THE EFFECT OF CONTROLLED ENVIRONMENTAL CONDITIONS ON THE PHOTOTHERMAL REQUIREMENT FOR GROWTH AND DEVELOPMENT, AND ON THE YIELD OF SELKIRK WHEAT

by

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ABSTRACT

The duration of the phases in the life cycle of a particular plant genotype is considered to be under environmental control and attempts have been made to mathematically express these intervals in terms of the data representing the prevailing environment. One such expression, involving the temperature level and length of photoperiod, is known as the "Photothermal Index" which represents the photothermal requirement for a certain interval. In the course of this study the concept of photothermal constants has been thoroughly tested for the common wheat variety Selkirk (*Triticum aestivum L.*) under artificial growing conditions. Controlled variations in temperature, photoperiod, moisture and fertility levels were possible and as an adjunct the effect of these variations on yield characteristics (tillering, seed number, seed size and protein percentage) were obtained.

It was found that the photothermal requirement is relatively constant for the periods emergence to heading and heading to maturity. However, certain exceptions were noted. The requirement increases with increasing fertility and when the temperature of the dark period is lower than that prevailing during the photoperiod. There is also an indication that for the period heading to maturity, low temperatures and low moisture levels reduce the requirement slightly. Tiller number was found to be greatest at temperatures of 54°F. and 60°F. but a higher proportion of spikes produced at 54°F. failed to set seed. Seed number was found to be favoured by a temperature of 60°F. while seed weight was highest at 54°F. Both characters are influenced by moisture levels. Protein percentage was unaffected by temperature but appeared to depend on the availability of soil nitrogen.

INTRODUCTION

Plant behaviour is determined by the genotype and its interaction with the environment. This was first shown by Johannsen (quoted by 12), who considered that variations within a pure-line were the result of environmental modifications of the genotype. To describe this variability he used the word "phenotype". An understanding of phenotypic variation is imperative to successful plant breeding, in the evaluation of plant types from diverse origins, in differentiation among the plants of segregating populations and in the critical interpretations of field trials (10).

In the past 50 years the work of many scientists has been devoted to the study of plant responses to the environment. It has been stressed by Dionne et al., (7) that before agronomists can establish environment-plant relationships, the role of the individual environmental factors in plant life must be known. In this connection they have determined the total amount of heat and light required by a plant to complete certain phases of its life cycle. This value, known as the photothermal requirement, is calculated by the multiplication of the duration in days, the photoperiod in hours and the temperature in degrees F. minus 40. Azzi (1) found it to be remarkably constant for the variety Frontana over a period of several years while Nuttonson (20) has drawn the same conclusion for the variety Marquis grown at widely separated locations over a single year. However, under natural conditions temperature cannot be separated from total insolation.

This present study was designed to critically examine the constancy of the photothermal requirement for the common wheat variety Selkirk (Triticum aestivum L.) under conditions where the temperature could be varied independently of light. The influence of moisture and fertility levels on the photothermal constancy was also studied. As an adjunct to this main study the effect of the treatments on yield characteristics (tillering, seed number, seed weight and percent protein) was measured.

LITERATURE REVIEW

Annual cereals, in the course of their development pass through a series of stages, namely, germination, foliage development, heading and maturity. The sequence of these stages is probably determined by gene controlled physiological processes, although the final expression of the genotype and the rate at which these stages follow each other is influenced by the prevailing environment (10).

Billings (2) has defined the environment of a plant as all of the external forces and substances affecting growth, structure and reproduction. The more important environmental factors, as listed by Klages (14) are light, temperature, water, essential minerals, CO_2 and O_2. Good (11) considers that, "Each and every plant species is able to exist and reproduce successfully only within a definite range of climatic and edaphic conditions. This range represents the tolerance of the species to external conditions". Within this tolerant range, however, plant growth is suppressed when any factor of the environment deviates from the optimum required for a particular species (2).

The study of plant responses to the environment covers an immense field because each environmental factor is subject to an infinite number of quantitative variations and because there is a constant interaction between all factors. The complexity of these variations and interactions, makes it exceedingly difficult to study and interpret the effects of a single environmental factor. For this reason many workers

(7, 14, 13, 3, 28) stress that the study of any individual factor necessitates the standardization of the other variables. However, Azzi (1) prefers to statistically assess the role of each individual factor from data collected on natural populations over a long period of time.

That portion of the sun's radiant energy that forms the visible spectrum is commonly referred to as light although radiation at either end of the spectrum has been shown to affect plant development. The radiant energy of light can be considered from three points of view, namely, intensity, quality and duration and each of these factors has been shown to influence plant growth and development (21, 9, 4, 5). With the exception of the reactions that are solely photochemical in nature, temperature has been shown to influence all bioprocesses including those that require light for their completion (3, 21).

In general, the rate of any reaction increases, 2 to 3 times, for every 10°C. (18°F.) rise in temperature between the temperatures of 32°F. and 95°F. (9). The tolerant temperature range for cellular metabolic activity depends on the phyiological maturity of the plant (3, 15). Maximov (15) has shown that the tolerant range for germinating wheat extends from 37°F. to 92°F. while Dionne _et_ _al_. (7) state that for the vegetative growth of wheat this range extends from 32°F. to 107.6°F. However, Azzi (1) has determined that growth of wheat is hardly possible below 40°F. while the lower limit for floral initiation is considered to be between 48°F. and 50°F. He also considers that the most critical period in the growth of wheat with respect to the temperature effect on yield is during the ten day period after heading. If the temperature prevailing over this phase is 55°F. or lower, the maturation period is extended considerably and many florets are infertile, or if fertile, the grain does not fill properly. When temperatures rise above an upper threshold, transpiration may be so great that symptoms of physiological drought set in which result in infertility and shrunken seeds (1). Thus the upper threshold level varies directly with the conditions of humidity and available soil moisture. With low humidity and little available soil moisture a temperature of 77°F. may be critical but if the moisture level is higher, temperatures up to 83°F. are not harmful and temporary excursions to 100°F. are not detrimental if of short duration.

