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THE INTERRELATION BETWEEN GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY TEMPERATURE, LIGHT AND NITROGEN

by

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CONTENTS

CHAPTER I

THE STUDY OF GROWTH AND DEVELOPMENT

A. INTRODUCTION

In higher plants the egg-cell is fertilized in the motherplant by the generative nucleus of the pollen tube and thus a stage of development begins which terminates in the production of the seed. This seed contains the young plant, which in order to reach maturity and have the ability to produce new seeds, must go through various stages of growth. Some of these stages are visible and can be detected directly, while others are invisible and can be recognized only by their external expression at a relatively later date. A group of stages represents growth of the plant which is defined as "the accumulation of dry matter and increase in size. The other group represents the physiological development or "the progress towards reproduction". Although the development of plants was early considered by some investigators (SACHS (1887) and VOECHTING (1893)), KLEBS (1918) may be regarded as the pioneer in the field of developmental physiology of plants. Until now, many hypotheses have been postulated by different investigators to explain the role of the different environmental factors in controlling the development of plants. Since none of these postulations yet is able to explain the developmental phenomenon without gaps on a general basis, additional and more extensive studies seem to be required. It is desirable to discuss some of the work in the field of developmental physiology in order to see to what extent the course of development is influenced by the different environmental factors.

KLEBS, according to WHYTE (1946), in his research on *Sempervivum funkii* recognized three separable developmental stages.

1. The ripeness-to-flower, a qualitative phase not recognizable morphologically, is regarded as a result of intensive C-assimilation with active transpiration and relatively limited uptake of nutrient salts. This ripeness-to-flower is favoured by high light intensity, provided the light energy is primarily used for increasing the carbohydrate content of the plant. Moreover, the importance of temperature in relation to light is emphasized, especially its effect on the rate of dissimilation.

2. The formation of flower primordia which would appear to be dependent upon light. It was found that with continuous strong light several days must elapse before primordia appear. It has also been demonstrated that the red rays stimulate the onset of flowering under both weak and strong light. The blue-violet rays, on the other hand, hinder the process and ultimately cause a reversion of the ripe-to-flower condition.

3. The formation of the inflorescence was found to be also dependent on light. In this case the light intensity required is higher than that necessary for the initiation of flower primordia. It was further stated that the formation of the inflorescence can also proceed even in the dark provided that the temperature applied is relatively low. In this case the formation of flowers is very poor.

LYSENKO (1935) formulated his theory of phasic development of annual seed plants. The main points in this theory can be summarized as follows:

1. He distinguished sharply between growth and development. The former is considered as the total of quantitative changes which cause increase in the mass or volume of the plant. The latter, on the other hand, is the total of internal qualitative changes which lead to reproduction.

2. The individual phases which proceed during development, may take place without being associated with any morphological changes. On the other hand, when certain conditions are available the developmental phases are expressed morphologically.

3. In the development of some annuals and biennials a definite sequence of phases is observed viz. a thermophase and a photophase. This means that the qualitative changes characteristic of the photophase can take place only after the vernalization phase, and not before, or even during it.

4. Concerning the factors required, it is concluded that for each phase a certain set of factors, determined by the natural conditions and properties of the plant in question, is necessary. Moreover, to pass through the different phases of its development, the same plant requires different sets of external factors.

KOPETZ (1936, 1937) has offered a theoretical interpretation for the relationship between the vegetative growth, the development of the annual plant and the environmental factors prevailing during the year. In principal, KOPETZ hypothesis as mentioned by WHYTE (1946), follows on from HARDER's statement, that a plant requires up to the time of flowering a certain minimum time of development, which remains constant for the race. KOPETZ has formulated his theory as follows.

1. A phase of pure vegetative development 'Vr' must be ended before the plant can proceed to reproductive development.

2. If any inhibiting factor is present after the first phase is ended, the plant will continue its vegetative growth; this additional period of growth is known as the luxury vegetative development 'V_l' which in fact can vary between nil and maximum. Thus, the total vegetative growth period '$V = V_r + V_l$' is dependent upon the time at which the favourable conditions for reproduction are present; i.e. 1. if the favourable conditions arise sometime later, after 'V_r' is complete it must be expected to increase; 2. if the favourable conditions are present before or during 'V_r', the plant must continue its vegetative growth until another period of favourable conditions is reached; 3. if the favourable conditions are present just after 'V_r' is ended, thus 'V' is equal to 'V_r' which means optimal progress towards reproduction.

It is of special interest to note that among these different views, some points of agreement can be recognized.

In the first place, there was a general agreement on the existence of the developmental phases through which any plant must go before proceeding towards its sexual reproduction. Secondly, it was agreed that some of these phases could be fulfilled within the plant without any morphological expression. Lastly, the influence of the environmental factors on different phases of development may change according to the factor or the group of factors that prevail during a certain phase.

The question arises to what extent growth and physiological development of the plant are influenced by the change of the environmental factors. In this respect, the environmental factors can be divided into two groups; decisive factors (temperature and photoperiod), and accessory factors (light intensity, light quality, water, nutrition, oxygen, etc). Generally, all factors have an almost equal effect on growth. On the other hand, physiological development of plants is mainly controlled by the two major factors mentioned above.

Some effects of temperature, light, and nutrition on the growth and development of some subtropical and temperate varieties of wheat are the main object of this study.

