approximately 3% to 1.8% from day zero to day 10, then it steadily increased for the floret a and c grains from the central spikelets (Fig. 5.6).

Between the cultivars no clear cut relation could be discerned in relation to nitrogen content of the grain (mgN/grain) and the number of grains set per ear (Fig. 5.7). Nevertheless it may be significant that those cultivars which produce a high nitrogen grain tend to set fewer grains. Thus for example in the floret a grains of the central spikelets, Triple Dirk had the highest nitrogen content and set the fewest grains per ear, while WW15 had the lowest nitrogen content it its grains and it set the most grains per ear.

At higher temperatures percent nitrogen and percent phosphorus of grains increased in all cultivars (Fig. 5.6, Table 5.1). At maturity percent nitrogen differed between the four cultivars, generally at all temperatures it was highest in Timgalen and least in WW15 (Fig. 5.8). However between the cultivars, at maturity, no consistent relationship could be observed between final yield per grain and percent nitrogen of grains. Nevertheless at each temperature nitrogen content (mgN/grain) was invariably greater for those cultivars which



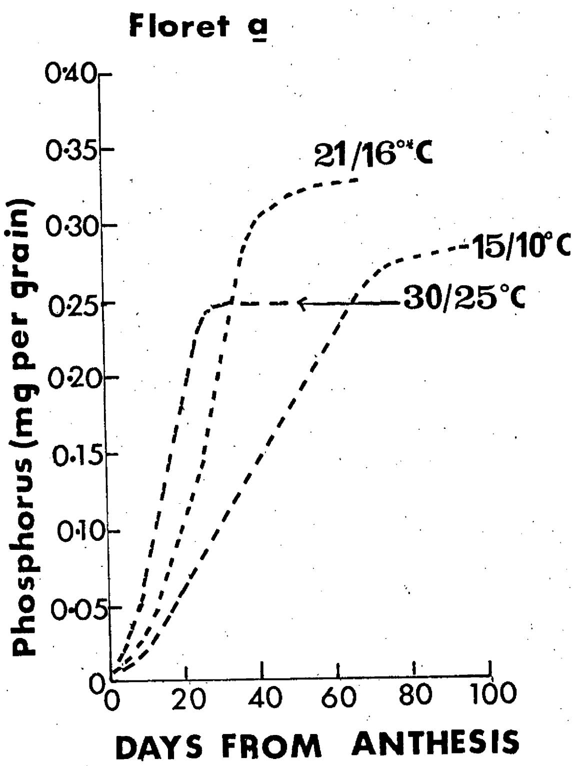
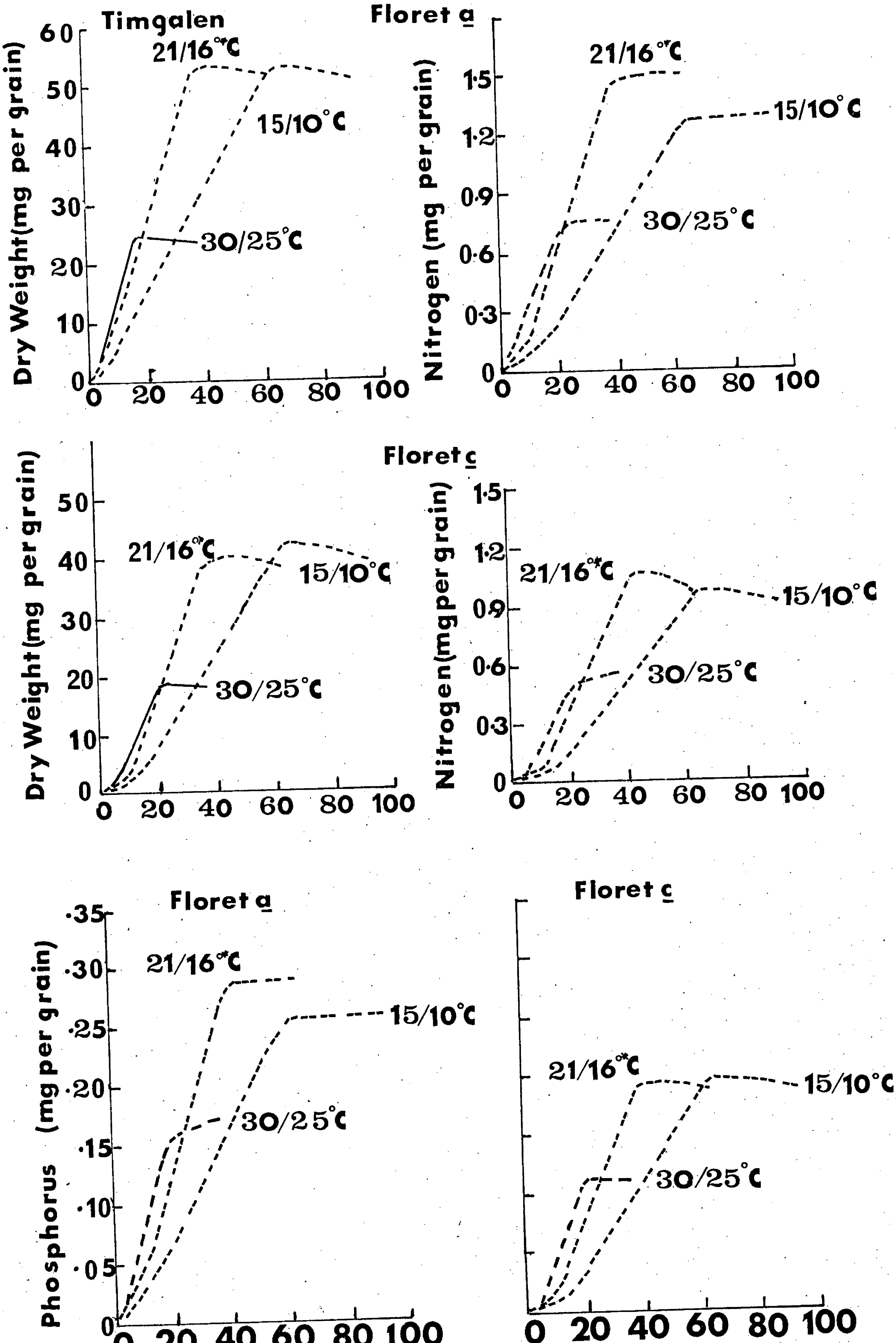
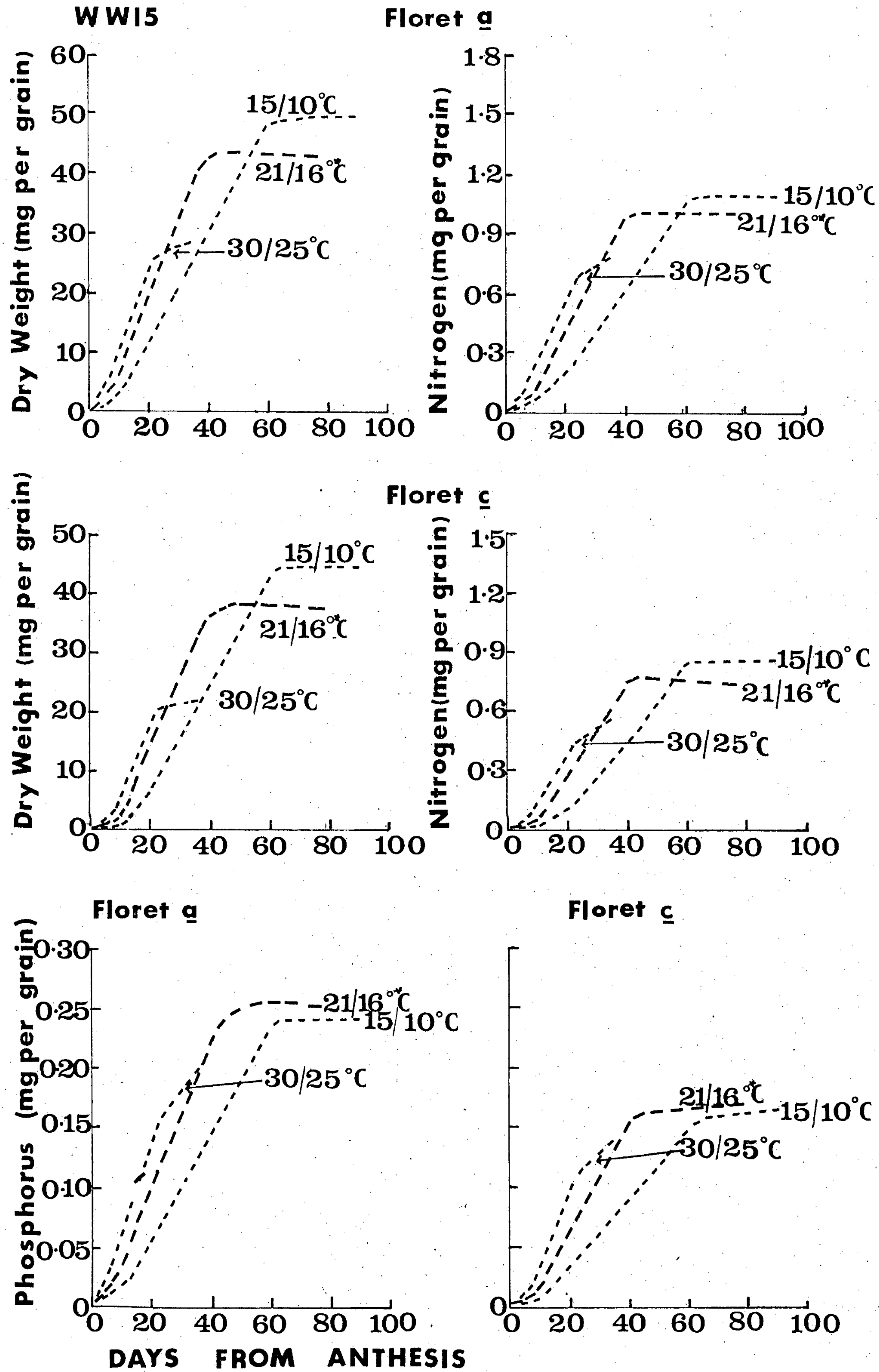
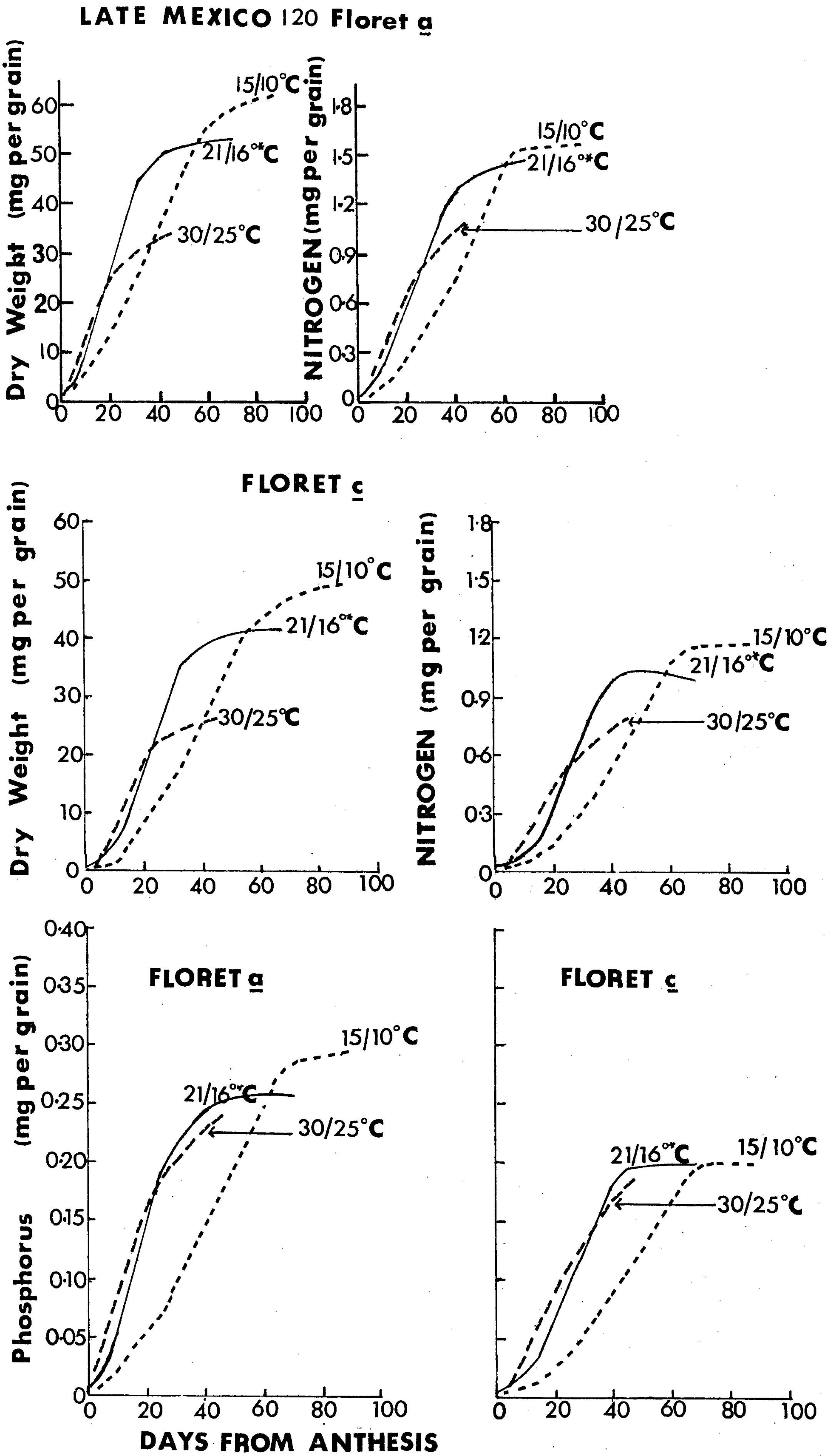


Figure 5.5 Experiment II. The accumulation of dry weight, nitrogen and phosphorus in the floret a and c grains from the central spikelets in Triple Dirk, Timgalen, WW15 and Late Mexico 120 at 15/10°C 21/16°*C and 30/25°C. Since very few grains set in the floret c positions in Triple Dirk at 21/16°*C and 30/25°C phosphorus and nitrogen accumulations were not determined.