The effect of light intensity is mainly through the relationship it bears to the rate of photosynthesis and consequently to the amount of available photosynthate (3). In wheat the maximum rate of photosynthesis is reached at 5300 foot candles provided CO_2 supply is adequate and temperature is optimal. However, the light energy is required only for the photodecomposition of water and not for CO_2 reduction, a process which may proceed in the dark at a rate which is governed by the prevailing temperature. This latter reaction may form a "bottle neck" in the process of photosynthesis as shown by Newton (19) who determined that, in wheat grown at 55°F., growth was at a maximum at 1400 foot candles whereas at 65°F. growth rate continued to increase up to 1800 foot candles.

Thus, warmer conditions are necessary to make greatest use of high light intensity.

In contrast to photosynthesis, respiration is independent of light. Temperature then is the major environmental factor that determines the rate at which chemical energy is released from sugar and partially stored in the form of adenosine triphosphate. For example, at 57°F. the intensity of respiration in wheat is 291 (ml O_2/hr /gm fresh weight) while at 76°F. this rate would be 582 to 727 (9).

Bonner and Galston (3) state that growth in plants is determined by the balance between the rate of photosynthesis and that of respiration. The total dry matter yield of the plant can be defined as the accumulation of photosynthate not used in respiration. Thus the conditions which lead to the greatest accumulation of photosynthate (i.e. conditions which favour a rate of photosynthesis far greater than the rate of respiration) results in greatest growth.

In addition to indirectly affecting growth through control of available photosynthate, light and temperature are important in the morphogenic development of plants. The photomorphogenic effects result particularly from the spectral composition and duration of light to which plants may be exposed (3, 28, 21, 9, 22, 18, 4, 27). Hypocotyl development is retarded by red light (9) but the rate of germination, coleoptile growth and extension of the subcrown internode are mainly influenced by temperature. Differentiation of the tiller primordia is reduced by the action of blue light (6), by high temperatures (1, 27, 16) and by the influence of long photoperiods (22, 8). Riddell and Gries (23), however, show that in certain varieties high temperatures increase tillering. Azzi (1) considers 65°F. as optimal for tiller production. Red light reverses the action of blue light by encouraging tillering and also causes a decrease in stem elongation with an accompanying increase in stem thickness (6). Riddell and Gries (23) associate short photoperiods with more stunted plants and a lower number of nodes although they claim that node number increases with increasing temperatures (23). The production of nodes (and therefore leaves) is, however, shown by Riddell and Gries (23) to be greatly influenced by the variety of wheat considered. In addition to affecting leaf number Crocker (6) reports that blue light decreases differentiation of leaf tissues. Red light, however, is said to stimulate leaf expansion while high temperatures (26) and long photoperiods (16) tend to reduce leaf size. In wheat red light is thought to promote flowering but the heads may be poorly developed (21). Plants heading out in blue light are similarly affected and there is a decrease in the number of florets formed (6). Temperatures which approach the limits of the tolerant range also reduce the number of fertile florets (1). The photomorphogenic effects of the spectrum are considered by many workers to be of particular significance and thus maintain that a spectral balance is a prerequisite for normal growth (3, 28, 21, 9, 4, 5, 6). Under artificial conditions the spectral composition of natural light is seldom attained (6).

In 1920 the relationship of day length and development (photoperiodism) was enunciated by Garner and Allard (quoted by 3, 28, 21, 9). The original theory now somewhat revised, leads to the present day conception that there are three main groups of plants, long day, short day and day neutral (3). In the case of long day and short day plants, initiation of the flowering primordia requires a specific treatment of day length, i.e. photoperiodic induction is essential, whereas with day neutral plants, initiation results as a consequence of a certain required amount of growth, i.e. a quantitative effect. Wheat is considered to be a long day plant although it has been shown by Riddell _et_ _al_. (22) that certain varieties will flower under a photoperiod as low as eight hours.

The completion of the life cycle in relation to time depends not only on photoperiod but more precisely on the photoperiod-temperature interaction. Increased temperatures are generally considered to hasten heading (1, 15, and 19) but with the varieties Chinese and White Federation 38, Riddell and Gries (23) have reported that increasing temperatures delay heading. They have reported that in these varieties initiation may be accelerated by prior exposure to cold temperatures. This acceleration, however, applies only to spring varieties that are normally considered to be late whereas initiation is delayed in those spring varieties normally considered to be early (25). Increasing both temperature and photoperiod is reported to decrease the period from initiation to heading and also the overall period to heading (23). The relationship between temperature and photoperiod in accelerating heading is reported by some workers (1, 20) to be additive while Riddell and Gries (22, 23) believe a greater response is shown to increasing photoperiod with certain varieties. For the period heading to maturity a reduction is reported with short photoperiods irrespective of temperature (16) while other authors (1, 17) claim that this period is also reduced by increasing temperatures.

As a result of the importance of the light-temperature interaction on the duration of a plant's life cycle, attempts have been made to quantitatively evaluate this relationship in terms of the flowering behaviour and morphological development of the wheat plant (1, 20). Earlier attempts considered only temperature and the proposal suggested was to sum all average daily temperatures above a certain base; 38°F. as used by Nuttonson (20) and 40°F. by Azzi (1). This sum, or as it was known, the "Remainder Index", would indicate the thermal quantity required and was calculated for the various phases in the life cycle (1, 20). This method, however, gives no weighting of efficiency to different temperatures and the detrimental effect of values outside the optimum range are ignored. In some cases this index has proven of value in predicting heading dates and in determining climatic analogues between parts of the U.S.A. and continental Europe. In more recent years, when photoperiod was also shown to affect the time of completion of the life cycle, attempts have been made to incorporate this effect into the Remainder Index by multiplying the latter by the length of the light period in hours. Such a product is referred to as the "Photothermal Index" (20) and since its inception it has been postulated that the photothermal requirement for a particular period of the life cycle is a constant for a particular variety. This has become known as the "Concept of Photothermal Constants" but its use has been confined only to field conditions (1, 20).

Azzi (1) measured the photothermal requirement for the variety Mentana over a number of years for the period sprouting to heading and found it to be constant at 15,520 photothermal units. For the period heading to maturity the figure was 9,800 (1). Nuttonson (20) tested the concept more thoroughly by gathering data on Marquis wheat at locations ranging from Alaska to Mexico. He found the crop took an average of 1,488 Day degrees (C.V. 11.4%) or when photoperiod is concerned its photothermal requirement was calculated as 21,700 (C.V. 7.8%).