B. REVIEW OF LITERATURE

1. *Growth and development as influenced by temperature.* The effect of temperature on growth processes and physiological development in plants is rather complicated, especially when other factors (light, nutrition, ... etc) are considered. In some cases the interrelation between temperature and other factors may be useful in differentiating between different rate limiting processes by their temperature responses. This is demonstrated in the photosynthetic process. At high light intensities and optimal CO_2 concentration the effect of temperature on photosynthesis is that upon a chemical process, at low light intensities and optimal CO_2 concentration the influence of temperature is that upon a photochemical process. At low (limiting) CO_2 concentration the effect of temperature can be interpreted on the basis of diffusion and solubility of CO_2 (VAN DEN HONERT (1928)).

Although the effect of temperature on plants was considered in different studies, the reviews on this subject are very few. This is due to the fact that in most studies the temperature was not a major factor. In the following review, the effect of temperature in relation to growth and development will be primarily considered. However, it is desirable also to quote some of the fundamental effects of temperature on metabolic and translocation processes in higher plants.

The differential effects of temperature on respiration and photosynthesis are well established. In their experiments with bean leaves, HEWITT and CURTIS (1948) found that the respiration loss of dry matter and carbohydrates from leaves increased progressively with the increase in temperature when plants were held in the dark at 4°, 10° and 20°C. This may indicate why many plants produce a more vigorous growth in the temperate regions than in the tropics. This was confirmed by WENT (1953), who reported that at lower temperatures the ratio of photosynthesis to respiration is over 10, while at higher temperatures respiration is increased relatively more, and low photosynthesis/respiration ratios are found. In this respect, light intensity is undoubtedly of major importance.

Concerning the sugar content of plants, the temperature seems to be of great importance. This was proven by ARREGUIN and BONNER (1949) who showed that the hydrolysis of starch in potato at low temperature can proceed successfully, while at higher temperatures, the whole process is inhibited as a result of phosphorylase inhibition. With carrots, CURTIS and CLARK (1950) (p. 679) stated that at any moisture content, the sugar percentage varies inversely with temperature.

WASSINK (1953), working with *Helianthus tuberosus* and *H. annuus* came to the conclusion that the temperature curve of starch hydrolysis mostly shows a pronounced maximum at about 0–3°C, a minimum around 10°C, and a renewed increase at temperatures above 15°C.

A factor which sometimes is of considerable physiological significance is the temperature effect on the translocation of metabolic products within the plant. In their experiments, WENT and HULL (1949) working with tomato, showed that translocation decreased with increasing temperature from 2°C upwards. WENT (1953) ascribed the low optimal night temperature for many plants to a Q_{10} less than 1 for the process of translocation of photosynthetic products. Experiments of HULL (1952) in which C^{14} labelled sucrose was applied to tomato and sugarbeet leaves, indicate an equal or greater translocation at lower temperatures. BÖHNING *et al.* (1953) working with tomato, however, concluded that Q_{10} for carbohydrate translocation in the range of 12° and 24°C was approximately 1.5.

The effect of temperature on the growth of cells, tissues or whole plants, was studied by some investigators. CHAO and LOOMIS (1947) stated that cell growth, especially cell elongation has a high Q_{10} which indicates that this process is controlled by a chemical reaction. HAMILTON (1948) has demonstrated that in *Avena sativa* the differentiation of shoot-tissues occurs much earlier in plants grown at 28 °C than at 16 °C. He also noted that the usual pattern of growth was observed at the lower temperature, while at the higher temperature rapid maturation of tissues and internodal cells occurred. This resulted in narrower leaves, shorter internodes, fewer adventitious roots and tillers, and inhibited panicle initiation. In their experiments with hyacinth and tulip HARTSEMA, LUYTEN and BLAAUW (1930) and LUYTEN, VERSLUYS and BLAAUW (1932) showed that during the development of these plants different optimal temperatures follow each other. This is due to a succession of morphological and physiological processes, each with its own optimal temperature.

It follows from that mentioned above that biochemical reactions and most biological processes are accelerated by increasing the temperature within a certain range, which differs according to the nature of the reaction or process. However, in some annuals and biennials, a certain quotum of low temperature seems to be required in order to induce or accelerate flowering. The capacity of the plant to respond to low temperature appears in the developing seed just after fertilization takes place. This capacity is progressively lost with approaching dormancy. In winter cereals low temperature is required when the dormancy of the ripe seed is broken and germination begins. If germinating seeds of winter wheat are kept at low temperature for some time, the resulting plants will flower much earlier than they otherwise would have done and may be used as spring wheat. This is the process of vernalization (jarovization) which commonly is defined as the treatment of seeds before sowing, by any technique designed to hasten the flowering of plants to which such seeds give rise. The possibility of inheritance of this new character has been the cause of conflicting ideas, which are beyond the scope of this study.

The vernalization process has also been successfully applied to non-cereal plants, such as mustard, lettuce, red clover, etc. The process also could be applied to different stages and different parts of the plant. GASSNER (1918) at an early date showed this by vernalizing wheat seedlings. Excised whole embryos on artificial media were vernalized by GREGORY and PURVIS (1938). PURVIS (1940) vernalized fragments of winter rye, consisting of the stem apex and leaf initials grown on an agar medium.

The practical application of the vernalization technique was first established by Russian agronomists as fully described in the Bulletins of the Russian Bureau of Genetics (1933–1935). MCKINNEY and SANDO (1933) published an English account of the technique which because of its importance, is given in a shortened form as follows: 1. Soaking the seeds in order to induce slight germination in the embryo. 2. Chilling the seeds at a temperature slightly above freezing point (0.5–1 °C). 3. For complete vernalization, six weeks of chilling are required. 4. The importance of aerating the seeds during the chilling period has been emphasized.