Timgalen
Floret a
Dry Weight (mg per grain)
Nitrogen (mg per grain)
21/16°C
15/10°C
30/25°C
0
10
20
30
40
50
60
0.3
0.6
0.9
1.2
1.5
20
40
60
80
100
Floret c
Dry Weight (mg per grain)
Nitrogen (mg per grain)
Floret a
Floret c
Phosphorus (mg per grain)
·05
·10
·15
·20
·25
·30
·35
DAYS FROM ANTHESIS


WW15
Floret a
Dry Weight (mg per grain)
Nitrogen (mg per grain)
15/10°C
21/16°C
30/25°C
Floret c
Floret a
Floret c
Phosphorus (mg per grain)
0·30
0·25
0·20
0·15
0·10
0·05
0
0 20 40 60 80 100
DAYS FROM ANTHESIS



LATE MEXICO 120 Floret a
Dry Weight (mg per grain)
NITROGEN (mg per grain)
15/10°C
21/16°*C
30/25°C
FLORET c
Dry Weight (mg per grain)
NITROGEN (mg per grain)
15/10°C
21/16°*C
30/25°C
Phosphorus (mg per grain)
FLORET a
FLORET c
15/10°C
21/16°*C
30/25°C
DAYS FROM ANTHESIS

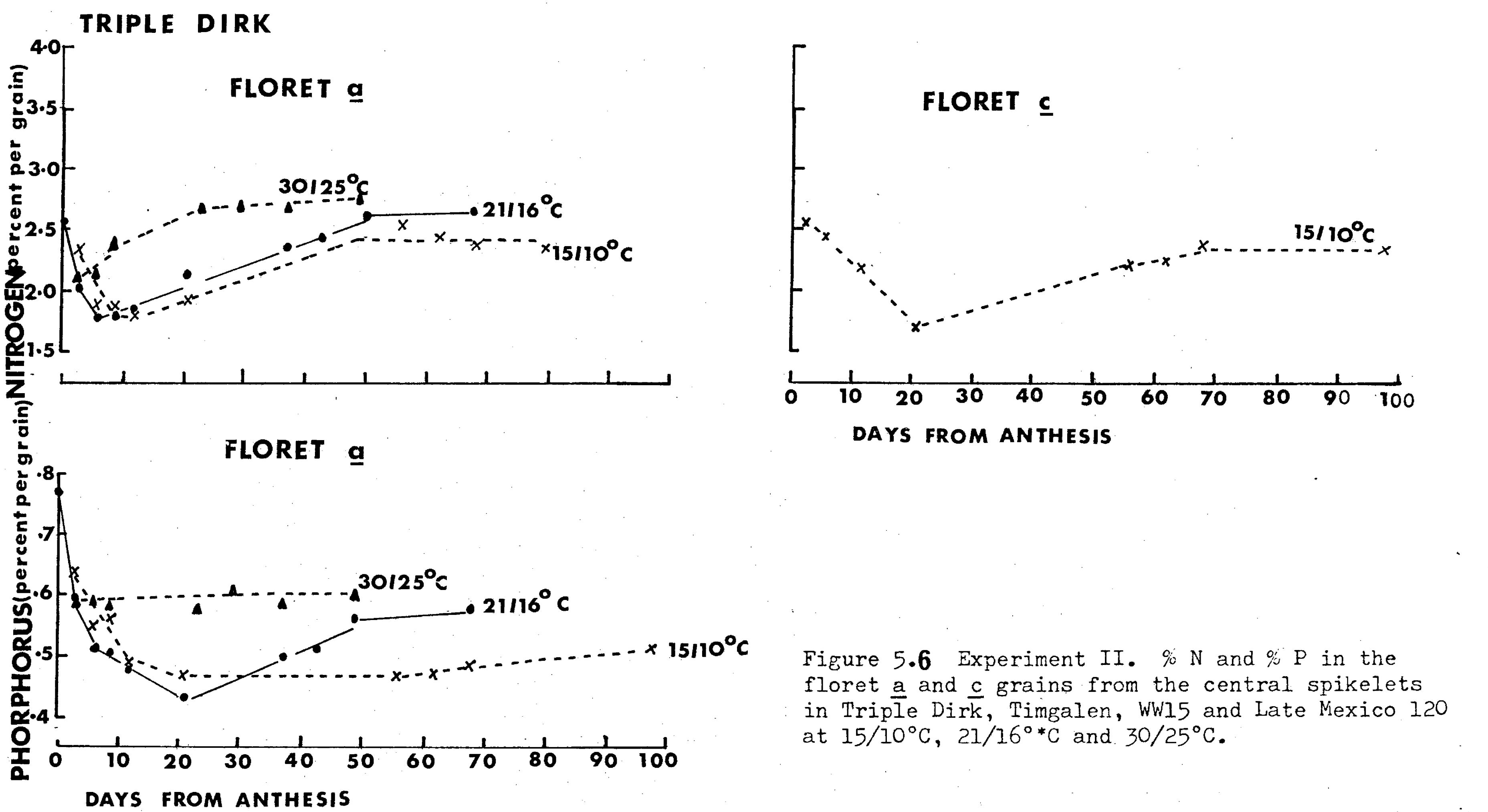
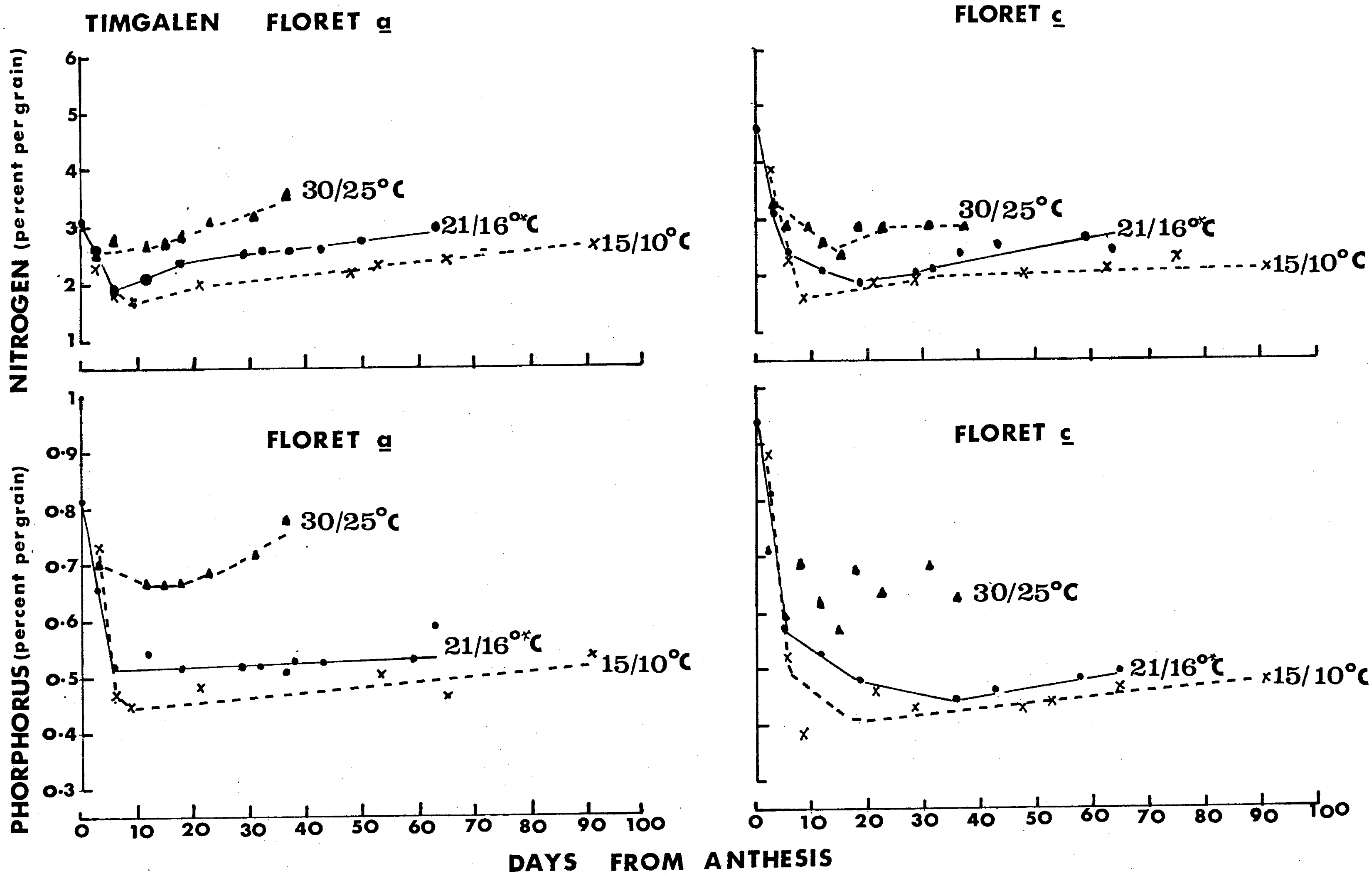
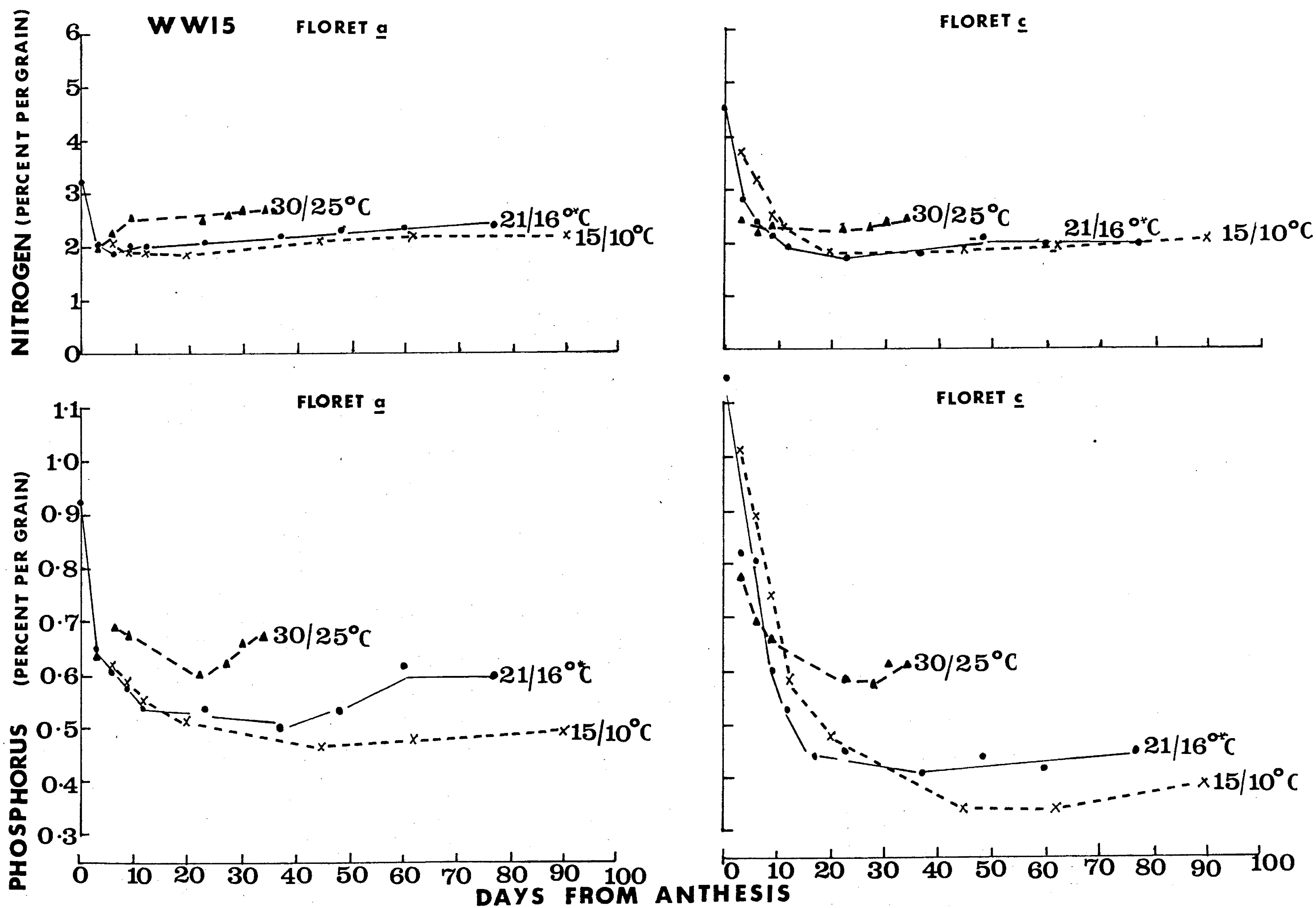
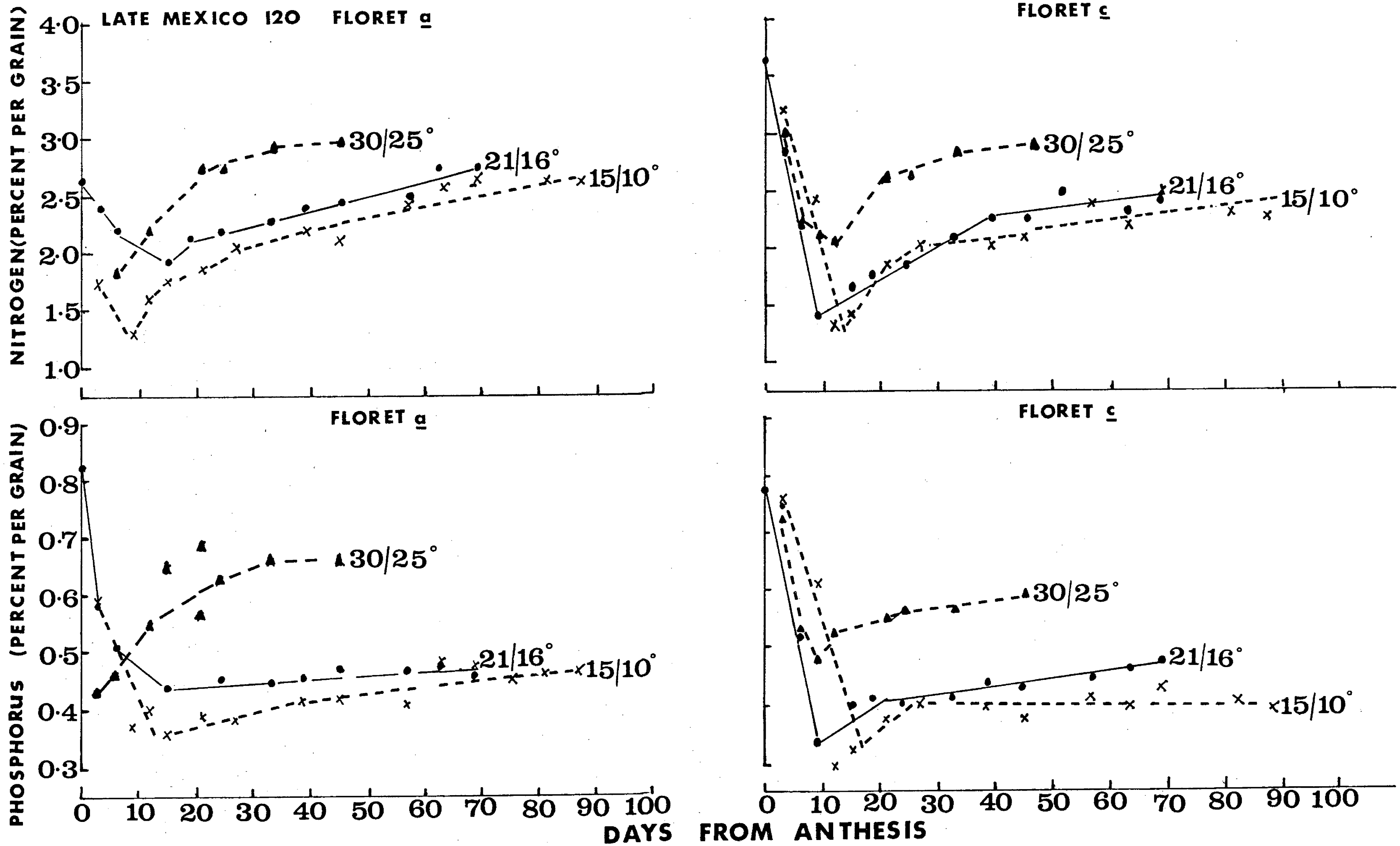


Figure 5.6 Experiment II. % N and % P in the floret a and c grains from the central spikelets in Triple Dirk, Timgalen, WW15 and Late Mexico 120 at 15/10°C, 21/16°*C and 30/25°C.