Except for the work of Azzi (1) and Nuttonson (20) no other reports on the photothermal requirements of wheat have been made, but it is possible to calculate the photothermal requirement for Chinese and White Federation 38 from evidence reported by Riddell and his co-workers (22, 23 and 24). From this data, which was obtained under controlled environmental conditions, it was calculated that the photothermal requirement for the period initiation to heading for White Federation 38 was a constant at 15,000 ± 600 photothermal units. However, for the period emergence to initiation for White Federation 38 the photothermal requirement varied from 8,000 photothermal units at 60°F. to 21,000 photothermal units at 80°F. irrespective of photoperiod. With the variety Chinese the photothermal requirement for either period was not a constant, e.g. for the period emergence to initiation it varied from 13,000 to 33,500 photothermal units and for the period initiation to heading it varied from 15,000 to 28,000 photothermal units. Thus it would appear that the constancy of photothermal requirements does not apply to all spring wheat varieties.

MATERIALS AND METHODS

Seed of the spring wheat variety Selkirk, originating from a single plant grown at Saskatoon in 1954 was used in all tests. The plants, therefore, were considered to be of the same genotype, and hence, the variability caused by genotype could presumably be ignored.

Seed was sown at a depth of one inch in pots placed in growth cabinets under controlled conditions. In each case two or three seeds were sown in each pot but only one plant was retained from the time of emergence. The soil was a mixture of three parts loam, one part sand and one part peat moss. Pots were of the four inch plastic type. Marble chips were placed in the bottom of the pot, covered by a layer from the top with the soil mixture. The volume of soil in each pot was identical throughout all tests. In all experiments except two, E and G, where the fertilizer effect was under test, the level of fertility in the soil was raised in order to eliminate fertility as a variable factor. One-half gram of 35 per cent ammonium nitrate and one-half gram of 24 per cent phosphate fertilizer were added to each pot. In all the experiments except C and D, where measured amounts of water were used, watering was carried out by overflowing each pot every second day.

Three growth cabinets were used in the studies. These were of a type manufactured in Winnipeg under the trademark Coldstream by the Fleming-Pedlar Company (see Figures I and II).

Figure I. End View of Growth Cabinet, showing the location of the controls and the growing room.

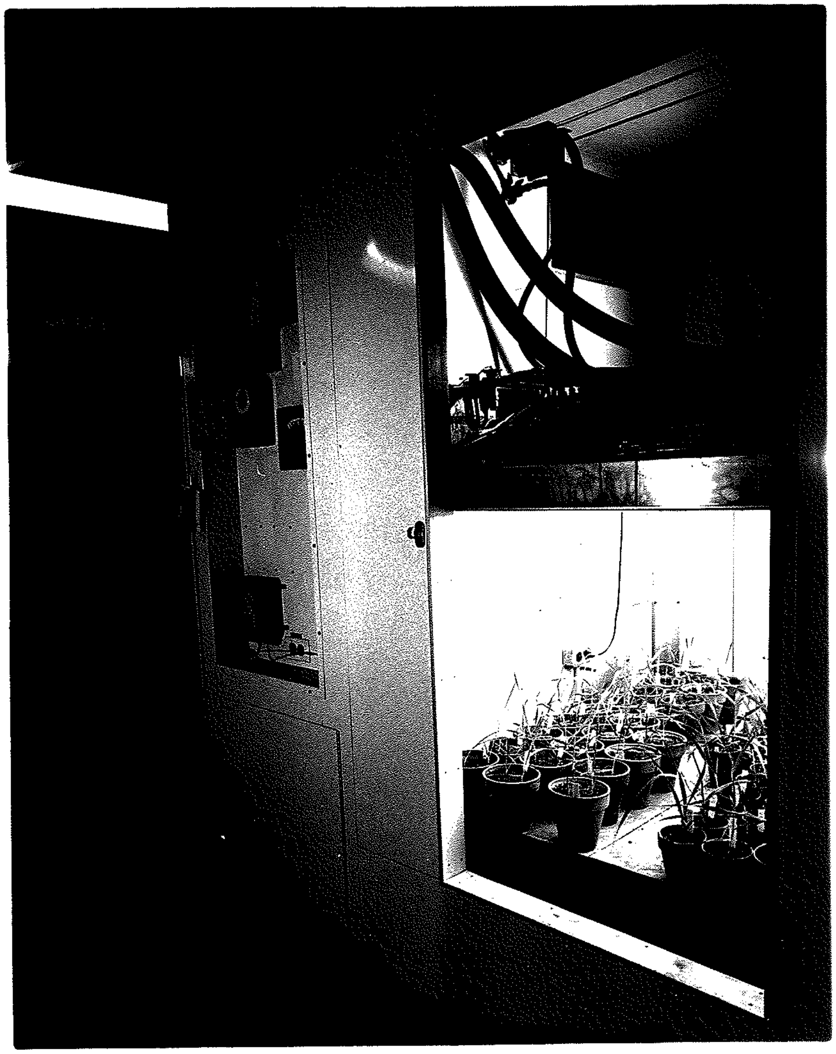

Figure II. Side View of Growth Cabinet, showing the growing room with platform, the adjustable light hood with its associated cooling unit and the air inlet.

This type of growth cabinet combines a growing area enclosed by doors with a movable light hood mounted above, and a platform raised above the floor on which the pots are placed. The cooling system is located at one end of the cabinet and consists of a refrigeration unit, a cooling radiator and a fan which moves the air through the radiator and returns it to the cabinet. Air is exhausted from the growing area through an opening below the platform and returned through an opening above the light hood. The air moves down into the growing area around the outside edges and through vents placed along the mid-line of the hood. In addition to the cooling unit, ballasts for lights and the control panel for temperature and light settings are located in the same portion of the cabinet. Light is supplied by 32 fluorescent tubes eight feet long of the standard reflector cool white type with eight incandescent 60 watt bulbs. The hood is so designed, that the tubes near the mid-line are farther away from the plants than those at the edges. The incandescent bulbs are located along the centre line. The fluorescent tubes supply most of the light and the incandescents supply additional light in the red portion of the spectrum that is lacking in the fluorescent light emission. Light intensity throughout the growing area, as measured by a Weston illumination meter (Model 756), varied between 1,000 and 1,600 foot candles on the platform when the lower edge of the light hood was 24 inches from it. Temperature may be controlled within the cabinets in the range 50° to 80°F. and air temperature fluctuates in a range of $\pm 2^{\circ}$F. about a specific setting. Water temperature measured in this range showed virtually no variation.