GREGORY and PURVIS (1936) were able to vernalize the seeds while attached to the mother plant, thus avoiding the difficulties of continuous loss of moisture. In this connection, LYSENKO (1928) was the first to claim that successful vernalization is possible provided that moisture content of the seeds during the chilling period is not less than 55 % of its air dry weight. Concerning the chilling temperature and its duration, there was a big range of differences in the technique used by various investigators, according to their aims in the experiments conducted and the plants used. In a previous review of the author (1951) some of these differences have been reported.

It is of special interest to note that GREGORY and PURVIS (1936) demonstrate that devernalization of seeds occurs at relatively high temperatures; furthermore, they proved the possibility of revernalization when devernalized seeds are again kept under conditions suitable for vernalization. In 1938 they also showed the importance of oxygen during the chilling period, demonstrating that seeds cannot be vernalized in nitrogen even when given all favourable conditions of water-content and temperature.

In order to explain the effect of low temperature on the flowering of winter annuals and biennials, according to SAID (1945) it was first suggested by MAXIMOV (1931) that a hormone-like substance in the endosperm of seeds retards reproduction. This substance could be destroyed by vernalization. Another suggestion which was offered by DEMOKOVSKII (1932) and later supported by SAPOZINIKOV (1935), is that the vernalization effect is caused by increasing the activity of the enzymatic system in the embryos of the seeds. In their experiments with winter rye and other plants PURVIS and GREGORY (1937) (see GREGORY 1948) have suggested that a substance 'B' is produced autocatalytically from the precursor 'A' in a reaction which is accelerated by low temperature. After they had discovered the processes of devernalization and revernalization they amended their scheme, and in 1952 formulated a new scheme.

$$\begin{array}{c} \text{E (leaf promoting substance)} \\ \uparrow \\ A \rightleftarrows A^1 \rightarrow B \rightleftarrows C \rightarrow D \text{ (flower promoting substance)} \end{array}$$

In this formula $A \rightleftarrows A^1$ denotes a reversible reaction which is controlled by temperature, while (B) is considered as the first stable product. The reaction $B \rightleftarrows C$ depends on darkness and light. It was assumed that in summer varieties, B is already present. LANG and MELCHERS (1947), working on the biennial *Hyoscyamus*, have offered a new suggestion, which in fact does not differ much from that of PURVIS and GREGORY. However, their interpretations for the reactions were significantly different.

$$\text{Precursor} \xrightarrow{\text{I}} \text{Thermolabile intermediate product} \xrightarrow{\text{II}} \text{End product}$$
$$\swarrow \text{III}$$

They assumed that the reactions I, II, III have normal positive temperature-coefficients, but that the temperature-coefficient of the destructive reaction III is greater than that of the other two. Thus, at intermediate and higher temperatures the intermediate product is removed by reaction III and no substrate is available for reaction II. This also explains why at very low temperatures vernalization does not take place. MELCHERS (1952) states "compared with the excellent agreement between the two schemes the question whether the intermediate product (A^1) is destroyed or is reconverted to the precursor (A) appears to me to be of minor importance".

The diurnal differences between day and night temperatures in relation to growth and development in plants, also have been studied. "Thermoperiodicity" is the term given by WENT to explain the response of plants to cyclic temperature variations. Although the annual thermoperiodicity is of great importance for the development of many deciduous trees and other plants of the temperate regions, the diurnal thermoperiodicity is not yet generally accepted as essential to the development of plants. However, WENT (1944), working with tomato showed that thermoperiodicity is due to the predominance of two different processes, the first process takes place during the day and requires relatively high temperatures, while the second takes place during the night and requires relatively low temperatures. From other work which has been discussed, it was suggested that thermoperiodicity is a general phenomenon in higher plants. DORLAND & WENT (1947) also have shown that the optimum night temperature for stem elongation of chili pepper plants gradually decreased from 30 °C to 8.5 °C as the plant progressed to maturity.

The influence of night temperature in relation to light intensity was studied by WENT (1945) who stated that in young tomato plants the optimum night temperature was shifted from 26 °C to 8 °C when the light intensity was decreased from full daylight to 200 foot candles. ROBBINS (1946) claimed that higher day and night temperatures could be tolerated during summer, owing to the higher light intensity. During winter, the night temperature should not exceed 13°–16 °C owing to the effect on carbohydrate depletion. It is of interest to note that VAN OVERBEEK (1948) had demonstrated that unseasonable flowering was induced in pineapple – Red Spanish variety – by lowering the minimum night temperature during late summer to a value approaching minimal winter temperature. He put forward the idea that the path by which low temperature causes flower formation in the pineapple, is via the organic acid and auxin metabolism.

WASSINK and WASSINK-VAN LUMMEL (1952) have investigated the influence of night temperature in relation to light intensity upon the flowering of *Iris*, var. Wedgwood. It was concluded that high night temperatures speed up development by accelerating synthetic processes which go on in the dark.

BANDURSKI *et al.* (1953) studied the effect of night temperature on tomato plants. They observed that the decrease in leaf colour at high night temperature was due to changes in leaf anatomy, leaves growing at 4 °C being compact with a minimal cross section of intercellular spaces. HIESEY (1953), working with *Poa ampla* and *Poa compressa* proved that the effect of night temperature on flowering, stem development, and leaf proportions, is of a quantitative nature.