TIMGALEN FLORET a
FLORET c
NITROGEN (percent per grain)
PHORPHORUS (percent per grain)
FLORET a
FLORET c
30/25°C
21/16°C
15/10°C
DAYS FROM ANTHESIS


WW15
FLORET a
FLORET c
NITROGEN (PERCENT PER GRAIN)
PHOSPHORUS (PERCENT PER GRAIN)
30/25°C
21/16°*C
15/10°C
DAYS FROM ANTHESIS


LATE MEXICO 120
FLORET a
FLORET c
NITROGEN (PERCENT PER GRAIN)
PHOSPHORUS (PERCENT PER GRAIN)
30/25°
21/16°
15/10°
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0
10
20
30
40
50
60
70
80
90
100
DAYS FROM ANTHESIS

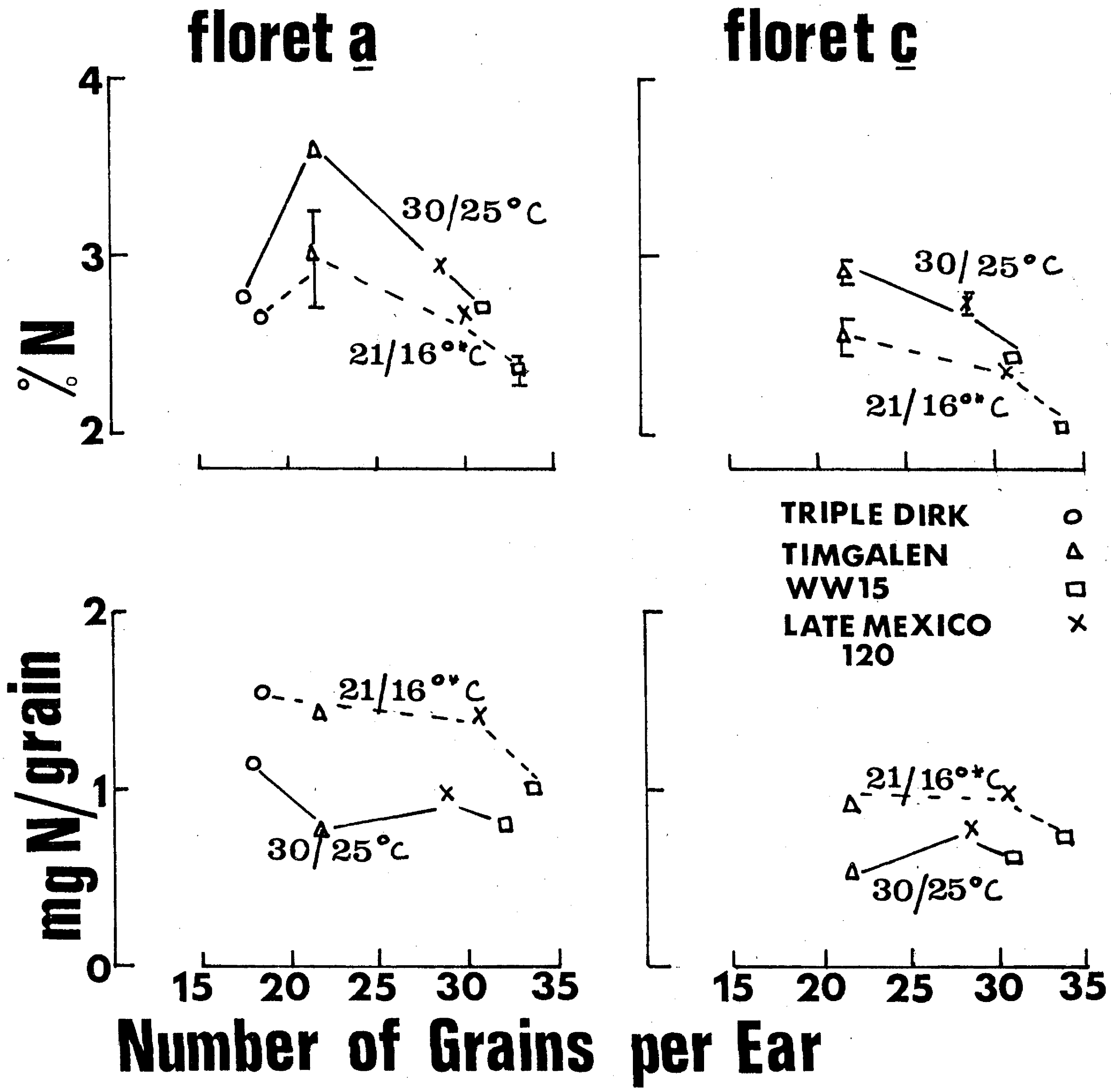


Figure 5.7 Experiment II. For mature a and c floret grains from the central spikelets (i) % N versus the number of grains per ear for each cultivar at 21/16°*C and 30/25°C and (ii) mgN/grain versus the number of grains per ear for each cultivar at 21/16°*C and 30/25°C. The error bar denotes 2 x S.D. Error bars have not been included when they fell within the length of the symbol used. (Table 5.1 for errors)

Temp. / floret position (Cultivar; %N, mgN/grain)		Triple Dirk: Percent nitrogen (± S.D.)	Triple Dirk: mg nitrogen per grain (± S.D.)	Timgalen: Percent nitrogen (± S.D.)	Timgalen: mg nitrogen per grain (± S.D.)	WW 15: Percent nitrogen (± S.D.)	WW 15: mg nitrogen per grain (± S.D.)	Late Mexico 120: Percent nitrogen (± S.D.)	Late Mexico 120: mg nitrogen per grain (± S.D.)
15/10°C	a	2.45±0.0	1.37±0.04	2.63±0.14	1.32±0.12	2.17±0.03	1.09±0.03	2.63±0.08	1.63±0.03
21/16°*C	a	2.68±0.03	1.54±0.01	3.05±0.28	1.46±0.00	2.37±0.06	1.02±0.05	2.71±0.03	1.47±0.01
30/25°C	a	2.78±0.02	1.16±0.01	3.60±0.02	0.77±0.01	2.69±0.02	0.81±0.03	2.97±0.01	1.06±0.04
15/10°C	c	2.37±0.07	0.92±0.05	2.18±0.16	0.94±0.04	2.01±0.08	0.88±0.06	2.28±0.02	1.18±0.06
21/16°*C	c			2.53±0.10	0.95±0.02	2.04±0.01	0.72±0.05	2.41±0.07	1.02±0.02
30/25°C	c			2.90±0.05	0.51±0.03	2.42±0.01	0.63±0.00	2.79±0.05	0.81±0.02
Temp. / floret position (Cultivar; %P, mgP/grain)		**Percent phosphorous (± S.D.)**	**mg phos. per grain (± S.D.)**	**Percent phosphorous (± S.D.)**	**mg phos. per grain (± S.D.**	**Percent phosphorous (± S.D.)**	**mg phos per grain (± S.D.)**	**Percent phosphorous (± S.D.)**	**mg. phos. per grain (± S.D.)**
15/10°C	a	0.51±0.01	0.29±0.00	0.54±0.02	0.27±0.02	0.49±0.02	0.24±0.02	0.45±0.02	0.28±0.01
21/16°*C	a	0.58±0.02	0.33±0.02	0.61±0.04	0.32±0.02	0.59±0.00	0.25±0.00	0.46±0.03	0.25±0.01
30/25°C	a	0.60±0.00	0.24±0.00	0.80±0.01	0.20±0.00	0.67±0.00	0.20±0.01	0.66±0.04	0.24±0.02
15/10°C	c			0.47±0.01	0.18±0.01	0.39±0.02	0.17±0.01	0.39±0.00	0.20±0.01
21/16°*C	c			0.50±0.01	0.19±0.00	0.46±0.00	0.17±0.00	0.47±0.00	0.20±0.02
30/25°C	d			0.62±0.00	0.11±0.01	0.60±0.04	0.16±0.01	0.69±0.02	0.20±0.00

Table 5.1 For mature a and c floret grains from the central spikelets, % N, % P, mgN/grain, mgP/grain are presented for the 15/10°C, 21/16°*C and 30/25°C temperature treatments experiment II.

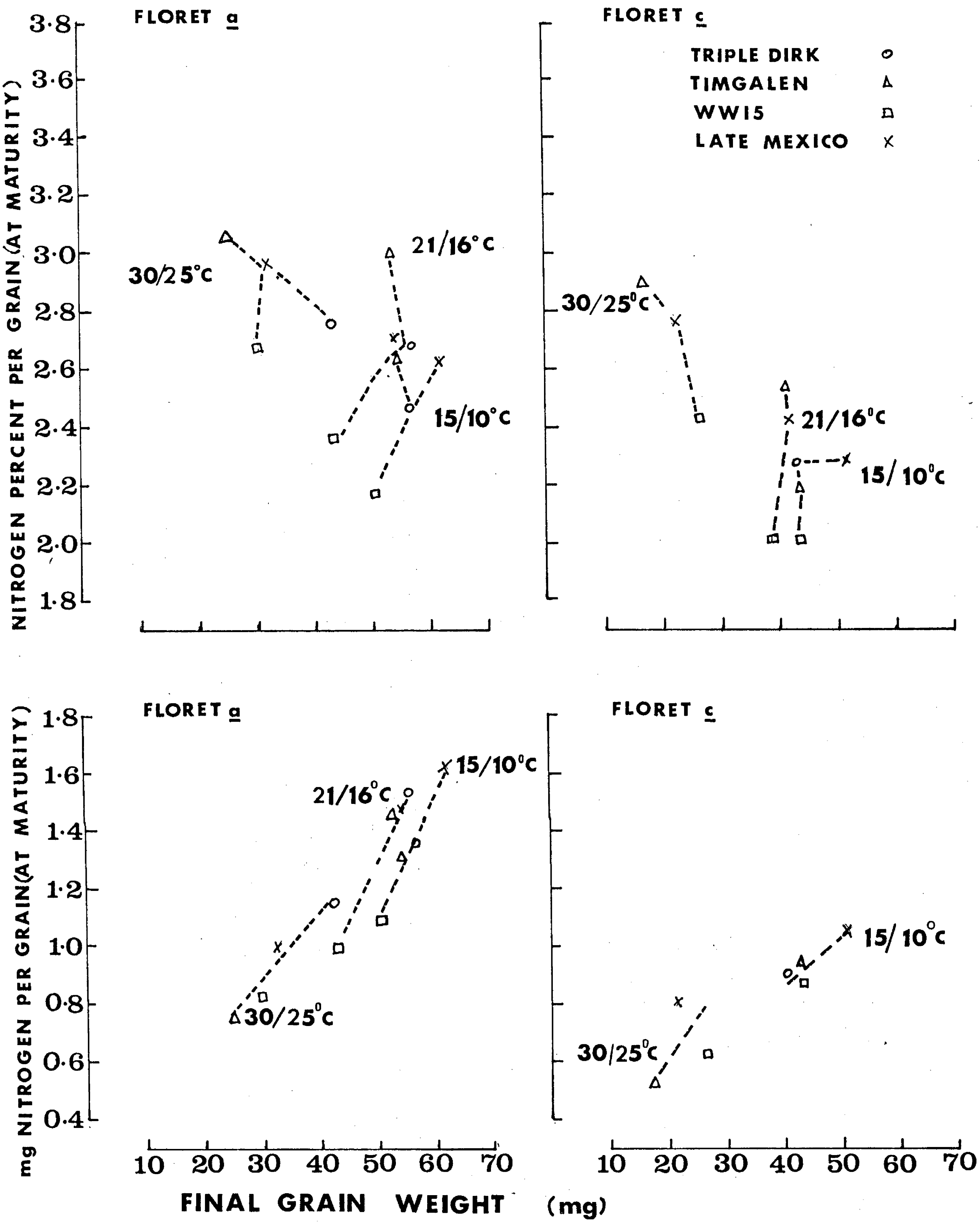


Figure 5.8 Experiment II. For mature a and c floret grains from the central spikelets (i) % N versus final grain weight at 15/10°C, 21/16°*C and 30/25°C in Triple Dirk, Timgalen, WW15 and Late Mexico 120 and (ii) mgN/grain versus final grain weight at 15/10°C, 21/16°*C and 30/25°C in each cultivar.

produced the heavest grain at maturity (Fig. 5.8).

For each cultivar the pattern of both %P and mgP/grain closely followed those of nitrogen, the major difference being that phosphorus was always present in very much smaller quantities (Figs. 5.5, 5.6, Table 5.1).

An understanding of the processes which terminate grain growth would undoubtedly aid investigations aimed at increasing yield. The results here suggest that, especially under lower temperatures, grain filling was not source limited. This suggests that future investigations of processes transporting carbohydrate to the grains merits further research. No relation could be discerned between nitrogen and phosphorus contents and duration of grain growth. Extensive studies of hormonal changes throughout the plant during grain filling are needed in order to determine which processes terminate grain growth.

CHAPTER 6

DISCUSSION

6.1 GRAIN SET

The number of potentially fertile florets in an ear are determined before anthesis (reviewed (Au 75), (Ev 74)) but during fertilization and the early stages of grain development inherent and environmental factors intervene and many florets which reach anthesis fail to set grains. Even in the most favourable conditions some 13 to 28% of florets which anthese fail to set grain. Furthermore under high temperature or low light intensities usually still fewer grains are set due to additional failures in the outer florets, especially in the upper spikelets. Therefore two queries arise:-

(i) Why under near-optimal growing conditions is it that florets which reach anthesis fail to set grain even though some previous studies indicate that several wheat cultivars have the photosynthetic capacity to fill more grains than are set in the ear ((As 68), (Br 72), (Ev 70))?

(ii) By what mechanisms does high temperature or low light intensity further reduce grain set?

Although high temperature at anthesis has been reported to cause sterility (Ho 59), it seems unlikely that failure of the outer floret grains at a high temperature in the present study was due to this cause as basal florets in the lower spikelets anthesed at approximately the same time and nevertheless set grains.

Factors influencing grain set have been intensively examined, but as yet an understanding of the controlling mechanism(s) is still inadequate ((La 76), (Ev 72), (Gi 73), (Ra 72), (Wa 70)). Three possible mechanisms have been proposed:- (i) a specific inhibitor ((Ra 70), (Ev 72)) (ii) that outer floret grains fail because they are unable to compete for metabolites such as photosynthate ((Ra 70),(Ra 72)) or nitrogen (Br 72) or perhaps (iii) that the failures are due to local (within the spikelet) limitations in the transport of assimilates.

(i) Previous investigations have indicated, at least in some cultivars, including Triple Dirk, that the setting of outer floret and distal spikelet grains may be inhibited by the presence of the basal ones (even when their fertilization is delayed (Ev 72)) as the former may be induced to set grain by the removal of the latter (Ra 70). Although this was observed for Triple Dirk, partial sterilization of the central spikelets in Late Mexico 120 (which set more grains per spikelet) caused no compensatory increase in grain set, perhaps indicating that grain setting in the outer florets was not in this cultivar inhibited by grains setting in the lower ones. This they suggested (Ra 70) may have been due to the apparantely slower initial development (lag) of grains within the ears of Late Mexico 120, but from this study no clear relationship between initial grain growth (lag) and the number of grains per ear or the number of grains per spikelet was observed except under winter irradiance combined with low temperature: those cultivars which set more grains per ear; Late Mexico 120 and WW15 generally had a longer lag than those cultivars which set less grains per ear eg. Triple Dirk.

Alternatively, it may be that the extent of this inhibition (ie., specific inhibitor "regulated" by the basal grains) is less effective in those cultivars which set more grains per spikelet because that cultivar (Triple Dirk) which set fewest grains per spikelet under optimum conditions (ie., has a more effective specific inhibitor mechanism) was generally more capable in adjusting its grain number to adverse conditions at anthesis, whereas those cultivars which set more grains per spikelet (ie., have a less effective specific inhibitor mechanism) under optimum conditions were generally less capable of adjusting their grain number to adverse environmental conditions (eg. Sonora, Late Mexico 120 and WW15). This aspect is by no means clear but it warrants future investigation.

(ii) The possibility that competition for assimilates within spikelets may be occuring is suggested by the fact that when assimilate availability was reduced by lowering the light intensity at anthesis, additional grains failed to set in the outer florets whereas the basal grains were unaffected. However in the field one would not expect light intensities to be so low (as in Experiment III) as to have this effect. At least, under near-optimal growing conditions it seems unlikely that failure of grain set is due to lack of an overall supply of photosynthetic assimilates as at this stage "excess" carbohydrate is being stored in the stems (Ra 71).

There is some support for the suggestion that a shortage of nitrogen may be a cause of the failure of grain set in the outer florets (Br 72) in that those cultivars which produced a high nitrogen grain tend to set fewer grains per ear (Fig. 5.8). However an alternative explanation would be that with fewer grains set, more nitrogen could be available for distribution to each.

(iii) The partitioning of assimilates between the various sites within the spikelet have for some time been regarded as having a controlling influence on grain formation. However if the cultivars examined in this study have similar vascular patterns to that of cv. Aotea (Ha 72) it appears unlikely that the vascular system within the spikelet is the main limitation to the setting of outer floret grains inasmuch that even under adverse environmental conditions some cultivars set up to four grains per spikelet (eg. Timgalen) even though the outer floret grains are connected by sub-vascular elements whereas in another cultivar (ie., Triple Dirk) florets which are directly linked with the main supply of the spikelet failed to set grains.

Whatever mechanism(s) regulates grain set in responce to a stress environment at anthesis:-

(i) it appears to 'operate' during fertilization and the early stages of development, that is, grain set had adjusted to the environmental stress by at least 11 days after first anthesis.

(ii) the extent grain adjustment varied between the cultivars. This in turn appears to influence the subsequent growth rate per grain, that is, cultivars which were less able to adjust their grain number to a stress condition at anthesis (and generally these were the cultivars which set more grains per spikelet under optimum conditions) generally showed a greater response than did that cultivar (Triple Dirk) which adapted more readily to a stress condition by adjusting its grain number. Therefore adjustment of grain number according to conditions at anthesis may mean that environmental conditions have far less effect on growth rate per grain and in this way grain size may be buffered against extreme variation.

It is emphasized that under more favourable growing conditions, for the several wheat cultivars examined, no consistant relationship between growth per grain and grain number per ear (or the mean number of grains per spikelet) was observed. In fact Rawson and Evans (Ra 71) observed that the cultivar with the most grains per ear also had the highest grain growth rate.

6.2 RATE AND DURATION OF GRAIN FILLING

Temperature affects both the rate and duration of grain filling. For temperatures up to 21/16°*C a decrease in the duration was largely compensated by an increase in grain growth rate but for temperatures above this value the severe reduction in duration was not compensated by an increase in grain growth rate and final grain weight was consequently reduced (4.2.1).