An area four feet six inches by six feet was measured out and centred on the growing platform. This area was then demarcated in a grid six inches by six inches. Pots were placed on the intersecting lines of this grid. Temperatures and light intensity were measured at these grid points, prior to beginning the experiment (see Appendix I).

Notes were taken on the number of days between emergence and heading and between heading and maturity. Heading was considered to have occurred when the last spikelet of the head emerged from the boot. Plants were considered to be mature when the chlorophyll had disappeared from the head. Numbers of tillers, weight of seed per tiller and protein percentage were also recorded in certain of the experiments.

The first experiments were used to determine which areas of each cabinet were environmentally similar. One hundred and thirty-four pots were placed in each cabinet at the time of planting. Of these 30 were discarded on the basis of poor germination or poor plant growth in the initial seedling stage. Of the 104 pots remaining, those located in certain areas which showed marked discrepancy from the normal were not included in the results. This discrepancy arose largely from irregular air circulation. However, the plants were left at each grid point to provide light competition for the surrounding plants.

Three general types of experiments were performed. For ease of presentation these are listed as individual experiments, although a certain interlocking of experiments occurred where pots were moved from cabinet to cabinet into conditions of different light and temperature:

Experiment A - This experiment was conducted to test the effect of temperature on the photothermal requirements for the periods emergence to heading and heading to maturity. Yield components were studied where possible. Three cabinets were employed, which were held at temperatures of 50°F., 60°F., and 70°F., respectively, throughout the growth cycle with a photoperiod of 18 hours.

Experiment B - In this experiment observations were made on the effect of photoperiod on the photothermal requirements for the same periods as in Experiment A. Two cabinets were kept at a constant temperature of 60°F. For one of these a 15 hour photoperiod and in the other a 21 hour photoperiod was maintained.

The design of subsequent experiments in the series was dependent on the results obtained in Experiments A and B. Since results indicated that the photothermal requirements for genetically similar plants were relatively constant, irrespective of variation in temperature and photoperiod, other experiments were designed to test this concept further by complex variations in light and temperature and by introducing variation in the edaphic conditions.

Experiment C - In this test the influence of temperature and moisture conditions on photothermal requirements in the heading to maturity stage was investigated. From Experiment A, 60 plants were removed from the cabinet held at 70°F. immediately after heading. Of these 30 were placed in a cabinet at 50°F. and 30 were placed in a cabinet at 60°F. and each held constant for an 18 hour photoperiod. These were further subdivided into three groups of 10 plants each of which were given differential water applications of 50, 100, and 150 ml respectively, every two days. A similar treatment was accorded 30 plants of those remaining in the cabinet at 70°F.

Experiment D - This experiment was designed to show the influence of a deficiency or an excess of moisture application on the photothermal requirements from emergence to heading and heading to maturity. Yield was also taken on these plants. Temperature was held constant at 60°F. with a photoperiod of 21 hours. This experiment was of a factorial type where two treatments of moisture application, namely 30 ml and 150 ml, were applied every other day at three growth stages, emergence to the fifth leaf stage, fifth leaf to heading and heading to maturity. This gave a total of eight treatment combinations, for example, 30 ml of water were applied throughout all of the three growth periods, in a second 30 ml were applied, throughout the first two periods and this was followed by 150 ml in the third period, and so forth.

Experiment E - In this test observations were made on the effect of nitrogenous fertilizers on the photothermal requirements for the period emergence to heading and on the yield of each plant. Temperature was kept constant at 60°F. with a photoperiod of 15 hours. Four fertilizer treatments were used. One gram of ammonium nitrate was applied at seeding and again at the fifth leaf stage in one series of pots; in the second only at seeding; in the third only at the fifth leaf stage; and in the fourth no fertilizer was applied.

Experiment F - In this test observations were made on the photothermal requirements for the period emergence to heading when temperature and photoperiod were altered at different points in the growth cycle. Plants were grown in a cabinet held at 50°F. with a photoperiod of 18 hours. At the third leaf stage 20 plants were removed and placed in a cabinet at 60°F. with a 21 hour photoperiod. A further 20 were removed at the fifth leaf stage and placed in the same conditions.

Experiment G - This experiment was designed to determine the photothermal requirements for the period emergence to heading when the temperatures during the 18 hours of light and 6 hours of darkness were 70°F. and 50°F. respectively. Fertilizer treatments were superimposed in this test. Four treatments were applied, namely, no fertilizer, one-half gram ammonium nitrate at seeding, one-half gram phosphate fertilizer at seeding, and lastly, one-half gram of each type at seeding. The fourth treatment as noted earlier was the standard fertilizer treatment for all soil except in Experiment E.

Photothermal constants were calculated in the following manner (Azzi 1):

Photothermal Constant = Number of days x (Temperature °F. - 40) x Photoperiod in hours.

Nitrogen determinations were made on the basis of the Kjeldahl Test.

RESULTS AND DISCUSSION

The experiments outlined in the section on materials and methods are presented separately in the interests of clarity. Information obtained for certain treatments which were applied in earlier experiments is presented in the table of later experiments wherever it is applicable.

Experiment A

In Table I are presented the results of this experiment.

Table I. The effect of variation in temperature on the photothermal requirement for two stages of plant growth. (Photoperiod - 18 hours).

Temperature	No. of Plants Measured	Days from Emergence to Head	Photothermal Units	Days Heading to Maturity	Photothermal Units
50	42	95.1* ± 3.2	21,416	72	12,980
60	60	60.4 ± 2.2	21,738	39	14,040
70	66	40.9 ± 1.6	22,140	25	13,500

* Because of failure of controls on the cabinet to maintain 50°F. during a short interval, the number of days to head was shortened. Calculation of photothermal requirements for this period comprise a summation of the actual temperatures recorded on the temperature chart.