2. *Growth and development as influenced by light.* Since the time INGEN HOUSZ showed that light is necessary for the evolution of oxygen by plants, a phenomenon which as such was discovered before by PRIESTLEY, the literature concerning various effects of light on different organisms, especially higher plants, has become vast. Thus, an attempt to give a complete review of this field cannot be entirely successful. The following references contain a more or less extensive dicussion of literature; BURKHOLDER (1936), WHYTE (1946), MURNEEK and WHYTE (1948), PARKER and BORTHWICK (1950), CURTIS and CLARK (1950), STOLWIJK (1954), WASSINK and STOLWIJK (1956). In order to keep to the subject of our study in the following review, growth and development as influenced by day-length will be taken mainly into consideration.

Although the term photoperiodism was first used and the phenomenon practically demonstrated by GARNER and ALLARD (1920), yet according to MURNEEK and WHYTE (1948) formative effects of diurnal length of exposure to natural light or artificial illumination have been observed or at least mentioned by several investigators previous to the discovery of photoperiodism. However, two important results could be derived from the experimental work of GARNER and ALLARD: the first is that the change in relative length of day and night is the decisive factor controlling the flowering of many plants, the second result is the possibility of modifying photoperiodism in plants by changing their environmental factors, such as temperature, light intensity, nutrition, etc. The fact that plants may require different photoperiods for inducing different phases of their development renders the classification by a more or less definite photoperiodic reaction (short-day or long-day) unsuitable. In this connection EGUCHI (1937) concluded that there are two stages in the course of flowering: the first being the stage of bud differentiation, and the second the stage of flowering, each of them requiring different photoperiods. On this basis, he offered his classification, in which nine photoperiodic types of plants were distinguished. WELLENSIEK *et al.* (1954) mentioned that if the induction and realization phases of flowering are favoured by different circumstances, one could understand the phenomenon of long-short day and short-long day plants. They further stated that, if induction only is considered, one may expect to find only short-day and long-day plants. It is of special interest to note that flowering of *Perilla* (a typical qualitative short-day plant) could be also induced under long-day conditions provided that the light intensity is relatively low. This supports WELLENSIEK's idea that the qualitative photoperiodical action does not exist.

The modifying effects of temperature, light intensity, light quality, nutrition and other environmental factors on photoperiodic response of plants have been studied by different investigators. However, many controversies among the results have been observed, a fact which is largely due to different techniques and also to the difficulties which arise from eliminating variations in environment.

GARNER and ALLARD (1931) stated that temperature has a profound influence the photoperiodism of plants. This fact was later supported by many investigators. Working with the short-day plant *Xanthium pennsilvanicum*, MANN (1940) stated that at 30°C a maximum rate of photoperiodic response resulted after 5 hours exposure, while at 10°C the maximum is not reached until photoperiods of about 15 hours are used. The word photothermal induction was suggested by OWEN *et al.* (1940) to designate the induction of flowering by both light and temperature. However, the combination of photoperiod and temperature as a factor influencing flowering has been proven before by CHROBOCZEK (1934) in his experiments with beets. This fact was confirmed later by CURTIS and CLARK (1950), who stated that too high or too low temperatures may counteract the tendency of the proper photoperiod to induce flowering. They added that after flowering has been initiated, or the induction period has passed, the rate at which the plant reaches the flowering condition is favoured by higher temperatures.

Concerning the effect of light intensity on the photoperiodic reaction of plants, there is evidence that, as far as the flower initiation is concerned, light intensity itself is of minor importance. This was reported early by KLEBS (1918) who noted that the stimulation of flower initiation requires, under continuous illumination, a lower light intensity than the growth and emergence of the inflorescence. On the other hand, SCULLY and DOMINGO (1947) stated that both light intensity and photoperiod are effective in the formation of floral primordia in certain varieties of the Castor bean (a long-day plant). Differences in total radiant energy did not show any significant effect as does the difference in day-length, in both *Xanthium* and Biloxi soybean. In this connection, PARKER and BORTHWICK (1950) concluded that active photosynthesis is indispensable in the photoperiodic response, through its effect on the plant as a whole. Thus the products of photosynthesis are essential for flowering as well as vegetative growth.

In many plants flowering could be induced even in complete darkness, provided enough storage material was present, or sugar was supplied. In fact the long-day plants as well as the short-day plants could be induced or inhibited to flower, when photosynthetically active light was given for a short daily period, provided that it is extended by supplementary light at a very low intensity, showing that duration of illumination rather than light intensity is a factor of significant effect in flower initiation. It seems of interest that CURTIS and CLARK (1950) stated that after the induction phase is passed, high light intensity as well as longer duration of illumination become effective in shortening the time to flowering. We may conclude that light intensity is not as significant a factor in inducing flowering as it is in flower development and fruit production.

When a long night period is interrupted by exposure to light, this may lead to flowering in long-day plants and to the suppression of flowering in short-day plants, provided both types were previously kept under short-day conditions. Moreover, the rate of induction had been proven to be influenced by light intensity as well as by duration of exposure. WELLENSIEK *et al.* (1954) have concluded that the possibility of a photosynthetical action of light interrupting the dark period is not generally accepted, but cannot be excluded from the available data.