Examination of the effect of temperature (during the linear phase of growth, Wardlaw unpublished) on CO_2 exchange by the ear led Wardlaw to suggest that increased respiratory losses at 30/25°C could account for at least part of the failure to observe a higher rate of dry matter accumulation in the ear, than at the lower temperatures. Spiertz (Sp 74) has also demonstrated that respiratory losses are greater at high than low temperatures. Also at high temperatures there may be a limit on some synthetic process within the grain, that is, an inability to increase the net rate of starch synthesis.

Assimilate movement* in wheat appears to be influenced by temperature effects on the source (flag leaf blade) and sink (ear) rather than on the transport system (stem) as translocation through the stem was found to be insensitive to temperature in the range 1°C to 40°C (Wa 74a). Furthermore, examination of the movement of ^{14}C-assimilates from the flag leaf to the ear indicate that the demand by the ear for assimilates is significantly higher at 30°C than 21°C (Wardlaw unpublished). This perhaps suggests that the faster grain growth rates at a high temperature may be due to a greater demand for assimilates by the grains.

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* the sources of carbohydrate to the grain have been discussed by Austin and Jones (Au 75) and Evans et al (Ev 74)

At the higher temperatures, grain growth rate does not appear to be limited by assimilate supply inasmuch that grain growth proceeds at a linear rate for most of its duration. In addition to current ear and flag leaf photosynthesis, the exposed green parts of the stem are capable of photosynthesis and this may be of some value under stress conditions (Wa 71). Furthermore the amount of grain carbon derived from the stem increases under stress conditions. (Ra 71).

However at a high temperature the faster grain growth rate is accompanied by a faster rate of senescence of the green plant tissue. It has been suggested by Bremner (Br 72) that leaf duration may be related to "movement of nitrogen" from the leaves "into the grains". Since %N in the grains was higher and leaf duration was shorter at the higher than lower temperatures this study does support the above suggestion.

It is not clear from this study or previous investigations (eg Sp 74) whether grain growth ceases at higher temperatures because of a lack of assimilates (due to more rapid senescence) or whether 'demand' by the grains for assimilates ceases earlier at the higher temperatures.

Clearly further experimentation, of the integrated plant responses, including the root system, to high temperature is required in order to clarify the above speculations. In particular it would be of special interest to examine growth rates (as influenced by environmental conditions)in relation to senescence.

At least at the lower temperatures, from the study here, it appears that grain growth rates were not limited by assimiliates inasmuch that when grain growth had ceased the ear and flag leaf were still green. This supports the deductions of Evans, Rawson and Wardlaw ((Ev 70), (Ra 71) (Wa 71)): that is, they found that under well-defined conditions grain growth rates were not limited by photosynthetic rate, as carbon balance sheets revealed that more assimilate was available for grain filling than was used. However caution is needed when generalizing to field conditions (Bi 75).

Asana and Williams (As 65) found no significant effect of night temperature on final grain weight. The results in this study suggest that a high night temperature does reduce final grain weight, however generally a high day temperature appears to have a more adverse effect on final grain weight than a high night temperature.

Effects of environmental factors on photosynthesis, photorespiration and dark respiration are beyond the scope of this study, but reference to this have been cited by Milthorpe and Moorby ((Mi 74), also (Kr 66), (Ho 69)). However one aspect may be relevant to the comparison of the effect of high day and high night temperatures on the grain growth rate, that is, as growth per grain was generally faster at the high day than high night temperature this may suggest that reassimilation of CO_2 by the glumes during the light period may confer some advantage to grain growth rate as Bremer and Rawson (Br 72a) have demonstrated that over the greater part of grain filling, the lemmas, which werephotosynthetically the most active of the glumes, accounted for some 15% of whole-plant photosynthesis.

Under the experimental conditions here, assimilate supply as influenced by light intensity was a major determinate of the rate but not the duration of grain filling. Also, the magnitude of the effect depended upon the extent to which grain set had been modified at anthesis.

The observation by Welbank Witts and Thorne (We 68) of a marked reduction in the duration of grain filling with increase in incident radiation for crops in the field is perhaps probably better explained as a temperature rather than a radiation response as there is likely to be a close association between radiation and temperature. Nevertheless it is difficult to generalize from single culm pot plants to field conditions, as in the crop situation, light may be more important due to mutual shading.

Marcellos and Single (Ma 72) examined the relation between days from anthesis to maturity and mean temperature in the field. Similarly Spiertz (Sp 74) examined the effect of temperature under phytotron conditions on the duration of grain filling. Overall their results agree with the results in this study which tends to confirm the overriding influence of temperature on this important parameter of yield, neither cultivar nor incident radiation having much effect.

The absence of any clear difference among the cultivars, examined in this study, in their duration of grain growth is striking. However differences between cultivars have been observed: Asana and Joseph (As 64) found that the grains of 'P6C281' increased at the same rate as those of 'NP720' but they continued to grow for a longer period and thereby formed larger grains. Nass and Reiser (Na 75) also found that cultivars varied in the duration of grain filling that is the duration varied from 38 to 46 days (standard error .32), however they found that "while the rate of filling appeared to be an important factor in determining the final weight, the length of the grain filling period (anthesis to maturity) by itself, was not.

Cultivar, temperature and light intensity all influenced the rate of grain growth per ear. This was found to be dependent on the number of grains per ear and correlated with the rate of flag leaf photosynthesis as influenced by light intensity. In turn final yield per ear at 21/16°*C was closely related to the rate of grain growth per ear, overall a similiar response to that noted by Nass and Reiser (Na75) above.

6.3 CULTIVAR

Grain growth rates not only varied among the cultivars but also in the extent they were influenced by treatments. This suggests that inherent differences exist among the cultivars, furthermore these differences were more apparent under stress conditions.

Adapting to a stress condition may not only imply the aborting of outer floret grains. Thus in Timgalen under summer irradiance combined with high temperature, ear grain number was not altered but the pattern of grain set was modified: grains which failed to set in "prime" central spikelet positions were compensated by more grains setting in the lower spikelets where so many did not set at the lower temperatures (Fig. 3.2). This "spreading out" of grains may confer some advantage to grain growth rate under stress conditions inasmuch that both sterile and fertile glumes are photosynthetic (Br 72a).

Differences between cultivars in their grain growth rates may be due to a combination of factors such as: (a) stem reserves: remoblization of stem reserves may be of greater importance in grain filling in some cultivars than others, especially under stress conditions (see (Bi 75) (Na 75) (Ra 71)) (b) presence of awns: awn structures show considerable photosynthetic activity and many double the net photosynthesis of the ear (Ev 72a). (c) photosynthetic rate, duration and respiratory losses also appear to vary between the cultivars (Ra 71), (Ev 70a)) (d) root functions: "roots may also synthesize amino acids, and act as a source of growth substances such as cytokinins for the shoot, but the significance of their role in this respect is not clear" ((Ev 74) see also (Wa 76b)).

Although differences in grain growth rates were observed among the cultivars, these differences were much smaller than those in grain number and grain growth rate per ear was in most cases proportional to grain number. In turn at 21/16°*C growth per ear was correlated with final weight per ear and therefore for the environmental conditions and cultivars in this study grain number per ear was a dominant componant of yield.

6.4 FINAL GRAIN SIZE AS INFLUENCED BY ITS POSITION WITHIN AN EAR.

A characteristic of individual grains within an ear is their variation in size. The results from this study support those of Rawson and Evans (Ra 70) and Evans et al (Ev 72), that is, that final grain size bears no simple relation to time of anthesis as suggested by Bonnett (Bo 67).

That the final dry weight of an individual grain is influenced by its spikelet and floret position has been previously observed (Ra 70) and in most cases the results in this study are in agreement (Section 4.6). However the reason(s) for the differences in grain size is not yet established, for example, why do the basal grains from the central spikelets grow faster, have slightly longer durations of filling and are more favoured to receive flag leaf assimilates than basal grains in the upper spikelets? (Ra 70) Rawson and Evans have demonstrated that the vascular capacity does not appear to be limiting factor but they suggest that demand for assimilates by the upper spikelet grains was limiting (Ra 70).

A possible approach to examine intrinsic differences between the grains may be (i) to determine whether the potential size of a grain is predetermined by events occurring before anthesis.

For example, is the potential size of a grain related to the growth of the floret and the growth of the ovary before anthesis: also (ii) to determine whether changes in growth substances* in the basal and outer floret grains from the commencement of ovary formation to maturity could provide the basis of a control of development of one grain by another.

Wardlaw has demonstrated that auxin production by the grains is not responsible for the control of assimilate translocation through the peduncle. (Wa 76).

In all cultivars reduction in the supply of assimilates under low light intensity affected the distribution of assimilate among the various grains within the central spikelets and final grain weight was more adversely affected when progressing from the basal to outer florets and this was largely because growth per grain was more adversely affected in the later. (Section 4.6.4) These results are similiar to those observed by Bremner (Br 72). Thus it may be implied for environmental conditions where light is limiting higher yields may be obtained by increasing spikelet number rather than seed set per spikelet were it not for the fact that grain growth appears to be most severely reduced in the upper spikelets (see Br 72).

The results in relation to the effect of temperature (Experiment I) on assimilate distribution among the grains are inconclusive, as at the higher temperatures, in all but one cultivar (Timgalen) some grains failed to set in the outer florets. In Timgalen, the distribution of assimilates was influenced by temperature: this

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* Wheeler (We 72) has reported "As wheat grains grow there is a sequence of growth substances in them. First cytokinins may regulate division in the grains, then gibberellin, and finally auxin, may regulate the accumulation of photosynthate in them".

effect was more marked for grains within than between spikelets (Section 4.6.2). On the other hand, for Late Mexico 120 and Sonora (in Experiment IV), for grains from the central spikelets, the grains appeared to be affected uniformly by temperature. Clearly further experimentation is required on how temperature effects assimilation distribution among the grains, within as well as between the spikelets.

6.5 CONCLUSION

From the discussion it is apparent that during and after anthesis many factors, inherent and/or environmental interfere to restrict the attainment of potential yield. High temperature and especially low light intensity can modify grain set. In the period which follows, ultimate grain size is reduced by high temperature largely due to a decrease in grain filling whereas under low light intensity it is reduced largely due to a decrease in grain growth. What factors terminate grain growth or why it is so much shorter at high temperatures?

Increased recognition of the structural features (that is, from stem to ear, within the ear and within the grain) and the role and interactions of biochemical features (during grain set, filling and at maturation) in the wheat plant are required as at present these are not well understood and limit our understanding of yield development in wheat from anthesis to maturity.

APPENDIX A

GRAIN GROWTH CURVES

Data illustrating the time course of growth of grains have already been presented in Section 2.6. Departures from the pattern of grain growth illustrated in Figure 2.1 were observed for the following cases: at the lower temperatures sometimes linear growth ceased abruptly on reaching final grain weight, for example WW15 at 15/10°C, (Fig. A1) or some loss of dry weight occurred following the rapid cessation of linear growth, for example Timgalen at 15/10°C (Fig. A.1). At the higher temperatures, on the other hand, there was often a more gradual approach to final grain weight. WW15 at 30/25°C in Figure A.1 gives some indication of this, but it was more pronounced in cv. Late Mexico 120.

At lower light intensities, also, there tends to be a more gradual approach to final grain weight (Fig. A.2). In fact, at the lowest light intensity used in experiment III (8070 lux), the grains in the third and fourth florets of central spikelets of cv Sonora maintained a "steady" growth rate until about 16-20 days after first anthesis, when cell division ceases in the endosperm (Wa 70). Thereafter the upper grains approached their final weight at a slower, "erratic" but steady rate (Fig. A.2). Such a course of growth was found in upper grains under adverse environmental conditions in cultivars setting many grains per spikelet: it was not found, for example, in the outer grains of Triple Dirk at the lowest light intensity in experiment III.

Only rarely, therefore, was there any difficulty in estimating the rate and duration of grain growth by the method described in Section 2.6.

Figure A.1 Experiment II. Increases in dry weight of the floret a grains from the central spikelets at 15/10°C in WW15 and Timgalen and at 30/25°C in WW15 and Late Mexico 120.

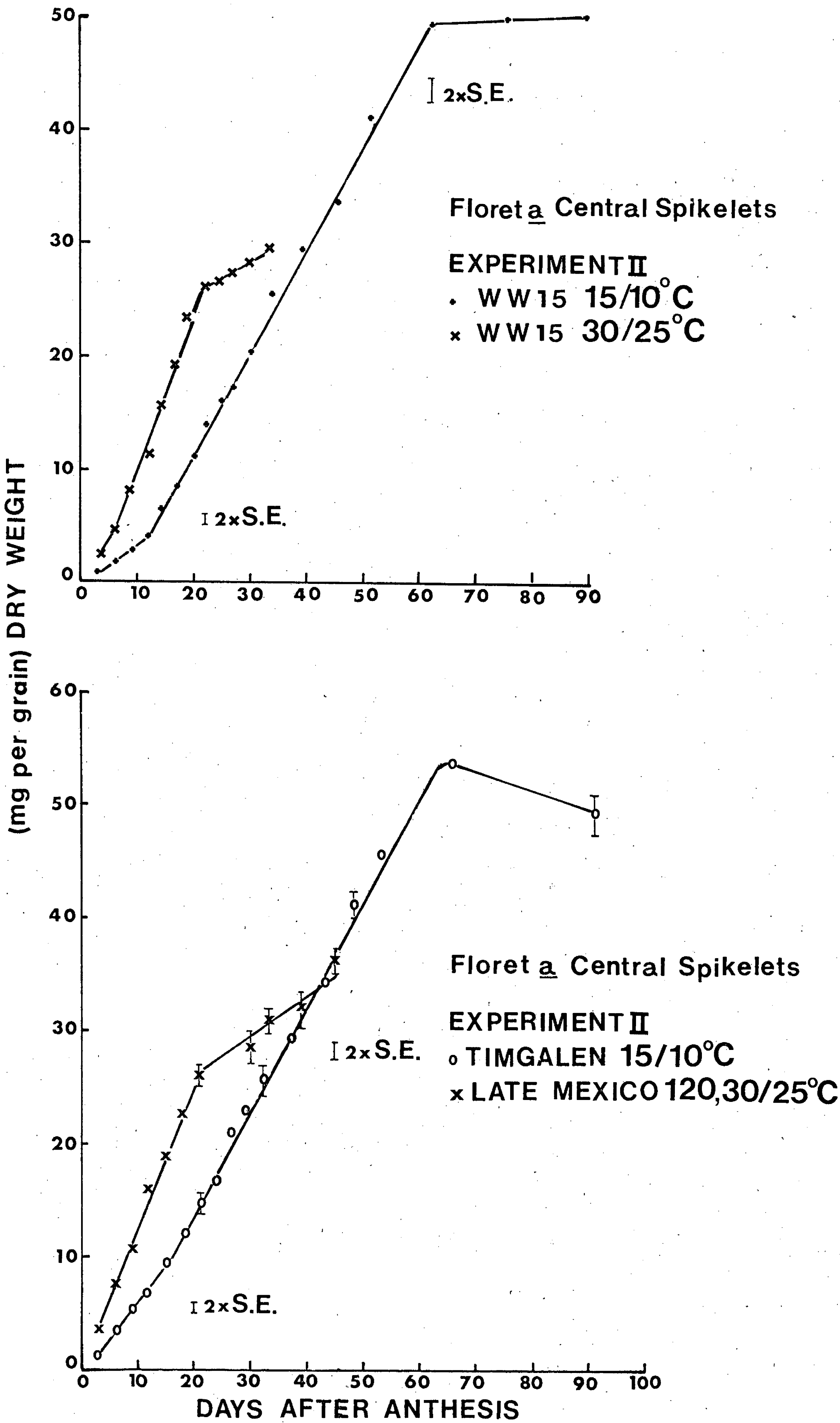
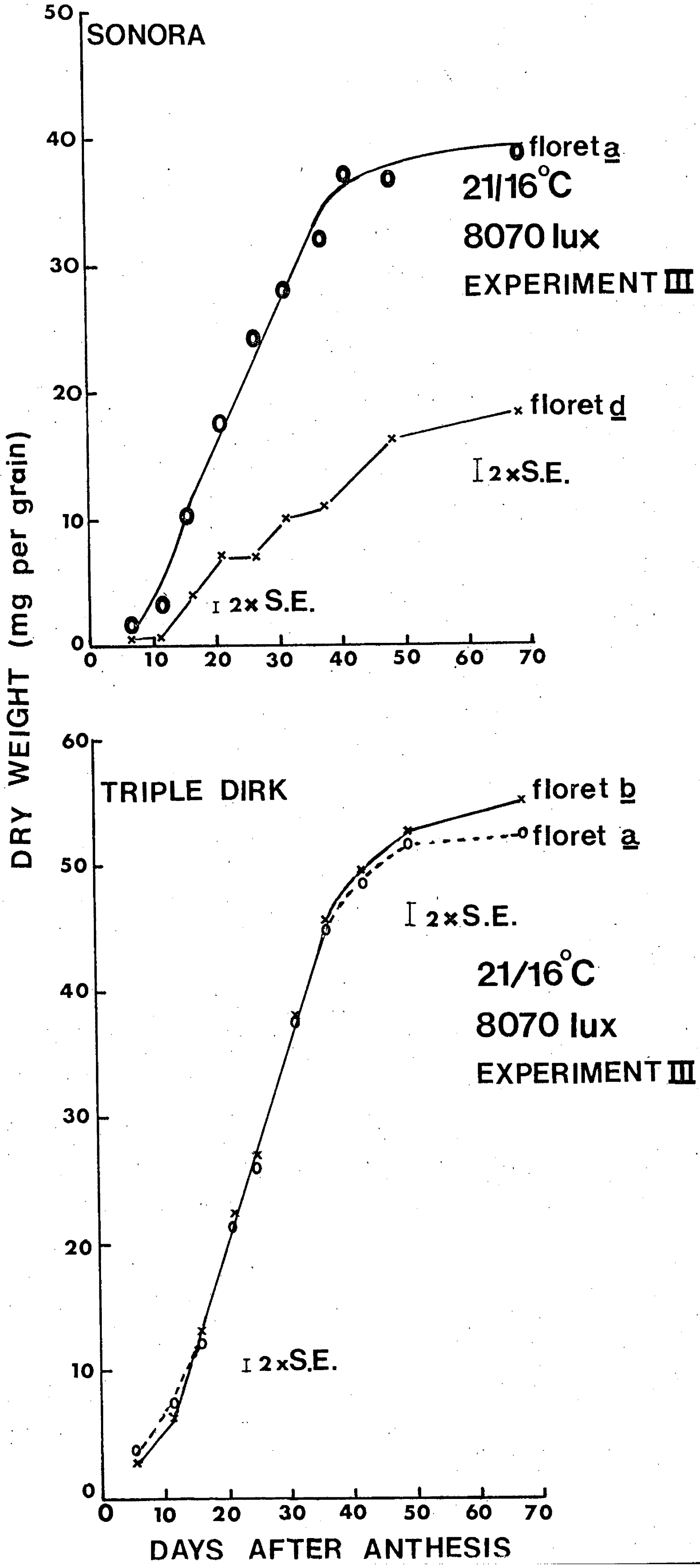