The results of this experiment indicate that the photothermal requirement for the period intervening between emergence and heading, and heading and maturity remains relatively constant despite a wide variation in temperature. This corresponds to the conclusions of Azzi (1). The variation among the results of the earlier period is less than that of the latter period.

Table 2. The effect of temperature variations at a constant photoperiod (18 hours light in a 24 hour cycle) on yield characteristics, and protein of main tiller seed (10 plants per treatment).

	Tillers			Main Tiller		Other Tillers		Main Tiller
Temperature	Fertile	Infertile	Total	No. Seeds	Seed Wt. Grams	No. Seeds	Seed Wt. Grams	% Protein in Grain
50	3.38	1.71	5.09	17.8	0.48	3.9	0.084	17.8
54*	3.72	0.90	4.62	26.1	1.01	12.5	0.417	17.4
60	3.04	-	3.04	36.7	1.19	24.8	0.927	17.7
70	1.97	1.04	3.01	34.5	0.87	18.6	0.643	17.8

* A number of plants growing at the one end of the cabinet at 50°F. were at a temperature of 53 to 55°F. because of the poor circulation of air in that region. These plants were normally considered to be discards, but in this case were harvested because of their visibly better head and seed sizes.

The number of tillers and the number of seeds and seed weight for main tillers and secondary tillers are presented in Table 2 together with the percentage protein based on seed from the main tiller.

It may be noted generally that temperature plays a significant role in determining the extent of development of the yield components. The extent of tillering at 60°F. and above was constant, whereas it increased as temperature decreased below 60°F. There appears to be a critical point or threshold between 54°F. and 60°F. below which the degree of tillering was increased. The highest percentage of fertility was noted for those tillers that matured at 60°F. and decreased below and above this point. Presumably the plants are subject to more rapid development at the higher temperatures and subject to intertiller competition for nutrients at the lower temperatures.

The theoretical threshold mentioned above (between 54°F. and 60°F.) appeared to affect the number of seeds per main tiller. At 60°F. and above, the number of seeds produced was fairly constant, whereas below 60°F., the number of seeds decreased as temperature decreased. In the case of secondary tillers, the most seeds were produced at 60°F. The number was lower at 70°F. and decreased even more in number at the lower temperatures. At the higher temperatures the rapidly growing main tiller reduced seed set on the secondary tillers, while at the lower temperature the greater number of tillers in the limited soil available, resulted in intertiller competition, so that a lower number of seeds per tiller were produced.

Grain weight also appeared to be affected by temperature. At 54°F. the highest individual seed weight was obtained and as temperature increased seed weight decreased, probably because increased respiration at the higher temperatures reduces the amount of carbohydrate that may be available for storage in the seed. Similarly, it may be suggested that at 50°F. the reduction in individual seed weight results from a decrease in the amount of photosynthate elaborated.

Temperature appeared to have no affect on the percentage of protein in the seed of the main tillers. The percentage of protein in the seed would appear to reflect the nitrogen status of the soil.

Experiment B

In Table 3 the effect on the photothermal requirement is recorded for three different photoperiods where temperature was maintained at 60°F.

These results indicate that the photothermal requirement remains relatively constant despite fluctuations in photoperiod. It may be noted that the photothermal requirement at 15 hours photoperiod was lower than that at 18 and 21 hours. It is possible that the longer dark period may allow physiological processes to reach their conclusion sooner than when the dark period is of shorter duration.

Table 3. The effect of variation in photoperiod on the photothermal requirement for two stages of plant growth at a constant temperature of 60°F.

Photo-period	No. of Plants Measured	Days from Emergence to Heading	Photo-thermal Units	Days from Heading to Maturity	Photo-thermal Units
15	20	67.2	20,160	44	13,200
18*	60	60.4	21,738	39	14,040
21	10	50.6	21,252	33	13,860

* Results from Experiment A

Because of the constancy of the photothermal requirements for the development of different phases in the life cycle of the wheat plant which were observed, the possibility existed, that if other environmental factors were varied, this constancy might not always apply. Thus further experiments were designed in which moisture and fertility were varied together with temperature and photoperiod.

Experiment C

In Table 4 are presented the results obtained when plants grown from emergence to heading at 70°F. were placed in different temperatures during the period heading to maturity. Three levels of moisture application were superimposed during this period. Photothermal requirements for the period heading to maturity, together with weight of grain per head, number of seeds per head, and percentage protein of the seed were recorded.

Table 4. The effect of variations in temperature and moisture application during maturation period on photothermal requirement, weight of grain and number of seeds per main tiller and protein content of seed.

Temperature								
Seeding to Heading	Heading to Maturity	No. of Plants Measured	Water Every 2nd Day (ml)	No. Days Head to Maturity	Photo-thermal Units	Wt. of Grain/ Head (gm)	No. Seeds/ Head	% Protein
70	70	10	50	24.5	13,110	0.81	32.6	17.9
		10	100			0.96	33.8	16.9
		10	150			1.04	35.1	16.9
70	60	10	50	36.0	12,960	1.01	35.1	17.5
		10	100			1.04	35.8	17.3
		10	150			0.98	34.2	17.5
70	54	6	50	44.0	11,088	1.13	33.6	17.8
		7	100			1.12	32.0	17.1
		7	150			1.01	28.6	16.8

When compared with the results of Experiment A, it was interesting to note that by lowering the temperature from 70°F. to 60°F. for the maturation period, the photothermal requirement was slightly lower than when the plant was reared at 70°F. throughout its life. When it was reduced to 54°F. for this period, the requirement was considerably lower. Moisture levels had no apparent effect on the interval between heading and maturity. In Experiment A, it was concluded that at 54°F. individual grain weight was greater. From the above results, it appears that this is again the case, but here the temperature has been varied only during the maturation period, which seems to indicate that the critical period in regard to grain weight occurs after heading. Moisture levels appeared to have little effect on grain weight at the lower temperatures, but at the higher temperature the lower moisture levels were probably a limiting factor.