As to the action spectrum of photoperiodically active light, RASUMOV (1933, 1941) has demonstrated that all the regions of visible light are effective in delaying flowering in short-day plants. If used for a short time during the night period, yellow, orange and red were most effective. Similar results were reported by KATUNSKY (1937), who showed that the order of effectiveness of various spectral regions was: red, yellow, orange, blue and green. KLESHNIN (1943) found that radiation from any part of the visible spectrum influenced the photoperiodic reaction. The intensities required, however, varied from one region to another. WITHROW and BENEDICT (1936), WITHROW and WITHROW (1940), PARKER *et al.* (1946, 1949), PARKER and BORTHWICK (1950) and BORTHWICK *et al.* (1946, 48, 50) have shown that two regions have a maximum effect on flowering; a narrow one in the violet near 400 m/μ and the other a broad one in the orange-red, extending from 560–720 m/μ. It is of special interest to note that the energies required to induce spike formation and stem elongation in some long-day plants were of the same magnitude as those required to prevent floral initiation in short-day plants under closely similar experimental conditions. WASSINK *et al.* (1950, '51, '52), STOLWIJK (1952, '54) published the results of experiments in which light of different wave lengths was given to the plants, either during the whole photoperiod or as supplementary light of relatively low intensities. They concluded that especially concerning the primary morphogenetic effects, two different reaction types prevail; a response to the spectral region between 520–700 m/μ with much less effect of blue and infra-red, while other plants or other phenomena in the same plant showed the opposite reaction type. These results obviously support those produced by FUNKE (1936, 37, 38, 39). The difference with FUNKE and also with the early work of BORTHWICK *et al.* was that WASSINK and his collaborators demonstrated the definite infrared effect. They also showed that this effect can be inhibited in *Cruciferae* by simultaneous or subsequent exposure to red or green supplementary light, see Stolwijk (1954).

There is evidence which indicated the importance of the blue-violet end of the spectrum for normal growth of the plants. This was established early by Popp (1926), who claimed that for normal vigorous growth blue light is essential, and its absence brings on conditions similar to those obtained when plants are grown in darkness, or at a very low light intensity, having long and weak stems. In the experiments conducted by Wassink *et al.* (1952), it has been proven that plants grown under continuous yellow and red light were relatively more elongated than those in the blue region, while the dry weight relations were as to be expected from the amounts of quanta supplied.

As to the action of pigments in relation to different photoperiodic reactions, Parker and Borthwick (1950) have stated that in the photoperiodically reactive plant, a photoreceptor exists absorbing far less in blue than in red, contrary to what is found in photosynthesis, in which the efficiency per unit incident energy of red is equal to that of blue. The mentioned authors and Hendricks (1953) stated that the receptive pigment may be regarded as related to phycocyanin.

Borthwick *et al.* (1952) have supported the idea that a photo-receptive system consisting of two pigments a "red absorbing" and an "infra-red absorbing" one, is present in various plants. These authors assumed a photochemical equilibrium which would be independent of the light intensity. In this connection Stolwijk (1954) has concluded that "When most of the quanta are absorbed by the red absorbing pigment, the reaction will proceed into the direction induced by red light. If, on the other hand, the infrared-blue absorbing pigment receives more quanta, the reaction will proceed into the 'infrared' direction". For more details, see Wassink and Stolwijk (1956).

In this review it is rather important to quote, as briefly as possible, the main points of different hypotheses which attempt to explain the mechanism of photoperiodism. The plants can be divided into two main groups with respect to their photoperiodic response in relation to flower initiation. The first group requires a minimum daily photoperiod without which the plants remain vegetative or at least their flowering is significantly retarded, while the second group requires a minimum uninterrupted night period without which flowering does not occur. The last part of the scheme offered by Purvis and Gregory (1937, 1952) describes the effect of day length on the development of winter cereals by way of a stable substance 'B' which under short-day conditions produces a substance 'C' from which the end product 'D' is produced under long-day conditions. On the other hand, if the plant remains under continuous short-day conditions, 'C' accumulates maintaining an equilibrium with 'B'. In his investigations on the photoperiodic induction of short-day plants Hamner (1942) suggested the existence of two substances 'A' and 'B'; the formation of the first is influenced by light intensity, while the second substance reacts in a dark reaction and is influenced by temperature. He further suggested that by combining the two substances, a flower initiating hormone 'C' is produced.

Light ——— A ⟩ C
Dark ——— B

van de Sande - Bakhuysen (1951) offered a suggestion rather similar to that of Hamner. The main difference is that Bakhuysen suggested that from the combination of 'A' and 'B' two substances could be produced, according to the length of the dark period; the first substance 'AB' which is light sensitive and the second 'BAB' which is light stable.

In a recent paper by WELLENSIEK *et al.* (1954), it has been stated that the products of photosynthesis may be considered necessary for flower initiation, rather than chemical reactions between substances such as 'A' and 'B'. They further suggested that flower formation is mainly controlled by the balance between the photosynthetic products and the removal of an inhibitory influence. There is no doubt that the last process can be induced within the plant under optimal conditions of temperature and day-length. The authors suggest that the inhibiting effect is connected with the auxin level.

As early as 1937, BÜNNING had offered a rather different theory which is based on the assumption that rhythmic processes exist in the organism, the period of which can be determined. Concerning photoperiodism it has been stated that the effects of light on the process of flowering depend on what phase of endogenous rhythm the plant is in, when it is illuminated. That phase of the internal rhythm in which light promoted flowering BÜNNING calls the "photophilic phase". The phase in which light either has no promoting effect or even is inhibitory, he calls the "scotophilic phase". This theory was strongly supported by MELCHERS (1952) and experimentally substantiated by CARR (1952) who, in his work with *Kalanchoe* grown under a 72 hrs cycle, was able to produce curves in which the phases proposed by BÜNNING were rather obvious. As was stated by CARR, the importance of BÜNNING's theory is that it can explain the effect of day length on both long-day and short-day plants in a uniform way.