Figure A.2 Experiment III. At the lowest light intensity of 8070 lux increases in the dry weight of (i) a grains from the central spikelets in Triple Dirk and Sonora and (ii) the outer floret grains from the central spikelets being the d and b grains respectively in Sonora and Triple Dirk.



Appendix B

INITIAL LAG MEASUREMENTS EXPERIMENTS I - IV

EXPERIMENT I INITIAL LAG (DAYS)

Floret Position / Cultivar, Spikelet Position, Temperature		Floret a	Floret b	Floret c	Floret d	Of Ears
Triple Dirk						
18/13°	Lower	4.4	5.4	9.5		5.0
	Central	4.3	5.0	5.0		
	Upper	3.7	5.4			
21/16°*C	Lower	2.4	3.4	5.4		4.7
	Central	3.1	5.4	2.4		
	Upper	3.1	4.1			
30/25°C	Lower	1.7	2.0			2.0
	Central	1.4	1.7			
	Upper	1.4	1.2			
Timgalen						
18/13°C	Lower	4.4	6.1	4.7		6.8
	Central	4.0	4.1	5.7	7.7	
	Upper	3.4	5.1	5.1		
21/16°*C	Lower	5.4	5.8	5.1		4.3
	Central	3.0	3.3	4.7	5.0	
	Upper	3.1	2.7	3.7		
30/25°C	Lower	3.7	4.1	3.1		3.1
	Central	2.0	3.0	2.0		
	Upper	1.7	1.7	2.0		
WW15						
18/13°C	Lower	4.5	8.0	10.0		6.0
	Central	3.2	4.2	6.0	6.5	
	Upper	3.0	4.0	4.3		
21/16°*C	Lower	5.2	5.0	7.0		5.0
	Central	3.0	4.2	4.8	6.2	
	Upper	3.0	3.8	4.2		
30/25°C	Lower	1.2	2.2	3.0		1.0
	Central	1.0	1.3	3.0		
	Upper	1.2	2.0	4.0		

EXPERIMENT I (cont.)

Floret Position / Cultivar, Spikelet Position, Temperature	Floret a	Floret b	Floret c	Floret d	Of Ears
Late Mexico 120					
21/16°*C Lower	4.1	6.1	6.4		4.0
Central	4.3	4.7	6.3	6.8	
Upper	2.7	2.7	2.7		
30/25°C Lower	2.4	3.3	2.4		3.0
Central	2.0	2.7	2.3	2.0	
Upper	2.7	3.3	3.3		

EXPERIMENT II

Floret Position / Cultivar, Spikelet Position, Temperature	Floret a	Floret b	Floret c	Of Ears
Triple Dirk				
15/10°C Central	4.0	5.9	7.9	4.0
21/16°*C Central	3.4	4.7	6.1	3.7
30/25°C Central	2.4	3.4		2.7
Timgalen				
15/10°C Central	4.7	7.1	8.7	8.6
21/16°*C Central	3.0	5.8	6.4	4.0
30/25°C Central	1.4	1.4	2.4	2.0
WW15				
15/10°C Central	7.9	9.9	10.7	11.5
21/16°*C Central	3.4	4.7	6.1	6.0
30/25°C Central	2.4	3.0	3.0	2.8
Late Mexico 120				
15/10°C Central	6.3	9.1	10.7	10.5
21/16°*C Central	3.0	5.8	6.4	5.8
30/25°C Central	1.7	1.4	3.1	3.8

EXPERIMENT III

Floret Position / Cultivar, Spikelet Position, Light Intensity	Floret a	Floret b	Floret c	Floret d	Of Ears
Triple Dirk					
8070 lux Central	5.2	6.8			7.0
16140 lux Central	6.0	7.0			7.0
34432 lux Central	7.0	8.0	8.0		7.0
48420 lux Central	7.0	7.5	9.0		7.0
21/16°*C Central	6.2	7.0	9.3		7.0
Sonora					
8070 lux Central	4.5	7.0	9.0	12.0	6.0
16140 lux Central	5.3	6.5	8.0	12.0	6.0
34432 lux Central	6.5	7.5	8.0	9.0	7.5
48420 lux Central	7.0	7.0	11.0	12.0	8.0
21/16°*C Central	7.5	9.0	11.0	12.5	9.0

EXPERIMENT IV

Floret Position / Cultivar, Spikelet Position, Temperature	Floret a	Floret b	Floret c	Of Ears	
Sonora					
21/16°*C Central	5.2	5.2	7.2	6.2	
21/16°C Central	5.2	5.8	7.2	7.2	
21/25°C Central	3.8	5.2	6.9	5.2	
30/16°C Central	3.7	3.7	6.4	5.1	
30/25°C Central	3.4	3.7	5.8	3.7	
Late Mexicon 120					
21/16°*C Central	3.9	6.0	7.7	5.0	
21/16°C Central	6.0	6.0	8.1	6.4	
21/25°C Central	3.7	5.4	6.7	3.7	
30/16°C Central	4.0	5.0	6.0	5.3	
30/25°C Central	3.4	3.7	5.0	3.7	

Appendix C

Relation between the rate and duration of grain filling EXPERIMENTS I-IV.

EXPERIMENT I

Table C.1(a), (b) and (c)

Treatment effects (a) 18/13°C to 21/16°*C (b) 21/16°*C to 30/25°C and (c) 18/13°C to 30/25°C on

(i) the <u>absolute</u> difference in growth rate per grain G (mg/day), ± S.D.

(ii) the <u>absolute</u> difference in the duration of grain filling, D (days) ± Error (Section 2.6)

(iii) the <u>absolute</u> difference in final dry weight per grain W (mg) ± S.E.$\bar{x}$

\+ denotes an increase in any of the above quantities
\- denotes a decrease.
Treatment effects are always observed from the lower to the higher temperature
n.s.d. - no significant difference at 95% confidence level

TABLE C.1 (a) 18/13°C to 21/16°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
<u>Triple Dirk</u>					
Lower	G	+0.17±0.08	+0.23±0.11	+0.01±0.06	
	D	-6.0 ±5.4	-6.1 ±6.7	-8.5 ±3.7	
	W	n.s.d.	-2.03±3.36	-3.65±2.96	
Central	G	+0.31±0.08	+0.42±0.08	0.14±0.11	
	D	-8.4 ±5.4	-7.6 ±4.3	-3.7 ±6.6	
	W	-1.04±2.08	-4.94±2.87	+1.24± 3.82	
Upper	G	+0.26±0.12	+0.23±0.19	-	
	D	- 5±5.4	-5.4 ±6.4	-	
	W	-1.78±2.70	-0.55±3.05	-	
<u>Timgalen</u>					
Lower	G	-0.22±0.05	+0.23±0.00	+0.21±0.09	
	D	-10.9 ±5.10	-13.90±6.10	-12.5 ±3.5	
	W	-4.80±2.74	-5.76±3.65	-5.87±1.28	

TABLE C.1 (a) continued

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Timgalen					
Central	G	+0.18±0.05	+0.17±0.05	+0.09±0.07	-0.09±0.19
	D	-8.7 ±3.0	-8.3 ±4.0	-9.6 ±5.3	-1.3 ±6.6
	W	-8.20±1.84	-8.78±1.90	-4.67±2.19	-0.12±2.52
Upper	G	+0.14±0.07	+0.12±0.08	+0.27±0.07	
	D	-13.5 ±4.1	-12.2 ±4.4	-14.2 ±5.7	
	W	-8.97±1.88	-8.42±2.45	+0.18±2.81	
WW15					
Lower	G	+0.30±0.09	+0.11±0.11	+0.16±0.2	
	D	-16.1 ±5.2	-9.5 ±5.3	-10.5 ±5.1	
	W	-7.14±2.01	-8.28±2.00	-9.11±2.00	
Central	G	+0.27±0.05	+0.31±0.07	+0.30±0.07	+0.32±0.21
	D	-13.2 ±6.0	-15.1 ±6.5	-10.8 ±4.6	-10.6 ±6.5
	W	-8.63±2.75	-8.08±3.0	-7.48±1.88	-3.45±2.19
Upper	G	+0.16±0.10	+0.20±0.10	+0.13±0.11	
	D	-11.0 ±5.0	-10.7 ±5.8	-12.7 ±8.0	
	W	-7.88±2.08	-6.97±2.60	-4.68±3.00	

TABLE C.1 (b) 21/16°* to 30/25°C

Spikelet Postion Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk					
Lower	G	+0.28±0.10	+0.22±0.13		
	D	-15.0 ±3.0	-13.9 ±4.7		
	W	-14.95±2.06	-16.85±2.75		
Central	G	+0.16±0.12	+0.20±0.16		
	D	-13 ±3.0	-11.7 ±3.3		
	W	-15.65±1.83	-17.14±1.83		
Upper	G	+0.23±0.11	+0.27±0.16		
	D	-14.7 ±3.1	-12.6 ±5.0		
	W	-13.44±2.35	-14.36±3.2		
Timgalen					
Lower	G	+0.44±0.17	+0.54±0.11	+0.28±0.14	
	D	-14.9 ±5.4	-13.6 ±5.4	-10.8 ±6.1	
	W	-14.57±2.10	-14.44±3.17	-8.14±2.66	
Central	G	+0.32±0.10	+0.36±0.12	+0.42±0.13	+0.32±0.22
	D	-13.3 ±3.4	-15.7 ±5.0	-9.7 ±6.0	-13.3 ±5.3
	W	-16.47±1.35	-16.53±2.03	-12.75±2.19	-5.84±2.52
Upper	G	+0.17±0.11	+0.33±0.15	+0.16±0.18	
	D	-8.8 ±4.7	-11.9 ±3.4	-3.1 ±4.7	
	W	-12.94±1.79	-12.2 ±2.22	-6.30±2.83	
WW15					
Lower	G	+0.18±0.10	+0.45±0.16	+0.01±0.23	
	D	-13.1 ±5.3	-17.1 ±4.9	-16.5 ±5.3	
	W	-14.76±2.52	-14.04±2.15	-15.83±2.45	
Central	G	+0.07±0.08	+0.14±0.11	+0.07±0.09	
	D	-10.7 ±6.3	-10.1 ±5.7	-12.2 ±5.9	
	W	-11.73±3.25	-14.46±2.99	-9.68±2.53	
Upper	G	+0.39±0.16	+0.32±0.12	+0.28±0.21	
	D	-17.1 ±5.2	-16.3 ±4.8	-18.3 ±6.8	
	W	-9.32±2.64	-10.40±2.39	-8.50±2.85	
Late Mexico 120					
Lower	G	+0.13±0.09	+0.07±0.09	+0.05±0.15	
	D	-12.2 ±4.9	-12.2 ±5.1	-10.9 ±5.4	
	W	-19.14±3.02	-19.82±2.65	-13.94±2.41	
Central	G	+0.12±0.06	+0.07±0.12	-0.10±0.16	
	D	-11.3 ±4.3	-15.7 ±4.7	-11.0 ±4.6	
	W	-17.18±2.48	-19.34±2.44	-15.92±2.06	
Upper	G	+0.17±0.13	+0.39±0.09	+0.17±0.12	
	D	-13.6 ±6.5	-15.6 ±4.4	-14.9 ±6.8	
	W	-12.87±2.34	-13.80±2.83	-13.10±3.65	

TABLE C.1 (c) 18/13°C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk Lower	G	+0.45±0.09	+0.55±0.10		
	D	-21.0 ±4.4	-20.0 ±5.4		
	W	-14.94±2.08	-18.87±3.35		
Central	G	+0.47±0.10	+0.52±0.09		
	D	-21.4 ±5.0	-19.3 ±3.0		
	W	-16.68±1.98	-22.07±2.63		
Upper	G	+0.49±0.08	+0.50±0.06		
	D	-19.7 ±3.7	-18.0 ±5.4		
	W	-15.22±2.47	-14.91±2.99		
Timgalen Lower	G	+0.66±0.15	+0.77±0.07	+0.49±0.13	
	D	-25.8 ±5.7	-27.5 ±6.7	-23.3 ±4.7	
	W	-19.37±2.52	-20.20±4.16	-14.02±2.09	
Central	G	+0.50±0.09	+0.54±0.10	+0.51±0.10	+0.23±0.21
	D	-22.0 ±3.0	-24.0 ±4.4	-19.3 ±5.3	-13.3 ±5.3
	W	-24.67±1.30	-25.31±2.0	-17.41±1.87	-5.84±2.12
Upper	G	+0.32±0.11	+0.45±0.12	+0.43±0.12	
	D	-22.3 ±3.4	-24.1 ±3.8	-17.3 ±4.4	
	W	-21.91±1.32	-20.62±2.2	-6.12±2.29	
WW15 Lower	G	+0.48±0.10	+0.56±0.19	+0.17±0.22	
	D	-29.2 ±6.1	-26.6 ±4.6	-27.0 ±5.4	
	W	-21.90±2.08	-22.47±2.2	-24.95±1.93	
Central	G	+0.34±0.07	+0.45±0.07	+0.37±0.10	
	D	-23.9 ±6.5	-25.2 ±7.2	-23.0 ±5.3	
	W	-20.36±3.46	-22.55±3.77	-17.15±2.92	
Upper	G	+0.55±0.11	+0.52±0.11	+0.41±0.21	
	D	-28.10±4.4	-27.0 ±5.0	-31.0 ±5.2	
	W	-17.20±2.77	-17.37±2.0	-13.19±2.39	

TABLE C.2 (a),(b) and (c). Examines similiar treatment effects as Table C.1. but instead of absolute differences, here, percent changes are presented for treatments (a),(b) and (c).