The number of seeds per head appeared to increase slightly with increased water supply at the higher temperature. At the 60°F. level, the seed weight remained essentially the same at all moisture levels but at 54°F. the higher moisture levels probably caused waterlogging, which resulted in a reduction in the number of seeds per head. Percentage protein in the seed did not appear to be materially affected by temperature, or by moisture levels. Again the protein content of the seed reflects the nitrogen content of the soil.

Table 5. The effect of application of two levels of moisture applied in combination with growth stage on the photothermal requirements, tillering capacity, yield of grain, and seed number at a temperature of 60°F. and a photoperiod of 21 hours (10 plants per treatment).

Treatment in Sub Periods I	II	III	Days to Head**	Photo-thermal Units	No. of Days from Head to Maturity	Photo-thermal Units	No. of tillers Fertile	Infertile	Main tiller Yield (gm)	Seed No.
A	A	A*			29	12,180	1.0	-	1.00	28.6
A	A	B			31	12,980	1.0	0.4	1.08	37.3
A	B	A			33	13,860	1.8	0.8	1.33	37.0
A	B	B	50.6	21,252	33	13,860	1.4	1.8	1.28	37.0
B	A	A			31	12,980	1.0	-	1.17	33.4
B	A	B			31	12,980	1.4	0.2	1.24	37.1
B	B									
B	B	A			33	13,860	2.2	0.4	1.09	37.0
B	B	B			33	13,860	2.8	0.8	1.06	38.4

* Treatment A - 30 ml moisture every second day, Treatment B - 150 ml moisture every second day, so that Treatment AAA - 30 ml moisture during each period. AAB - 30 ml in first two periods followed by 150 ml in the third period.

** Since there was no apparent variation in number of days to heading among the different moisture treatments, an average figure is given.

*** Sub Periods I - Emergence to fifth leaf. II - Fifth leaf to heading.
III - Heading to maturity.

Experiment D

Because of the inconclusive results for the effect of moisture level in Experiment C, it was decided to test this factor further, using two levels of water application, namely, 30 ml (A) and 150 ml (B), applied every other day. These were applied in different combinations over the growth period of the plant, using the periods emergence to fifth leaf, fifth leaf to heading, and heading to maturity. A total of eight treatment combinations are therefore possible. Temperature and photoperiod were maintained at a constant level of 60°F. and 21 hours, respectively.

Records of photothermal requirements, number of tillers, seed number and yield per main tiller were collected and are shown in Table 5.

From these results it appeared that the moisture treatments had no effect on the photothermal requirements up to heading. However, in the period heading to maturity, the photothermal requirement was reduced in all those treatments where 30 ml were applied during the period fifth leaf to heading. Tiller initiation was seriously reduced under these conditions and for maximum tillering it would appear that an adequate amount of water is essential from emergence to heading, the most critical period being from the fifth leaf to heading (i.e. the tillering stage). When adequate moisture was applied over this period tiller production was stimulated. However, if this period had been preceeded by a dry period, the secondary tillers would not grow at the rate set by the main tiller and showed a large degree of infertility. Conversely when adequate moisture was supplied from emergence to heading, the secondary tillers closely followed the main tiller so that finally there was a greater proportion of fertile heads. The yield of the main tiller heads is reduced when drought conditions prevail up to heading or when an excess of moisture is used through this period. In this latter case, the greater number of tillers initiated probably resulted in intertiller competition which reduced the main tiller yield. The number of main tiller kernels is unaffected by moisture levels except in those cases where drought prevailed from the fifth leaf stage to maturity.

Table 6. The effect of nitrogenous fertilizer on the photothermal requirement, number of tillers per plant, and on the yield, number of seeds and protein content of seed from the main tiller (Temperature 60°F. and photoperiod of 15 hours) (Average of eight plants per treatment).

Treatment	Days to Head	Photo-thermal Units	Av.No.of Tillers/ Plant	Av. Yield/ M.T.gm	No. Seeds/ M.T.	% Protein
(FF)	69.95±2.7	20,979	1.2	0.50	25.3	27.00
(FN)	69.09±3.8	20,727	2.6	1.05	36.0	22.75
(NF)	61.95±3.1	18,585	2.6	0.75	36.0	24.05
(NN)	63.00±2.0	18,900	1.8	1.33	39.1	12.70

FF - Fertilized at seeding and again at fifth leaf stage

FN - Fertilized at seeding only

NF - Fertilized at fifth leaf only

NN - Not fertilized

<u>Experiment E</u>

In Table 6, the effect of nitrogenous fertilizer on the photothermal requirement, tillering, grain weight, and seed number produced per main tiller is presented, together with protein percentage of the seed. The temperature was maintained at 60°F. and the photoperiod at 15 hours.

Application of fertilizer during the seedling stage greatly increased the interval to heading, while fertilizer applied at the fifth leaf stage only, did not have this effect, being essentially the same as the control. As a result, the photothermal requirements for those plants fertilized at seeding was greater. The average number of tillers was greatest when only one fertilizer application was made, whether applied at seeding or at the fifth leaf stage. When fertilizer was applied at both stages, a reduction in number of tillers occurred. This undoubtedly reflects a toxic effect from excess fertilizer, since a two-gram application to the pot volume of soil amounts to approximately 1500 lbs. of fertilizer per acre. In the average yield of the main tiller, the control showed the highest seed weight. Apparently, although the single application of fertilizer was not toxic for the vegetative growth of the plant, it may have been toxic in the development of seeds, or the additional growth resulted in intertiller competition. The greatest effect was noted where fertilizer was applied at the fifth leaf stage. In the number of seeds per main tiller, the control showed the highest number. When one application of fertilizer was applied, growth stage at the time of application had no effect, but under two applications, the greatest reduction occurred. The most surprising result of the experiment was the tremendous increase in percentage protein. Where fertilizer was applied at two stages, protein was more than double that of the control. The results give some indication that fertilizer applied at the fifth leaf stage has a greater effect in increasing protein than that applied at seeding. However, with an application of fertilizer at seeding, the yield of the main tiller was only twenty-one percent lower than the check, but the protein was increased by seventy-nine percent. It should be pointed out that protein percentage was determined by the Kjeldahl test and measures crude protein, some of which may be non-elaborated nitrogen.