3. *Growth and development as influenced by N-concentration.* Since the relation of the nitrogenous content of green plants to flower initiation and flower development had been studied by many investigators, many attempts were made to show a quantitative correlation between the nitrogen and carbohydrate content of the plant and its progress towards reproduction. However, the results produced by different investigators did not always agree. This is largely due to differences in solutions used and in their concentrations, and differences in plant material (stems, leaves, whole plant, etc.) used for analysis, plant age, and different types of chemical determinations. In this respect, it is preferable to carry out the plant analysis at different stages of growth for comparative study.

The importance of the C/N ratio, the value of which varies directly with the conditions of the plant, was first noted by FISCHER (1916) who claimed that a high C/N ratio favours flowering while a relatively low C/N ratio is suitable for the vegetative growth. KRAUS and KRAYBILL (1918) and KRAUS (1925), in their experiments with the tomato which was subjected to varying amounts of nitrates, could establish a fairly constant relationship between the N-content of the plant and its vegetative and fruiting behaviour; strong vegetative growth appeared to be correlated with high nitrate conditions. On the other hand, when nitrate was restricted, the plants were less vegetative, carbohydrates accumulated, fruiting at first increased and somewhat later fruit-setting ceased and even the differentiation of flowers stopped. However, CAMPBELL (1924) was able to demonstrate that the nitrate-nitrogen content of some weeds was relatively high just before blooming, and zero at full maturity. STEELE, (1949, p. 300) has reported that the changes in the carbohydrate/nitrogen relationship in the tissue of the plant are effective in producing two types of growth. A vigorous growth with little flowering is favoured by a low ratio, while a high ratio generally gives a good development of the reproductive tissues, in spite of the fact that for flowering and fruit-setting the availability of nitrogenous compounds is required.

Concerning the opposite point of view, ARTHUR *et al.* (1930) have proved that no relationship was found to exist between C/N ratio and flowering in either long-day plants (radish and lettuce) or short-day plants such as *Salvia splendens*. It is of interest to note that the C/N ratio could be changed by other factors such as light intensity and light duration. PARKER and BORTHWICK (1939), working with Biloxi soybean, concluded that, although differences occur in nitrogen and carbohydrate content under different photoperiodic treatments, these differences do not seem to have any direct causal relation to induction of flowering. According to MURNEEK and WHYTE (1948), CAILACHJAN (1944) concluded that the development of the plant from the vegetative to the reproductive stage is not decisively influenced by variation in the mineral nutrient solution. He also observed that it had no influence on a plant's reaction to nitrogen whether it belonged to the short or to the long-day group. Furthermore he also refuted the idea that a large increase in nitrogen nutrition prevents plants from entering the reproductive phase. According to CAILACHJAN, plants are divided into three groups with different nitrogen requirements.

WITHROW (1945), working with various long-day and short-day plants, has concluded that nitrogen is not a determining factor in floral initiation, as are temperature and photoperiod, but that the time at which visible buds appear could be altered in some species by changing the nitrogen supply. This was confirmed to some extent by CROCKER (1948), who showed that the day length rather than the chemical composition or C/N ratio, determined the flowering of all photoperiodically reactive plants, while also in day-neutral plants, flowering occurred over a wide range of C/N ratios. It is of special interest to quote here that, although it has been cited on many occasions that changes in the C/N ratio within the plant cause it to shift from one phase to another, a big mass of evidence still opposes this view. However, the effect of C/N ratio in connection to flower development and fruit formation is not denied. DEATS (1925) noticed that the amount of starch present in the stems of tomato plants, was directly proportional to the length of day. Thus he considered that the day length might influence the form of plant development by change in the C/N ratio. Nevertheless, the fact that the plant, under suitable photoperiod, could flower over a wide range of C/N ratios, makes this consideration unreliable.

The influence of nitrogen on growth was studied by various investigators. WITHROW (1945) showed that in both short and long-day plants, abundant nitrogen generally produces, taller and heavier plants. When both types were grown under long-day conditions, plants were relatively taller than those grown under short-day conditions, provided they all had the same nitrogen supply. It was also demonstrated that limitation of nitrogen has a marked effect on the anatomy of the stem. LOUSTALOT and WINTER (1948) showed that a low nitrogen level has a marked depressive effect on the growth of seedlings of *Cinchona ledgeriana*, but a statistically significant difference between plants receiving 18 and 81 p.p.m. of nitrogen was not observed. In this respect, WALLACE (1951), dealing with cereals, noticed that with relatively low nitrogen, dwarfed thin shoots with pale leaves, few tillers, and poor ears are produced.

There is also a big mass of evidence that root/top ratio could be affected by changing the amount of nitrogen supplied to the plants. As far as it is known to the author, REID (1924) was the first to show that available high nitrogen supply could furnish favourable conditions for shoot growth, provided sufficient carbohydrate was available, while low nitrogen supply favours root growth. This was later confirmed by WEISMAN (1950), who concluded from his experiments on wheat that, when nitrogen was lacking, there was a significantly greater root and a decreased shoot elongation. CURTIS and CLARK (1950) also reported that top/root ratio was higher when nitrogen is increased and lower when nitrogen is decreased. In a recent paper, BOSEMARK (1954) stated that the increase in root length in cases of nitrogen deficiency is mainly due to an increase in cell length, whereas the growth inhibition with high nitrogen supply is caused by the reduction in cell elongation and cell multiplication.

Concerning the effect of nitrogen on the yield, it is generally agreed that the available nitrogen is a very important factor in determining the yield and quality of many crop plants. With moisture and temperature, available nitrogen in the soil largely determines the relation between protein and starch content of the wheat kernels: MARTIN and LEONARD (1949) and ALSBERG (1945). In this respect, it was noted early by DAVIDSON and LE CLERE (1917, 18, 23) that the highest yield of wheat was produced when inorganic nitrogen had been used during the early stages of growth, while its application at the time of heading increases the protein content.