TABLE C.2 (a) 18/13°C to 21/16°*C

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk					
Lower	G	+11±5	+18±7	+ 1±5	
	D	-14±7	-15±9	-22±6	
	W	n.s.d.	- 3±6	- 8±7	
Central	G	+19±5	+16±5	+10±9	
	D	-20±7	-19±6	- 9±8	
	W	- 3±4	- 7±5	+ 3±8	
Upper	G	+17±8	+15±13		
	D	-13±8	-14±9		
	W	- 3±5	- 1±6		
Timgalen					
Lower	G	+15±4	+15±6	+15±7	
	D	-25±7	-31±8	-29±5	
	W	- 9±5	-10±7	-12±3	
Central	G	+13±3	+11±3	+ 7±6	- 8±19
	D	-21±4	-19±6	-25±8	- 4±10
	W	-13±3	-14±3	- 9±5	-0.4±8
Upper	G	+ 9±5	+ 8±5	+21±7	
	D	-32±6	-28±6	-38±11	
	W	-16±4	-15±5	-0.5±8	
WW15					
Lower	G	+21±7	+ 8±6	+13±10	
	D	-31±6	-20±7	-22±6	
	W	-13±4	-14±4	-17±4	
Central	G	+18±4	+20±5	+21±6	+30±25
	D	-28±8	-32±8	-25±6	-25±9
	W	-15±6	-14±5	-15±4	-10±7
Upper	G	+14±9	+16±9	+14±14	
	D	-23±6	-23±7	-28±11	
	W	-16±5	-15±5	-14±10	

TABLE C.2 (b) 21/16°*C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk					
Lower	G	+15±6	+11±6		
	D	-42±5	-40±7		
	W	-26±4	-29±6		
Central	G	+12±6	+12±5		
	D	-39±6	-35±6		
	W	-28±4	-30±4		
Upper	G	+12±5	+15±10		
	D	-45±6	-39±10		
	W	-25±5	-27±7		
Timgalen					
Lower	G	+22±9	+26±6	+17±9	
	D	-46±12	-44±13	-36±14	
	W	-29±5	-29±8	-20±7	
Central	G	+17±6	+18±6	+22±8	+25±20
	D	-42±7	-46±11	-34±13	-42±11
	W	-31±3	-31±5	-28±5	-18.7±2
Upper	G	+10±7	+18±9	+11±9	
	D	-30±10	-38±7	-14±11	
	W	-27±4	-26±5	-18±9	
WW15					
Lower	G	+12±7	+25±9	+0.8±15	
	D	-37±10	-46±9	-45±10	
	W	-29±6	-28±5	-36±7	
Central	G	+ 5±5	+ 8±7	+ 5±6	
	D	-32±11	-31±11	-37±11	
	W	-24±8	-28±7	-23±8	
Upper	G	+26±12	+20±8	+24±20	
	D	-46±10	-46±9	-56±14	
	W	-23±6	-25±6	-29±11	
Late Mexico 120					
Lower	G	+13±5	+ 4±5	+ 3±11	
	D	-36±9	-38±10	-33±10	
	W	-34±7	-35±6	-30±6	
Central	G	+ 7±4	+11±5	- 7±8	
	D	-34±9	-45±9	-33±9	
	W	-32±6	-34±5	-33±5	
Upper	G	+12±10	+25±5	+17±14	
	D	-38±12	-48±9	-42±13	
	W	-27±6	-29±7	-35±12	

TABLE C.2 (c) 18/13° to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk					
Lower	G	+24±5	+28±6		
	D	-50±7	-50±8		
	W	-26±4	-31±4		
Central	G	+26±5	+26±5		
	D	-51±8	-47±7		
	W	-25±4	-35±5		
Upper	G	+27±5	+28±5		
	D	-49±5	-48±10		
	W	-28±5	-27±7		
Timgalen					
Lower	G	+34±8	+37±4	+30±9	
	D	-59±12	-62±13	-54±11	
	W	-35±5	-36±9	-30±6	
Central	G	+26±5	+27±5	+28±6	+18±18
	D	-57±6	-57±9	-50±11	-44±10
	W	-41±3	-41±4	-34±5	-19±8
Upper	G	-19±7	+25±7	+30±9	
	D	-52±6	-55±6	-44±8	
	W	-38±3	-37±5	-18±7	
WW15					
Lower	G	+30±7	+31±10	+14±17	
	D	-57±10	-57±8	-57±9	
	W	-39±5	-38±5	-47±6	
Central	G	+22±5	+26±5	+25±7	
	D	-51±11	-53±11	-52±10	
	W	-35±8	-38±8	-35±8	
Upper	G	+36±8	+33±8	+35±20	
	D	-58±8	-59±8	-68±11	
	W	-35±6	-36±6	-39±10	

EXPERIMENT II

TABLE C.3 (a), (b) and (c)

Treatment effects (a) 15/10°C to 21/16°*C. (b) 21/16°*C to 30/25°C and (c) 15/10°C to 30/25°C on

(i) the absolute difference in growth rate per grain G. (mg/day) ± S.D.

(ii) the absolute difference in the duration of grain filling, D (days) ± Error (Section 2.6)

(iii) the absolute difference in final dry weight per grain W (mg) ± S.E. $\bar{X}$.

+ denotes an increase; - a decrease.
Treatment effects are always observed from the lower to the higher temperature.

TABLE C.3 (a) 15/10°C to 21/16°*C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+ 0.65±0.08	+ 0.62±0.04	+ 0.49±0.17
	D	-25.8 ±5.2	-22.6 ±4.4	-25.6 ±8.9
	W	n.s.d	n.s.d	- 2.39±2.45
Timgalen Central	G	+ 0.70±0.06	+ 0.72±0.06	+ 0.73±0.11
	D	-25.3 ±5.8	-26.5 ±4.4	-22.9 ±9.3
	W	- 1.52±1.93	- 1.74±1.78	- 2.52±3.23
WW15 Central	G	+ 0.30±0.07	+ 0.21±0.06	+ 0.15±0.7
	D	-19.7 ±7.4	-19.7 ±5.10	-15.6 ±7.6
	W	- 7.08±0.84	- 8.44±1.84	- 4.10±2.23
Late Mexico 120 Central	G	+ 0.53±0.06	+ 0.60±0.06	+ 0.45±0.07
	D	-28.2 ±5.2	-26.0 ±5.6	-23.7 ±9.9
	W	- 8.18±2.21	- 8.88±2.36	- 9.22±3.21

TABLE C.3 (b) 21/16°*C to 30/25°C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+ 0.29±0.10	+ 0.24±0.05	
	D	-11.5 ±4.0	-12.9 ±4.4	
	W	-13.41±2.24	-14.01±2.50	
Timgalen Central	G	- 0.20±0.13	- 0.43±0.09	- 0.51±0.17
	D	-15.4 ±5.4	- 9.7 ±6.1	-14.1 ±6.8
	W	-28.11±2.40	-28.36±2.64	-24.19±3.06
WW15 Central	G	+ 0.24±0.07	+ 0.23±0.11	+ 0.09±0.10
	D	-12.6 ±5.4	-13.9 ±4.4	-13.9 ±6.6
	W	-12.98±1.11	-14.84±2.04	-13.87±2.14
Late Mexico 120 Central	G	- 0.22±0.15	- 0.33±0.05	- 0.35±0.10
	D	-11.2 ±8.1	- 6.1 ±7.8	- 8.7 ±8.5
	W	-22.15±3.36	-23.17±3.37	-18.78±3.01

TABLE C.3 (c) 15/10°C to 30/25°C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+ 0.93±0.10	+ 0.86±0.06	
	D	-37.3 ±5.2	-35.5 ±4.4	
	W	-13.05±2.11	-15.04±2.0	
Timgalen Central	G	+ 0.49±0.10	+ 0.29±0.08	+ 0.21±0.15
	D	-40.7 ±4.8	-36.2 ±6.5	-37.0 ±9.3
	W	-29.63±1.87	-30.11±2.12	-26.70±3.00
WW15 Central	G	+ 0.54±0.09	+ 0.43±0.09	+ 0.24±0.08
	D	-32.3 ±6.8	-33.6 ±4.10	-29.5 ±7.0
	W	-20.06±1.74	-23.29±1.71	-17.96±2.03
Late Mexico 120 Central	G	+ 0.32±0.15	+ 0.27±0.06	+ 0.10±0.10
	D	-39.4 ±8.3	-32.4 ±8.6	-32.4 ±12.0
	W	-30.33±2.88	-32.06±2.92	-28.60±3.26

TABLE C.4 (a),(b) and (c) examines similiar treatment effects as Table C.3 but instead of absolute differences,here percent changes are presented. Experiment II.

TABLE C.4 (a) 15/10°C to 21/16°*C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+42±6	+39±3	+41±17
	D	-42±6	-38±5	-44±10
	W	n.s.d.	n.s.d.	- 6±6
Timgalen Central	G	+44±4	+43±4	+48±7
	D	-43±7	-46±5	-41±11
	W	- 3±4	- 3±3	- 6±7
WW15 Central	G	+24±6	+17±5	+15±8
	D	-36±8	-36±6	-30±9
	W	-14±3	-15±4	- 9±5
Late Mexico 120 Central	G	+34±4	+35±5	+33±7
	D	-45±7	-45±7	-42±11
	W	-13±4	-14±4	-18±7

TABLE C.4 (b) 21/16°*C to 30/25°C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+16±6	+13±3	
	D	-32±7	-36±8	
	W	-23±5	-24±5	
Timgalen	G	-13±9	-26±7	-34±15
	D	-47±9	-31±13	-42±14
	W	-53±7	-53±8	-58±12
WW15 Central	G	+17±5	+15±7	+ 8±10
	D	-35±10	-38±8	-38±12
	W	-23±5 -30	-29±5	-35±7
Late Mexico 120 Central	G	-14±11	-20±3	-26±9
	D	-32±16	-19±14	-27±16
	W	-41±9	-42±9	-46±10

TABLE C.4 (c) 15/10°C to 30/25°C

Spikelet Position, Cultivar		Floret a	Floret b	Floret c
Triple Dirk Central	G	+51±7	+47±5	
	D	-61±7	-60±7	
	W	-23±5	-26±4	
Timgalen Central	G	+35±8	+23±7	+21±15
	D	-68±9	-62±12	-66±14
	W	-54±6	-55±7	-60±12
WW15 Central	G	+37±8	+30±7	+21±8
	D	-58±9	-61±6	-57±11
	W	-40±5	-42±4	-41±6
Late Mexico 120 Central	G	+23±11	+20±5	+10±11
	D	-63±14	-55±14	-57±16
	W	-49±8	-50±7	-55±10

EXPERIMENT III

TABLE C.5 (a) and (b) The effect of decreasing the light intensity from (a) 48420 lux to 8070 lux and (b) from 48420 lux to 16140 lux at 21/16°C on

(i) the absolute difference in growth rate per grain G (mg/day) $\pm$ S.D. at

(ii) the absolute difference in the duration of grain filling D (Days) $\pm$ Error (Section 2.6)

(iii) the absolute difference in final dry weight per grain W (mg) $\pm$ S.E.$\bar{x}$.

+ denotes an increase - a decrease.

Experiment III

TABLE C.5 (a) 48420 lux to 8070 lux

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk Central	G D W	- 0.45$\pm$0.07 + 7.5 $\pm$6.6 - 1.92$\pm$2.91	- 0.54$\pm$0.08 + 6.5 $\pm$6.0 - 5.87$\pm$3.21	Grains failed to set at 8070 lux	
Sonora Central	G D W	- 0.67$\pm$0.12 + 4.30$\pm$5.9 -19.13$\pm$2.13	Growth linear -21.67$\pm$3.02	not -33.28$\pm$3.64	Some grains failed at 8070 lux

TABLE C.5 (b) 48420 lux to 16140 lux

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk Central	G D W	- 0.08$\pm$0.04 + 1.50$\pm$4.5 + 0.71$\pm$1.67	- 0.12$\pm$0.08 + 1.0 $\pm$3.9 - 0.18$\pm$1.64	Grains failed to set at 16140 lux	
Sonora Central	G D W	- 0.45$\pm$0.11 + 0.5 $\pm$5.3 -13.81$\pm$1.96	- 0.47$\pm$0.12 + 0.5 $\pm$5.0 -13.98$\pm$2.28	- 0.55$\pm$0.10 + 4.8 $\pm$7.6 -13.72$\pm$3.28	-0.21$\pm$0.14 +5.6 $\pm$6.9 -10.34$\pm$2.06

TABLE C.6 (a) and (b) the same as C.5 except changes are presented as percentages for (a) and (b).

TABLE C.6 (a) 48420 lux to 8070 lux

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk Central	G	-25±5	-29±6	Grains failed to set at 8070 lux	
	D	+19±9	+18±9		
	W	- 3±2	-10±2		
Sonora Central	G	-41±11	Growth	not linear	Some grains failed to set at 8070 lux
	D	+11±8			
	W	-33±3	-35±6	-64±8	

TABLE C.6 (b) 48420 lux to 16140 lux

Spikelet Position Cultivar		Floret a	Floret b	Floret c	Floret d
Triple Dirk Central	G	- 4±2	- 6±3	Grains failed to set at 16140 lux	
	D	+ 7±10	+ 3±6		
	W	+ 1±3	0±4		
Sonora Central	G	-27±8	-27±9	-33±8	-18±12
	D	+ 2±8	+ 2±7	+14±12	+17±12
	W	-24±4	-23±4	-26±8	-27±6

EXPERIMENT IV

TABLE C.7 (a), b(i), b(ii), c(i), c(ii) The effect of (a) extending the day temperature at 21/16°C from eight to twelve hours.

(b) the effect of increasing the day temperature by 9°C at a night temperature of (i) 16°C (ii) 25°C.

(c) the effect of increasing the night temperature by 9°C at a day temperature of (i) 21°C (ii) 30°C on (i) the absolute difference in growth rate per grain G (mg/day), ± S.D.

(ii) the absolute difference in the duration of grain filling D (days) ± Error (Section 2.6)
(iii) the absolute difference in final dry weight per grain W (mg) ± S.E.$\bar{x}$.

+ denotes an increase, - denotes a decrease

TABLE C.7 (a) Extending the day temperature at 21°C from eight to 12 hours at a night temperature of 16°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G D W	+ 0.36±0.08 - 2.4 ±5.3 + 5.86±1.90	+ 0.40±0.07 - 5.10±4.7 + 5.69±2.0	+ 0.41±0.08 - 5.7 ±4.7 + 7.49±1.77
Late Mexico 120	G D W	+ 0.67±0.13 - 7.0 ±7.0 +10.06±3.83	+ 0.74±0.09 - 5.0 ±6.1 + 9.98±3.73	+ 0.60±0.09 - 5.0 ±6.1 +10.61±3.32

TABLE C.7 b(i) Increase from 21/16°C to 30/16°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G D W	+ 0.03±0.14 -10.6 ±3.9 -14.90±1.64	- 0.08±0.17 - 6.9 ±4.7 -15.90±1.74	+ 0.10±0.12 - 8.7 ±3.5 -12.86±1.77
Late Mexico 120 Central	G D W	- 0.07±0.18 - 5.1 ±5.1 -14.37±3.2	- 0.18±0.15 - 6.2 ±5.4 -15.68±3.47	- 0.12±0.09 - 5.4 ±5.7 -13.89±3.41

TABLE C.7 b(ii) Increase from 21/25°C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G	+ 0.01 ± 0.12	+ 0.06 ± 0.08	+ 0.07 ± 0.14
	D	- 5.9 ± 2.4	- 4.9 ± 3.9	- 3.2 ± 3.7
	W	- 6.42 ± 1.45	- 7.06 ± 1.67	- 5.36 ± 1.17
Late Mexico 120 Central	G	+ 0.16 ± 0.23	+ 0.13 ± 0.20	+ 0.33 ± 0.21
	D	- 6.1 ± 5.4	- 5.40 ± 5.6	- 6.4 ± 5.7
	W	- 8.89 ± 2.95	- 9.82 ± 3.39	- 8.24 ± 3.64

TABLE C.7 c(i) Increase from 21/16°C to 21/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G	+ 0.07 ± 0.11	+ 0.01 ± 0.07	+ 0.14 ± 0.08
	D	- 6.0 ± 3.6	- 4.0 ± 4.6	- 5.7 ± 3.7
	W	-12.38 ± 1.70	-13.90 ± 1.96	-12.16 ± 1.45
Late Mexico 120 Central	G	- 0.32 ± 0.19	- 0.37 ± 0.14	- 0.34 ± 0.16
	D	- 0.7 ± 5.1	- 1.5 ± 5.4	- 0.3 ± 5.7
	W	- 7.71 ± 3.10	- 8.41 ± 3.28	- 6.30 ± 3.48

TABLE C.7 c(ii) Increase form 30/16°C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G	+ 0.05 ± 0.15	+ 0.14 ± 0.18	+ 0.11 ± 0.18
	D	- 1.3 ± 2.7	- 2.0 ± 4.0	- 0.2 ± 3.5
	W	- 3.90 ± 1.39	- 5.14 ± 1.46	- 4.66 ± 1.49
Late Mexico 120 Central	G	- 0.08 ± 0.22	- 0.07 ± 0.21	+ 0.12 ± 0.14
	D	- 1.7 ± 5.4	- 1.7 ± 5.6	- 1.3 ± 5.4
	W	- 2.23 ± 3.05	- 2.56 ± 3.58	- 0.65 ± 3.58

TABLE C.8 (a), b(i), b(ii), c(i), c(ii) the same as Table C.7 (a), b(i), b(ii), c(i), c(ii) but instead of absolute differences percent changes for the above treatments are given.