Experiment F

In the preceeding experiments, the temperature was held constant throughout the growing period, except in Experiment C, in which temperature treatments were changed in the period heading to maturity. Since no information was available on the effect of varying temperature and photoperiod during the interval from emergence to heading, Experiment F was designed to obtain this information.

Table 7. The effect on photothermal requirement of changing temperature and photoperiod for different growth stages.

Stages of Growth	No. of Plants Measured	Temperature °F	Photo-period Hours	Duration in Days	Photo-thermal Units	Total Photo-thermal Units
Emergence to heading (from Experiment A)	42	50	18	95.1±3.2	21,416	21,416
Emergence to third leaf		50	18	35.5	6,390	20,628
Third leaf to heading	20	60	21	33.9±1.2	14,238	
Emergence to fifth leaf		50	18	62.1	11,178	19,716
Fifth leaf to heading	20	60	21	20.3±1.2	8,538	
Emergence to heading (from Experiment B)	20	60	21	50.6		21,252

In Table 7 are presented the results obtained for photothermal requirement when plants, initially grown at 50°F. and 18 hours photoperiod, were transferred at the third and fifth leaf stages to a temperature of 60°F. and 21 hours photoperiod. For comparison, the results from Experiment A and Experiment B are included, where plants were grown from emergence to maturity, at 50°F. and 18 hours and 60°F. and 21 hours, respectively.

The results from Experiment A and Experiment B show that the photothermal requirement at each level was essentially equal. However, when the plants were transferred at the third leaf stage to the higher temperature and photoperiod, the total photothermal requirement was reduced. When this transfer was made at the fifth leaf stage, this reduction was even more apparent. This reduction is considered to be associated with the change in temperature and not the change in photoperiod. The increased exposure to the colder temperature of 50°F. is thought to be responsible for the decrease in the photothermal requirement. The reasons for this are not understood although it may be speculated that they are analagous to those in operation when extended exposure to cold treatments results in hastening heading and maturity in late spring wheat varieties (25).

Experiment C

In the preceeding experiment no attempt was made to vary temperature over each 24 hour cycle. In order to get controlled diurnal variation this experiment was designed with the object of providing 70°F. during the light period and 50°F. during the dark period. On this was superimposed fertilizer treatments designed to test the effect of nitrogenous and phosphate fertilizers. Besides the control, nitrogen alone, phosphate alone, and nitrogen and phosphate together, were applied at seeding. The last treatment corresponds to the standard level of fertility, used in all the preceeding experiments, except where fertilizer was used as a variable.

Table 8. The effect of diurnal temperature variation and fertilizer treatment on the photothermal requirement and tillering capacity at 70°F. during the light period, 50°F. during the dark and photoperiod of 18 hours (10 plants per treatment).

Treatment at Seeding	Days to Head	Photo-thermal Units #1	Photo-thermal Units #2	Number of Tillers	
				Fertile	Infertile
A - nil	45.2±1.8	24,408	20,310	1.4	1.2
B - $\frac{1}{2}$ gm N	49.9±1.2	26,346	22,455	1.0	0.3
C - $\frac{1}{2}$ gm P	48.1±0.7	25,974	22,050	3.0	2.0
D- $\frac{1}{2}$ gm P $\frac{1}{2}$ gm N	50.3±1.2	27,162	22,635	2.0	0.9

#1 Photothermal units calculated using only the temperature during the light hours (as in Experiments A to F), when "day" and "night" temperatures were the same.

#2 Photothermal units calculated using Went's (28) phytotemperature which takes into consideration a lower night temperature according to the formula: Phytotemperature = Tmax. - $\frac{1}{4}$(tmax. - tmin.). The factor $\frac{1}{4}$ presumably comes from the relationship of dark period of six hours to the 24 hour period.

In Table 8, data on the days to head, photothermal requirement, and number of tillers for each of the four fertilizer treatments are recorded.

It appears from the table that application of fertilizer tends to increase the number of days to head over the check, the smallest increase resulting from the phosphate application. It is interesting to note that the plants treated with the nitrogen and phosphate together (the standard treatment on other tests) headed about ten days later than was the case when the temperature was maintained at 70°F. throughout the 24 hour period. This is reflected in the greatly increased values for the photothermal requirements (see #1, Table 8). The diurnal variation in temperature must be considered as the reason for this increase. Accordingly, the photothermal units were calculated using Went's formula, which takes night temperature into account (see #2, Table 8). The resulting figures, although about five percent above the expected, compare favourably with the values obtained when temperature was constant during the entire 24 hour period. The slight increase in value may be partially explained on the premise that it takes some time at the beginning of each light period for the temperature to reach 70°F. Application of phosphate tends to increase the number of tillers, whereas nitrogen appears to decrease the number of tillers.

It must be assumed that the soil was receiving either excess nitrogen, or was deficient in phosphate.

SUMMARY AND CONCLUSION

In this study it has been shown that the photothermal requirement for the periods emergence to heading and heading to maturity for the spring wheat variety, Selkirk, remained relatively constant despite fluctuations in temperature between 50°F. and 70°F. and despite fluctuations in photoperiod between 15 hours and 21 hours. These results confirm the findings of Azzi (1) and Nuttonson (20) but do not fully support the results calculated by the author from the data presented by Riddell and Gries (23). From this data, for the period initiation to heading it was found that the photothermal requirement for the variety White Federation 38 remains a constant at different levels of photoperiod and temperature, while for the variety Chinese there is an increasing requirement with increasing temperatures but not with increasing photoperiod. This indicates that varieties differ in the response they show to varying temperatures with regard to reproductive development. The lower temperature level used in this study appeared to cause a reduction in the photothermal requirement for the period heading to maturity. The reasons for this are not clear. It is possible that at the higher temperatures growth exceeded that required before subsequent stages could be initiated, giving the impression that at a low temperature development proceeds faster per degree of temperature than is the case at higher temperatures. This conclusion is supported by the results reported by

Riddell and Gries (23) wherein they claim that, for the varieties Chinese and White Federation 38, higher temperatures encouraged vegetative growth and delayed heading. It was also noted in this study that at the low level of photoperiod the photothermal requirement was slightly reduced. This may be related to the longer dark period and confirms the report of Nanda _et al_. (16) which states that only short photoperiods decrease the interval from heading to maturity. Their conclusion, however, that an increase in temperature has no effect in hastening maturity, is not supported. When the temperature during the dark period was lower than the temperature during the photoperiod, the photothermal requirement from emergence to heading was increased. However when an adjustment was made to the formula to calculate the photothermal requirement they were very similar, i.e., the adjusted value was found to correspond closely to that obtained when the temperature level was not reduced for the dark period.