VAN DE SANDE BAKHUYZEN (1937), working with wheat grown under constant conditions, concluded that the two outstanding factors controlling nitrogen intake during the time the leaves grow in size, are photosynthesis and the increase in xeromorphic character of the growing organs (p. 298).

CHAPTER II

MATERIALS AND METHODS

1. PLANT AND SOIL MATERIAL

Uniform seeds from pure lines of four different wheat varieties were used. Two of these varieties were secured from the Botanical Section, Ministry of Agriculture, Egypt, while the other varieties were obtained from the Netherland Grain Centrum, Wageningen/Holland. These four varieties are:

a.	*Triticum vulgare* var. Hindi	(42 chromosomes)
b.	„ *piramidale* var. Baladi	(28 „)
c.	„ *vulgare* var. Heine VII	(42 „)
d.	„ *vulgare* var. Peko	(42 „)

Seeds ready for sowing were previously soaked in pure water for 24 hrs at 20 °C, in order to secure a higher germination percentage. In this respect, a preliminary experiment was made to determine the time required for complete germination at different temperatures (10°, 20°, and 27 °C). In this experiment, the dry weight per 100 germinated seeds was determined every 24 hrs, from the time of sowing until the dry weight began to increase. The results are shown in Fig. 1. The importance of these curves becomes clear, when it is necessary to begin the treatments with plants at the same physiological stage, especially in the case of the temperature experiments.

For growing the plants, earthenware pots of different capacities were used; in

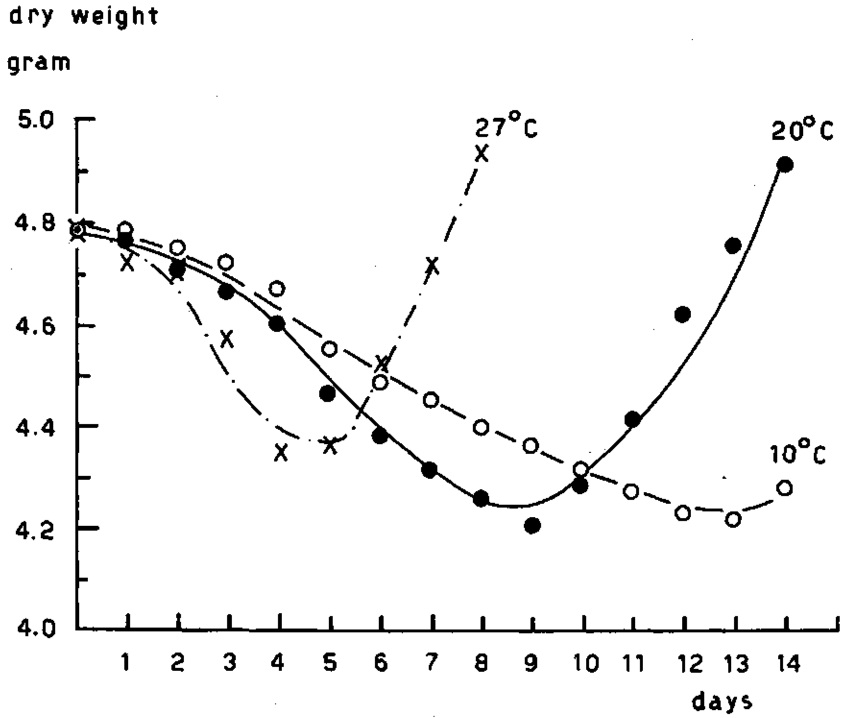


FIG. 1. Germination curves at different temperatures in Hindi variety. Average dry weight of 100 germinated seeds.

each of these pots 4–7 seeds were sown and later thinned to 2–4 plants, according to the capacity of the pot. The thinning was also useful to obtain more uniformity of the plants at the beginning of the experiment. Three different kinds of soil were used during these experiments: organic matter and sand, pure sand, and heavy clay soil. During growth the plants were fed by a standard artificial nutrient solution. Every pot was given from 100–300 ml weekly. In the nutrition experiment some alterations were made according to the requirements of the experiment. Relative humidity was kept within 65–75 % by means of hygrometer which was checked every now and then by means of spirometer. In all cases water requirements for the plants were regularly fulfilled. Experiments showing irregular growth, caused either by diseases or insects, were discontinued. Weed control was carried out from time to time by eradication of the weeds as soon as they appeared.

2. CONTROL OF TEMPERATURE, CHILLING OF SEEDS AND EXPERIMENTS ON OXYGEN SUPPLY

For studying the temperature effect on plant growth and development, four constant temperature rooms were used (2°, 10°, 20° and 27 °C). In these rooms the temperature was nearly constant during the whole year, except in hot summer days in which the temperature became about 1°–3 °C. higher, especially in the warmer rooms. However, additional batteries of fans were used in these two rooms, for dissipating the heat produced during artificial illumination of the plants.

In order to vernalize the wheat seeds, they were previously soaked in water at 20 °C for about 7–9 hrs, according to the variety. This period was sufficient to supply the seeds with water. They require a minimum of 55 % of their air dry weight which percentage is necessary to activate the embryo sufficiently to be vernalized, but avoids the troubles of progressed germination. The seeds were then ready for chilling and were transferred to a vernalizing box designed by the author, which was satisfactory for keeping constant the moisture content of the seeds. Moreover, a suitable atmosphere was insured by absorbing the CO_2 respired from the seeds in a concentrated solution of KOH. At the same time the seeds were in direct contact with the atmosphere surrounding the petri dishes in which they were kept by means of 3 n-shaped rods between each petri dish and its cover. A simplified diagram for the vernalization box is given in Fig. 2. The box was then kept in the refrigerating cabinet; in which the temperature was constantly kept at 1 °C during the period of chilling. The KOH solution was renewed weekly, and each box was regularly supplied with distilled water in order to avoid drying of the filter papers covering the walls of the box.