TABLE C 8(a) Extending the day temperature at 21°C from eight to twelve hours at a night temperature of 16°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G D W	+20±5 - 7±17 +11±4	+20±4 -16±16 +10±4	+23±4 -17±15 +15±4
Late Mexico 120 Central	G D W	+31±7 -20±22 +17±7	+31±4 -15±20 +16±7	+29±5 -15±21 +20±7

TABLE C.8 b(i) Increase from 21/16°C to 30/16°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G D W	+ 2±8 -35±16 -28±4	- 4±9 -25±20 -28±4	+ 6±7 -32±15 -26±4
Late Mexico 120 Central	G D W	- 3±8 -18±20 -24±6	- 7±7 -22±22 -25±6	- 6±5 -21±24 -27±8

TABLE C.8 b(ii) Increase from 21/25°C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora	G D W	+ 0.4±7 -24 ±11 -16 ±4	+ 3±4 -21±19 -17±4	+ 3±7 -15±18 -14±3
Late Mexico 120 Central	G D W	+ 8 ±12 -23 ±24 -17 ±6	+ 6±10 -25±25 -18±7	+16±11 -26±24 -18±9

TABLE C.8 c(i) Increase from 21/16°C to 21/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G	+ 4±6	+ 0.3±4	+ 7±4
	D	-20±13	-15 ±18	-20±15
	W	-23±4	-25 ±4	-25±3
Late Mexico 120 Central	G	-15±10	-16 ±7	-17±9
	D	- 3±18	- 5 ±20	- 1±22
	W	-13±6	-14 ±6	-12±7

TABLE C.8 c(ii) Increase from 30/16°C to 30/25°C

Spikelet Position Cultivar		Floret a	Floret b	Floret c
Sonora Central	G	+ 3±8	+ 7±10	+ 5±9
	D	- 7±14	-10±20	- 1±19
	W	-10±4	-13±4	-13±4
Late Mexico 120 Central	G	- 4±11	- 3±10	- 6±7
	D	- 8±25	- 3±26	- 6±27
	W	- 5±7	- 6±8	- 2±9

APPENDIX D Growth rate of individual grains and ears EXPERIMENTS I - IV. ± S.D.

EXPERIMENT I

Floret position / Cultivar, Spikelet Position, Temperature		Floret a mg day^{-1}	Floret b mg day^{-1}	Floret c mg day^{-1}	Floret d mg day^{-1}	OF EARS mg day^{-1}
Triple Dirk 18/13°C	Lower	1.405 ± 0.068	1.431 ± 0.077	1.307 ± 0.086		32.74 ±0.801
	Central	1.355 ± 0.560	1.464 ± 0.059	1.142 ± 0.096		
	Upper	1.333 ± 0.803	1.297 ± 0.098			
21/15°*C	Lower	1.572 ± 0.092	1.758 ± 0.129	1.319 ± 0.036		43.32 ± 1.28
	Central	1.663 ± 0.095	1.785 ± 0.096	1.280 ± 0.117		
	Upper	1.598 ± 0.150	1.528 ± 0.281			
30/25°C	Lower	1.850 ± 0.101	1.982 ± 0.116			45.71 ± 1.06
	Central	1.821 ± 0.133	1.982 ± 0.122			
	Upper	1.823 ± 0.073	1.794 ± 0.028			
Timgalen 18/13°C	Lower	1.300 ± 0.032	1.309 ± 0.049	1.139 ± 0.083	1.045 ± 0.178	43.93 ± 1.86
	Central	1.437 ± 0.035	1.470 ± 0.033	1.329 ± 0.044		
	Upper	1.388 ± 0.067	1.348 ± 0.047	1.019 ± 0.071		
21/16°*C	Lower	1.521 ± 0.073	1.535 ± 0.120	1.347 ± 0.097	0.959 ± 0.202	44.70 ± 1.86
	Central	1.618 ± 0.063	1.642 ± 0.066	1.423 ± 0.108		
	Upper	1.531 ± 0.077	1.466 ± 0.105	1.291 ± 0.080		

EXPERIMENT I cont.

Floret position / Cultivar, Spikelet Position, Temperature	Floret a mg day^{-1}	Floret b mg day^{-1}	Floret c mg day^{-1}	Floret d mg day^{-1}	CF EARS mg day^{-1}
Timgalen					
30/25°C Lower	1.956 ± 0.262	2.079 ± 0.087	1.624 ± 0.177	1.276 ± 0.230	57.20 ± 1.23
Central	1.938 ± 0.146	2.006 ± 0.166	1.839 ± 0.147		
Upper	1.704 ± 0.141	1.793 ± 0.186	1.454 ± 0.172		
WW15					
18/13°C Lower	1.088 ± 0.078	1.278 ± 0.038	1.102 ± 0.102	0.746 ± 0.256	51.31 ± 0.95
Central	1.213 ± 0.046	1.288 ± 0.038	1.099 ± 0.069		
Upper	0.981 ± 0.052	1.036 ± 0.086	0.759 ± 0.108		
21/16°*C Lower	1.383 ± 0.092	1.391 ± 0.077	1.265 ± 0.136	1.066 ± 0.151	55.19 ± 0.40
Central	1.478 ± 0.057	1.601 ± 0.105	1.394 ± 0.066		
Upper	1.138 ± 0.152	1.233 ± 0.112	0.885 ± 0.120		
30/25°C Lower	1.566 ± 0.105	1.843 ± 0.232	1.275 ± 0.315		59.4 ± 2.06
Central	1.549 ± 0.094	1.739 ± 0.114	1.464 ± 0.117		
Upper	1.533 ± 0.165	1.554 ± 0.122	1.167 ± 0.300		
Late Mexico 120					
21/16°*C Lower	1.590 ± 0.063	1.664 ± 0.043	1.350 ± 0.111	1.103 ± 0.168	97.71 ± 2.13
Central	1.496 ± 0.034	1.632 ± 0.136	1.432 ± 0.051		
Upper	1.213 ± 0.094	1.179 ± 0.103	0.863 ± 0.205		
30/25°C Lower	1.717 ± 0.117	1.730 ± 0.131	1.396 ± 0.188	0.728 ± 0.346	103.5 ± 2.128
Central	1.613 ± 0.081	1.706 ± 0.095	1.333 ± 0.270		
Upper	1.385 ± 0.168	1.574 ± 0.081	1.040 ± 0.036		

EXPERIMENT II

Floret Position / Cultivar, Spikelet Position, Temperature	Floret a mg day^{-1}	Floret b mg day^{-1}	Floret c mg day^{-1}	OF EARS mg day^{-1}
Triple Dirk				
15/10°C Central	0.908 ± 0.070	0.958 ± 0.051	0.697 ± 0.097	20.95 ± 0.62
21/16°*C Central	1.554 ± 0.078	1.582 ± 0.019	1.188 ± 0.241	25.49 ± 0.82
30/25°C Central	1.839 ± 0.118	1.823 ± 0.068		30.80 ± 1.38
Timgalen				
15/10°C Central	0.901 ± 0.031	0.957 ± 0.042	0.782 ± 0.056	18.86 ± 1.01
21/16°*C Central	1.598 ± 0.081	1.676 ± 0.072	1.508 ± 0.109	33.69 ± 1.71
30/25°C Central	1.394 ± 0.169	1.248 ± 0.108	0.994 ± 0.233	24.06 ± 1.84
WW15				
15/10°C Central	0.919 ± 0.081	1.034 ± 0.040	0.885 ± 0.048	32.86 ± 0.50
21/16°*C Central	1.215 ± 0.046	1.241 ± 0.070	1.039 ± 0.097	29.82 ± 1.31
30/25°C Central	1.459 ± 0.097	1.467 ± 0.142	1.127 ± 0.107	33.72 ± 0.83
Late Mexico 120				
15/10°C Central	1.048 ± 0.053	1.109 ± 0.067	0.901 ± 0.083	32.94 ± 0.86
21/16°*C Central	1.583 ± 0.057	1.714 ± 0.047	1.351 ± 0.061	42.65 ± 0.98
30/25°C Central	1.367 ± 0.240	1.379 ± 0.045	1.003 ± 0.129	35.97 ± 1.21

EXPERIMENT III

Floret Position / Cultivar, Spikelet Position, Light Intensity	Floret a mg day^{-1}	Floret b mg day^{-1}	Floret c mg day^{-1}	Floret d mg day^{-1}	OF EARS mg day^{-1}
Triple Dirk					
21/16°*C Central	1.553 ± 0.029	1.710 ± 0.074	1.216 ± 0.258		42.28 ± 1.06
8070 lux Central	1.340 ± 0.112	1.304 ± 0.138			27.99 ± 1.09
16140 lux Central	1.710 ± 0.063	1.726 ± 0.103			40.17 ± 0.73
34432 lux Central	1.996 ± 0.130	2.074 ± 0.131	1.655 ± 0.225		59.27 ± 2.17
48420 lux Central	1.789 ± 0.018	1.845 ± 0.013	1.490 ± 0.063		42.69 ± 2.36
Sonora					
21/16°*C Central	1.612 ± 0.046	1.743 ± 0.056	1.630 ± 0.076	1.258 ± 0.096	69.74 ± 0.97
3070 lux Central	0.967 ± 0.159				37.70 ± 2.12
16140 lux Central	1.187 ± 0.140	1.274 ± 0.164	1.105 ± 0.096	1.010 ± 0.115	43.07 ± 1.35
34432 lux Central	2.036 ± 0.053	2.130 ± 0.031	1.982 ± 0.053	1.296 ± 0.100	79.26 ± 0.53
48420 lux Central	1.634 ± 0.077	1.739 ± 0.078	1.658 ± 0.104	1.224 ± 0.157	66.34 ± 1.43

EXPERIMENT IV

Floret Position / Cultivar, Spikelet Position, Temperature	Floret a mg day^{-1}	Floret b mg day^{-1}	Floret c mg day^{-1}	CF EARS mg day^{-1}
Sonora				
21/16°*C Central	1.425 ± 0.040	1.562 ± 0.034	1.373 ± 0.030	39.56 ± 0.39
21/16°C Central	1.783 ± 0.126	1.965 ± 0.109	1.782 ± 0.114	52.88 ± 0.94
21/25°C Central	1.858 ∓ 0.097	1.971 ± 0.039	1.926 ± 0.041	53.41 ± 0.57
30/16°C Central	1.815 ± 0.146	1.890 ± 0.224	1.886 ± 0.124	55.62 ± 1.65
30/25°C Central	1.865 ± 0.143	2.026 ± 0.137	1.996 ± 0.236	51.33 ± 3.05
Late Mexico 120				
21/16°*C Central	1.502 ± 0.058	1.601 ± 0.027	1.441 ± 0.092	40.76 ± 1.09
21/16°C Central	2.171 ± 0.200	2.345 ± 0.146	2.036 ± 0.088	62.66 ± 0.29
21/25°C Central	1.855 ± 0.177	1.971 ± 0.135	1.698 ± 0.223	48.45 ± 2.819
30/16°C Central	2.096 ± 0.156	2.170 ± 0.149	1.911 ± 0.096	65.01 ± 0.85
30/25°C Central	2.011 ± 0.273	2.099 ± 0.265	2.028 ± 0.186	62.25 ± 2.49

APPENDIX E

Duration of grain filling for individual grains and ears. EXPERIMENTS I - IV. $\pm$ Error (Section 2.6)

EXPERIMENT I

Cultivar, Temperature	and Spikelet Position	Floret a days	Floret b days	Floret c days	Floret d days	Per Ear days
Triple Dirk	Lower	42.0 $\pm$ 3.4	41.7 $\pm$ 3.7	38.0 $\pm$ 2.0		43.7 $\pm$ 3.7
18/13°C	Central	41.7 $\pm$ 3.7	40.6 $\pm$ 2.0	40.0 $\pm$ 3.0		
	Upper	38.0 $\pm$ 3.0	37.6 $\pm$ 3.4			
Triple Dirk	Lower	36.0 $\pm$ 2.0	34.6 $\pm$ 3.0	29.5 $\pm$ 1.7		32.3 $\pm$ 4.7
21/16°*C	Central	33.3 $\pm$ 1.7	33.0 $\pm$ 2.3	36.3 $\pm$ 3.3		
	Upper	33.0 $\pm$ 2.4	32.2 $\pm$ 3.0			
Triple Dirk	Lower	21.0 $\pm$ 1.0	20.7 $\pm$ 1.7			20.0 $\pm$ 1.0
30/25°C	Central	20.3 $\pm$ 1.3	21.3 $\pm$ 1.0	20.0 $\pm$ 1.3		
	Upper	18.3 $\pm$ 0.7	19.6 $\pm$ 2.0			
Timgalen	Lower	43.4 $\pm$ 2.7	44.4 $\pm$ 3.7	43.0 $\pm$ 1.0		41.0 $\pm$ 4.0
18/13°C	Central	40.7 $\pm$ 1.3	42.3 $\pm$ 1.7	38.3 $\pm$ 2.3	33.3 $\pm$ 3.3	
	Upper	43.0 $\pm$ 1.4	43.7 $\pm$ 2.4	36.6 $\pm$ 2.7		
Timgalen	Lower	32.5 $\pm$ 2.4	30.5 $\pm$ 2.4	30.5 $\pm$ 2.4		36.7 $\pm$ 4.0
21/16°*C	Central	32.0 $\pm$ 1.7	34.0 $\pm$ 2.3	28.7 $\pm$ 3.0	32.0 $\pm$ 3.3	
	Upper	29.5 $\pm$ 2.7	31.5 $\pm$ 2.0	22.4 $\pm$ 3.0		
Timgalen	Lower	17.6 $\pm$ 3.0	16.9 $\pm$ 3.0	19.7 $\pm$ 3.7		19.0 $\pm$ 1.7
30/25° C	Central	18.7 $\pm$ 1.7	18.3 $\pm$ 2.7	19.0 $\pm$ 3.0	18.7 $\pm$ 2.0	
	Upper	20.7 $\pm$ 2.0	19.6 $\pm$ 1.4	19.3 $\pm$ 1.7		

EXPERIMENT I (continued)

Cultivar, Temperature and Spikelet Position		Floret a days	Floret b days	Floret c days	Floret d days	Per Ear days
WW15	Lower	51.5 ± 3.0	46.5 ± 2.5	47.5 ± 2.6		53.8 ± 3.6
18/13°C	Central	46.9 ± 3.2	47.9 ± 4.0	44.0 ± 2.0	42.6 ± 3.5	
	Upper	48.0 ± 2.0	46.0 ± 3.0	45.5 ± 3.2		
WW15	Lower	35.4 ± 2.2	37.0 ± 2.8	37.0 ± 2.5		36.5 ± 3.0
21/16°*C	Central	33.7 ± 2.8	32.8 ± 2.5	33.2 ± 2.6	32.0 ± 3.0	
	Upper	37.0 ± 3.0	35.3 ± 2.8	32.8 ± 4.8		
WW15	Lower	22.3 ± 3.1	19.9 ± 2.1	20.5 ± 2.8		22.0 ± 3.5
30/25°C	Central	23.0 ± 3.3	22.7 ± 3.2	21.0 ± 3.3		
	Upper	19.9 ± 2.2	19.0 ± 2.0	14.5 ± 2.0		
Late Mexico	Lower	33.9 ± 2.5	32.5 ± 2.7	32.9 ± 2.7		35.0 ± 4.0
120, 21/16°*C	Central	33.0 ± 2.0	35.0 ± 2.7	33.3 ± 2.3	29.0 ± 2.7	
	Upper	35.6 ± 3.8	34.2 ± 2.4	35.6 ± 4.1		
Late Mexico	Lower	21.7 ± 2.4	20.3 ± 2.4	22.0 ± 2.7		21.7 ± 2.0
120, 30/25°C	Central	21.7 ± 2.3	19.3 ± 2.0	22.3 ± 2.3	27.3 ± 5.6	
	Upper	22.0 ± 2.7	18.6 ± 2.0	20.7 ± 2.7		