The influence of moisture and fertility levels on the photothermal requirement have not been reported upon in the literature, although it is often considered in agronomy texts (1) that low levels of moisture and phosphate fertilizers hasten heading whereas high moisture levels and the application of nitrogenous fertilizer have a delaying effect. From the results of this study the moisture level was found to have little effect on the interval emergence to heading, but dry conditions did reduce the requirement for the period heading to maturity. The application of both nitrogen and phosphate fertilizer increased the photothermal requirement when compared to those plants which were not fertilized.

A lower number of tillers was found at high temperatures which confirms the reports of several workers (17, 26, and 27). Azzi (1) considers 65°F. to be the optimum temperature for tiller production, but in this study, it was found that a higher tiller count was obtained at temperatures below 60°F. Tiller number was also found to depend on an adequate supply of moisture from the fifth leaf to heading and was reduced at low moisture levels. When a dry period existed during the seedling stage (emergence to fifth leaf) the secondary tillers were outstripped in growth by the main tiller and a proportion proved to bear infertile heads. The tillering response shown to fertilizer applications was opposite to that expected (1). Nitrogen decreased tillering whereas phosphate fertilizer encouraged it. It can only be assumed that the soil was lacking in phosphate and that the application of nitrogen exaggerated the unbalance between the nutrient levels.

Grain weight and seed number produced per main tiller were studied in relation to temperature. It was found that 60°F. favoured seed production but that at 54°F. individual seed weight was greatest. The process of fertilization is slowed down by lower temperatures and at 50°F. it was noted that the apical spikelets and third florets were usually infertile. At higher temperatures only the apical spikelets were so affected. The finding that 54°F. results in highest individual seed weight does not fully confirm the report that 55°F. is the lower threshold with respect to grain weight (1). It was found that below 54°F. seed weight did decrease rapidly, particularly with respect to the secondary tillers, but Azzi (1) claims that the range 60°F. to 70°F. is optimal for seed weight. It was also shown in the present study, that low moisture levels associated with high temperatures tend to decrease grain weight whereas high moisture levels at low temperatures reduce the seed number. When high moisture applications at optimum temperatures are considered, it was found that the increase in the number of tillers results in a lower grain weight, presumably the result of tiller competition. Low moisture application at optimum temperatures brings about a reduction in both seed number and grain weight, particularly if the drought was experienced over the period fifth leaf to heading. This latter result confirms the report of Azzi (1) that the most critical time in respect to the effect of moisture on yield is a water deficiency during the 14 day period prior to head emergence.

Finally one of the most interesting findings of the study was that the percentage nitrogen found in the grain of the main tiller was unaffected by variations in temperature and appeared to be more closely associated with the level of available nitrogen in the soil. It was considered that the level of nitrogen application was so high that leaching could not reduce this level to a point where there was less than the maximum which the plant could use. Secondly and more important is, that as the soil had previously been sterilized, there was a reduced microorganism population to compete for the added nitrate.

A significant feature emerging from this study is that the response of the variety Selkirk is very different from that shown by Riddell and Gries (23) for the variety Chinese. High temperatures encourage earlier heading in Selkirk although they decrease tiller production, whereas with Chinese, high temperatures delay heading but encourage vegetative differentiation. The linked response of heading and vegetative development with temperature is interesting and worthy of further experimentation.

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Appendix I.

A Study of the Variations found within the Cabinets

Temperature recordings and light readings were found to vary somewhat throughout the cabinet. Before the study commenced, an effort was made to measure these variations.

Generally it was found that the air temperature within the cabinet was constantly varying 2°F. above and below the temperature for which it was set. This was correlated directly to the manner in which the refrigeration unit cuts in and out. To obtain a measure of how much the plant would be affected, petri dishes full of water were used, and it was found that the water maintained a constant temperature uninfluenced by the cycle of operation of the cooling unit. Subsequent studies were done using a six-inch by six-inch grid, laid out on the growing platform. Generally speaking, it was found that the temperature was highest in the centre and fell off towards the edges. This pattern was not constant, however, and it was concluded that the factor responsible was the manner of air circulation within the cabinet, over which there was no control. The pattern of air circulation appeared to vary depending on the setting of the light hood.

Light intensity was also checked on the same grid, using a Weston meter, fitted with a movable sensitive element which allowed readings to be obtained from within the closed cabinet. Generally speaking, it was found that light intensity at the centre measured 300 to 400 foot candles more than at either end. The nature of this decrease was gradual. It was found that intensity values also decreased between 100 to 200 foot candles from the centre line to the extreme edge of the light bank. The general trend for light intensity would be diagramatically represented by a low pyramid. In addition it was found that light intensity decreased when the light hood was moved further from the platform. The light intensity at the same setting of the hood was very similar in two of the cabinets, but in the third cabinet, where the light emission was stronger throughout, it was necessary to raise the hood four inches higher, in order to obtain the same light intensity at platform level.

The general conclusion reached during the standardization of the cabinets was that the variation pattern in light and temperature was extremely complex over the platform, and would have to be accepted as a base for experimentation, since modifications to eliminate them could not be made. Experiment A, in addition to testing for the effect of temperature on photothermal requirements was also designed to test for variations in plant growth conditions within individual cabinets. In this trial, the complete outside row of pots was considered as discards, while the remainder were analysed for variation in the number of days to head. It was found that at 70°F. there was little variation (S.E. 1.56, C.V. 3.9%). At 60°F. (S.E. 5.07, C.V. 8.4%), and at 50°F. (S.E. 14.07, C.V. 14.8%), the variation was greater as a result of higher temperature prevailing in the end of the cabinet, furthest from the air inlet, where air circulation was impaired. To overcome this variation, it was found necessary to discard a second row in the cabinet at 60°F. and four additional rows in the cabinet, held at 50°F. In both cases the period up to heading was similar for the remaining pots.