EXPERIMENT II

Cultivar, Temperature and Spikelet Position		Floret a days	Floret b days	Floret c days	Per Ear days
Triple Dirk					
15/10°C	Central	61.7 ± 3.2	58.9 ± 2.4	58.5 ± 5.5	61.3 ± 3.5
21/16°*C	Central	35.9 ± 2.0	36.3 ± 2.0	32.9 ± 3.4	33.5 ± 3.0
30/25°C	Central	24.4 ± 2.0	23.4 ± 2.4		25.4 ± 2.8
Tingalen					
15/10°C	Central	59.3 ± 2.8	57.7 ± 2.4	56.1 ± 5.9	57.7 ± 1.6
21/16°*C	Central	34.0 ± 3.0	31.2 ± 2.0	33.2 ± 3.4	32.8 ± 1.5
30/25°C	Central	18.6 ± 2.4	21.5 ± 4.1	19.1 ± 3.4	19.8 ± 1.5
WW15					
15/10°C	Central	55.3 ± 4.4	55.3 ± 2.4	52.2 ± 4.0	57.5 ± 5.8
21/16°*C	Central	35.6 ± 3.0	35.6 ± 2.7	36.6 ± 3.6	40.5 ± 6.6
30/25°C	Central	23.0 ± 2.4	21.7 ± 1.7	22.7 ± 3.0	26.5 ± 3.9
Late Mexico 120					
15/10°C	Central	62.8 ± 3.2	58.5 ± 3.2	56.5 ± 6.7	59.0 ± 8.5
21/16°*C	Central	34.6 ± 3.0	32.2 ± 2.4	32.8 ± 3.2	35.5 ± 4.0
30/25°C	Central	23.4 ± 5.1	26.1 ± 5.4	24.1 ± 5.3	24.3 ± 2.5

EXPERIMENT III

Cultivar, Light Intensity and Spikelet Position	Floret a	Floret b	Floret c	Floret d	Per Ear
Triple Dirk Cen. 21/16°*C	36.0 ± 1.5	35.8 ± 1.8	32.2 ± 3.0		36.5 ± 2.2
Central 8070 lux	39.5 ± 4.8	38.0 ± 4.1			38.9 ± 5.3
Central 16140 lux	33.5 ± 2.7	32.5 ± 2.0			32.2 ± 2.8
Central 34432 lux	30.0 ± 1.5	30.5 ± 3.5	30.5 ± 3.5		35.5 ± 4.5
Central 48420 lux	32.0 ± 1.8	31.5 ± 1.9	28.0 ± 3.0		33.3 ± 3.5
Sonora Cen. 21/16°*C	34.5 ± 1.5	33.0 ± 2.2	30.0 ± 2.1	30.0 ± 2.5	33.5 ± 3.0
Central 8070 lux	38.3 ± 3.1	38.0 ± 2.5	40 - 42*	40 - 42*	36.0 ± 4.3
Central 16140 lux	34.5 ± 2.5	33.5 ± 2.5	33.2 ± 5.4	33.1 ± 3.8	35.8 ± 3.8
Central 34432 lux	30.5 ± 1.5	31.5 ± 1.8	31.0 ± 2.1	30.2 ± 2.8	31.5 ± 3.5
Central 48420 lux	34.0 ± 2.8	35.0 ± 2.5	28.4 ± 2.2	27.5 ± 3.1	33.3 ± 3.2

* Approximate value.

EXPERIMENT IV

Cultivar, Light Intensity and Spikelet Position	Floret a days	Floret b days	Floret c days	Per Ear days
Sonora Central 21/16°*C	32.5 ± 3.1	32.5 ± 2.0	33.1 ± 2.7	32.5 ± 4.1
Central 21/16°C	30.1 ± 2.2	27.4 ± 2.7	27.4 ± 2.0	27.4 ± 3.4
Central 21/25°C	24.1 ± 1.4	23.4 ± 1.9	21.7 ± 1.7	22.7 ± 3.0
Central 30/16°C	19.5 ± 1.7	20.5 ± 2.0	18.7 ± 1.5	20.5 ± 3.0
Central 30/25°C	18.2 ± 1.0	18.5 ± 2.0	18.5 ± 2.0	19.2 ± 2.7
Late Mexico 120				
Central 21/16°*C	34.6 ± 4.4	32.3 ± 3.1	30.9 ± 3.4	34.6 ± 5.0
Central 21/16°C	27.6 ± 2.7	27.4 ± 3.0	26.2 ± 2.7	26.6 ± 4.4
Central 21/25°C	26.9 ± 2.4	25.9 ± 2.4	25.9 ± 3.3	28.9 ± 5.4
Central 30/16°C	22.5 ± 2.4	21.2 ± 2.4	20.8 ± 3.0	20.2 ± 3.9
Central 30/25°C	20.8 ± 3.0	20.5 ± 3.2	19.5 ± 2.4	20.2 ± 2.7

APPENDIX F Final dry weight of individual grains and ears. EXPERIMENTS I - IV. $\pm$ S.E. $\bar{x}$

EXPERIMENT I

Floret Position / Cultivar, Spikelet Position, Temperature		Floret a mg $\pm$ S.E.$\bar{x}$	Floret b mg $\pm$ S.E.$\bar{x}$	Floret c mg $\pm$ S.E.$\bar{x}$	Floret d mg $\pm$ S.E. $\bar{x}$	Of Ears mg $\pm$ S.E.$\bar{x}$
Triple Dirk						1548.98 $\pm$ 53.92
18/13°C	Lower	57.74 $\pm$ 1.29	61.01 $\pm$ 1.98	45.07 $\pm$ 2.17		
	Central	57.83 $\pm$ 1.12	62.90 $\pm$ 1.84	45.48 $\pm$ 2.09		
	Upper	54.77 $\pm$ 1.41	54.56 $\pm$ 3.99			
21/16°*C	Lower	57.75 $\pm$ 1.27	58.97 $\pm$ 1.38	41.43 $\pm$ 0.79		1430.94 $\pm$ 72.48
	Central	56.80 $\pm$ 0.97	57.96 $\pm$ 1.03	46.72 $\pm$ 1.73		
	Upper	52.99 $\pm$ 1.29	54.02 $\pm$ 1.64			
30/25°C	Lower	42.8 $\pm$ 0.79	42.14 $\pm$ 1.37			912.09 $\pm$ 17.28
	Central	41.15 $\pm$ 0.87	40.82 $\pm$ 0.79			
	Upper	39.55 $\pm$ 1.96	39.65 $\pm$ 1.58			
Timgalen						1860.22 $\pm$ 75.68
18/13°C	Lower	54.79 $\pm$ 1.58	55.91 $\pm$ 2.32	47.47 $\pm$ 0.35		
	Central	60.86 $\pm$ 0.90	61.87 $\pm$ 0.94	50.96 $\pm$ 0.94	31.35 $\pm$ 1.06	
	Upper	57.05 $\pm$ 0.71	56.14 $\pm$ 1.22	34.85 $\pm$ 1.14		
21/16°*C	Lower	49.99 $\pm$ 1.16	50.15 $\pm$ 1.33	41.59 $\pm$ 0.93		1683.84 $\pm$ 69.40
	Central	52.65 $\pm$ 0.94	53.09 $\pm$ 0.97	46.29 $\pm$ 1.25	31.24 $\pm$ 1.46	
	Upper	48.08 $\pm$ 1.18	47.73 $\pm$ 1.23	35.03 $\pm$ 1.67		
30/25°C	Lower	35.41 $\pm$ 0.94	35.71 $\pm$ 1.84	33.45 $\pm$ 1.73		1111.75 $\pm$ 39.44
	Central	36.18 $\pm$ 0.40	36.56 $\pm$ 1.06	33.54 $\pm$ 0.93	25.40 $\pm$ 1.06	
	Upper	35.14 $\pm$ 0.61	35.52 $\pm$ 1.00	28.72 $\pm$ 1.15		

EXPERIMENT I (Continued)

Floret Cultivar, Position Spikelet Position, Temperature	Floret a mg $\pm$ S.E.$\bar{x}$	Floret b mg $\pm$ S.E.$\bar{x}$	Floret c mg $\pm$ S.E.$\bar{x}$	Floret d mg $\pm$ S.E.$\bar{x}$	Of Ears mg $\pm$ S.E.$\bar{x}$
WW15					2793.50 $\pm$ 62.32
18/13°C Lower	56.45 $\pm$ 0.78	59.14 $\pm$ 0.96	52.90 $\pm$ 0.72		
Central	57.43 $\pm$ 1.63	60.04 $\pm$ 1.95	49.55 $\pm$ 1.31	32.93 $\pm$ 1.06	
Upper	48.97 $\pm$ 1.11	47.80 $\pm$ 1.17	33.86 $\pm$ 1.39		
21/16°*C Lower	49.30 $\pm$ 1.22	50.87 $\pm$ 1.03	43.78 $\pm$ 1.24		2518.23 $\pm$ 53.63
Central	48.80 $\pm$ 1.12	51.96 $\pm$ 1.06	42.08 $\pm$ 0.75	29.47 $\pm$ 1.14	
Upper	41.09 $\pm$ 0.97	40.83 $\pm$ 1.12	29.18 $\pm$ 1.70		
30/25°C Lower	34.55 $\pm$ 1.29	36.67 $\pm$ 1.24	27.95 $\pm$ 1.21		1463.7 $\pm$ 63.57
Central	37.08 $\pm$ 1.83	37.50 $\pm$ 1.83	32.40 $\pm$ 1.79		
Upper	31.78 $\pm$ 1.17	30.43 $\pm$ 0.96	20.68 $\pm$ 1.15		
Late Mexico 120					3406.19 $\pm$ 136.11
21/16°*C Lower	56.56 $\pm$ 1.48	57.26 $\pm$ 1.50	46.06 $\pm$ 1.08		
Central	54.32 $\pm$ 1.17	56.21 $\pm$ 1.22	47.93 $\pm$ 1.06	32.65 $\pm$ 0.71	
Upper	47.98 $\pm$ 1.41	48.30 $\pm$ 1.46	37.88 $\pm$ 2.06		
30/25°C Lower	37.42 $\pm$ 1.54	37.44 $\pm$ 1.15	32.13 $\pm$ 1.32		2237.85 $\pm$ 69.67
Central	37.13 $\pm$ 1.31	36.83 $\pm$ 1.22	32.01 $\pm$ 1.00		
Upper	35.11 $\pm$ 0.94	34.49 $\pm$ 1.37	24.77 $\pm$ 1.58		

EXPERIMENT II

Cultivar, Spikelet Position / Floret Position		Floret *a* mg $\pm$ S.E.$\bar{x}$	Floret *b* mg $\pm$ S.E.$\bar{x}$	Floret *c* mg $\pm$ S.E.$\bar{x}$	Of Ears mg $\pm$ S.E.$\bar{x}$
Triple Dirk					
15/10°C	Central	56.50 $\pm$ 1.08	58.14 $\pm$ 0.70	40.23 $\pm$ 1.35	1367.15 $\pm$ 84.12
21/16°*C	Central	56.86 $\pm$ 1.21	57.19 $\pm$ 1.30	37.83 $\pm$ 1.13	980.24 $\pm$ 50.96
30/25°C	Central	43.45 $\pm$ 1.02	43.10 $\pm$ 1.30		672.75 $\pm$ 46.12
Timgalen					
15/10°C	Central	54.56 $\pm$ 0.70	55.10 $\pm$ 0.63	43.92 $\pm$ 1.59	1065.04 $\pm$ 89.57
21/16°*C	Central	53.05 $\pm$ 1.23	53.36 $\pm$ 1.15	41.40 $\pm$ 1.65	1111.14 $\pm$ 69.25
30/25°C	Central	24.94 $\pm$ 1.17	24.99 $\pm$ 1.49	17.22 $\pm$ 1.41	437.34 $\pm$ 16.93
WW15					
15/10°C	Central	50.28 $\pm$ 0.74	55.01 $\pm$ 0.75	43.88 $\pm$ 1.06	1834.22 $\pm$ 71.05
21/16°*C	Central	43.20 $\pm$ 0.71	46.57 $\pm$ 1.09	39.78 $\pm$ 1.17	1606.93 $\pm$ 61.34
30/25°C	Central	30.22 $\pm$ 1.01	31.73 $\pm$ 0.96	25.91 $\pm$ 0.97	1077.31 $\pm$ 37.87
Late Mexico 120					
15/10°C	Central	62.42 $\pm$ 0.86	64.48 $\pm$ 0.96	51.74 $\pm$ 1.73	2015.15 $\pm$ 93.68
21/16°*C	Central	54.24 $\pm$ 1.35	55.59 $\pm$ 1.41	42.52 $\pm$ 1.48	1547.47 $\pm$ 69.17
30/25°C	Central	32.09 $\pm$ 2.02	32.42 $\pm$ 1.96	23.14 $\pm$ 1.53	801.82 $\pm$ 15.38

EXPERIMENT III

Cultivar, Light Intensity	Floret Spikelet Position	Floret a mg $\pm$ S.E.$\bar{x}$	Floret b mg $\pm$ S.E.$\bar{x}$	Floret c mg $\pm$ S.E.$\bar{x}$	Floret d mg $\pm$ S.E.$\bar{x}$	Of Ears mg $\pm$ S.E.$\bar{x}$
Triple Dirk						
21/16°*C						
8070 lux	Central	61.91 $\pm$ 0.63	63.15 $\pm$ 0.79	48.9 $\pm$ 1.41		1777.66 $\pm$ 45.46
16140 lux	Central	55.58 $\pm$ 2.28	52.63 $\pm$ 1.92			1202.34 $\pm$ 66.09
34432 lux	Central	58.22 $\pm$ 2.95	58.33 $\pm$ 1.15			1381.21 $\pm$ 50.32
48420 lux	Central	63.88 $\pm$ 0.64	64.21 $\pm$ 1.06	49.28 $\pm$ 2.11		2017.13 $\pm$ 52.80
	Central	57.51 $\pm$ 0.63	58.51 $\pm$ 1.30	41.10 $\pm$ 1.39		1614.41 $\pm$ 78.09
Sorora						
21/16°*C	Central	56.19 $\pm$ 0.78	60.17 $\pm$ 1.09	51.82 $\pm$ 1.28	35.85 $\pm$ 0.93	2189.26 $\pm$ 80.67
8070 lux	Central	39.23 $\pm$ 1.11	39.71 $\pm$ 1.49	19.13 $\pm$ 2.59		1217.60 $\pm$ 56.20
16140 lux	Central	44.55 $\pm$ 0.94	47.40 $\pm$ 0.75	38.69 $\pm$ 2.23	28.56 $\pm$ 0.91	1729.52 $\pm$ 67.56
34432 lux	Central	62.06 $\pm$ 0.64	64.33 $\pm$ 0.48	58.27 $\pm$ 0.67	41.45 $\pm$ 0.96	2609.48 $\pm$ 77.25
48420 lux	Central	58.35 $\pm$ 1.02	61.38 $\pm$ 1.53	52.41 $\pm$ 1.05	38.90 $\pm$ 1.15	2312.89 $\pm$ 78.52

EXPERIMENT IV

Floret Position / Cultivar, Spikelet Position, Temperature		Floret a mg $\pm$ S.E.$\bar{x}$	Floret b mg $\pm$ S.E. $\bar{x}$	Floret c mg $\pm$ S.E.$\bar{x}$	Of Ears mg $\pm$ S.E.$\bar{x}$
Sonora					
21/16°*C	Central	47.35 $\pm$ 1.04	50.77 $\pm$ 0.97	41.81 $\pm$ 0.92	1300.93 $\pm$ 48.97
21/16°C	Central	53.21 $\pm$ 0.86	56.46 $\pm$ 1.02	49.30 $\pm$ 0.84	1515.69 $\pm$ 71.04
21/25°C	Central	40.82 $\pm$ 0.85	42.56 $\pm$ 0.94	37.14 $\pm$ 0.60	1153.59 $\pm$ 57.34
30/16°C	Central	38.31 $\pm$ 0.78	40.63 $\pm$ 0.72	36.44 $\pm$ 0.93	1118.64 $\pm$ 51.51
30/25°C	Central	34.41 $\pm$ 0.61	35.49 $\pm$ 0.74	31.78 $\pm$ 0.56	998.88 $\pm$ 44.62
Late Mexico 120					
21/16°*C	Central	49.10 $\pm$ 1.94	51.93 $\pm$ 1.83	41.58 $\pm$ 1.60	1404.51 $\pm$ 75.91
21/16°C	Central	59.16 $\pm$ 1.89	61.90 $\pm$ 1.91	52.19 $\pm$ 1.73	1656.56 $\pm$ 83.73
21/25°C	Central	51.45 $\pm$ 1.211	53.50 $\pm$ 1.37	45.89 $\pm$ 1.75	1417.98 $\pm$ 87.47
30/16°C	Central	44.79 $\pm$ 1.32	46.23 $\pm$ 1.57	38.30 $\pm$ 1.68	1124.04 $\pm$ 82.24
30/25°C	Central	42.56 $\pm$ 1.74	43.67 $\pm$ 2.02	37.65 $\pm$ 1.90	1166.06 $\pm$ 66.47

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