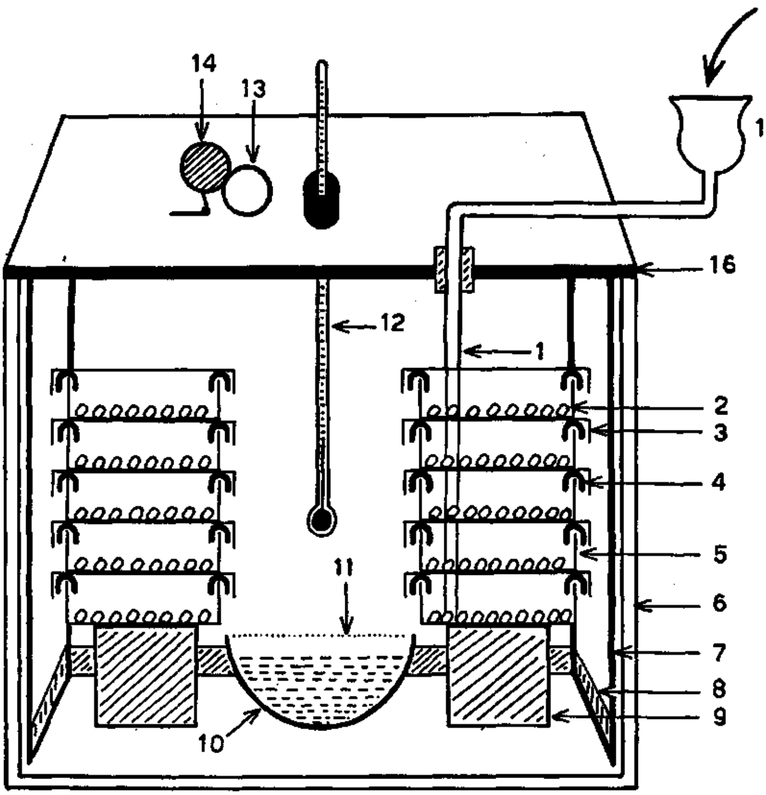


FIG. 2. Vernalization box: 1, water supply tube; 2, layer of seeds; 3, petri dish cover; 4, small glass spacer; 5, petri dish base; 6, glass box; 7, filter paper lining; 8, layer of distilled water; 9, wooden block to support dishes; 10, KOH container; 11, wire mesh; 12, thermometer; 13, ventilation opening; 14, cover; 15, water reservoir; 16, wooden top.

In experiments in which the roots were supplied with oxygen at different temperatures, plants were grown in root tubes, placed in a glass box, 17 cm long, 30 cm wide and 30 cm deep. The box is divided in two compartments, separated from each other by a glass plate, the edges of which are firmly fitted in the middle of the box-lid by means of a groove. In each compartment, 4 root-tubes (with or without soil) were placed through holes in the lid. In the bottom of each tube a piece of glass-wool was placed preventing the soil from falling through the end of the tube and permitting a direct connection between the outside and the inside of the tube. At the beginning of the experiment, the box was filled with water. One of its compartments was supplied with oxygen from an oxygen-cilinder, through a glass tube fitted with a porous block at the tip to distribute the gas in fine bubbles under 2 atmospheres pressure; see Fig. 3. If not mentioned in the text, the temperature used was 20-23°C.

FIG. 3. Two chambers oxygen box connected with an oxygen tank.

3. CONTROL AND MEASUREMENT OF LIGHT

For the light experiments, different equipments and different methods of light measurement were used, according to the factor studied or to the kind of light in which the plants were grown.

For the photoperiodic response under natural illumination, the plants were grown outdoors in pots in the equipment described by WASSINK and STOLWIJK (1952). This equipment essentially consists of two cabinets which easily can move on iron rails and were wheeled over the plants at the same time. In this way in one of these cabinets the natural day was reduced to 10 hrs (short-day treatment), while in the other two Philips 40 W fluorescent tubes were mounted for extending the natural day light to 16 hrs (long-day treatment). During the supplementary illumination, the light intensity was relatively low (360 ergs/cm^2/sec) in order to avoid difficulties resulting from differences in photosynthesis between the two treatments. The day light extension was automatically controlled by means of an electric clock. In summer time, a fan was used for ventilating the equipment.

In the experiments conducted indoors, plants received 10 hrs daylight of relatively high intensity, which under long-day conditions was extended by 6 hrs of low light intensity. In some treatments, plants received day illumination in the green house and were then transferred to have supplementary light which was always automatically controlled.

For the experiments in which light intensity was studied as a major factor, the light saturation was previously determined[1]. The evolution of O_2 per unit leaf area at different light intensities was measured in a WARBURG apparatus; 9 vessels of uniform capacity (42 ml.) were used. Each of these vessels was supplied with 10 ml. of WARBURG buffer solution nr. 9, 0.5 M. Inside the vessel CO_2 concentration was about 1.2 %. Discs of 0.5 cm diameter were taken from the two upper leaves of the plant. Each vessel containing 10 of these discs, placed on a perforated perspex plate, was exposed to a certain light intensity

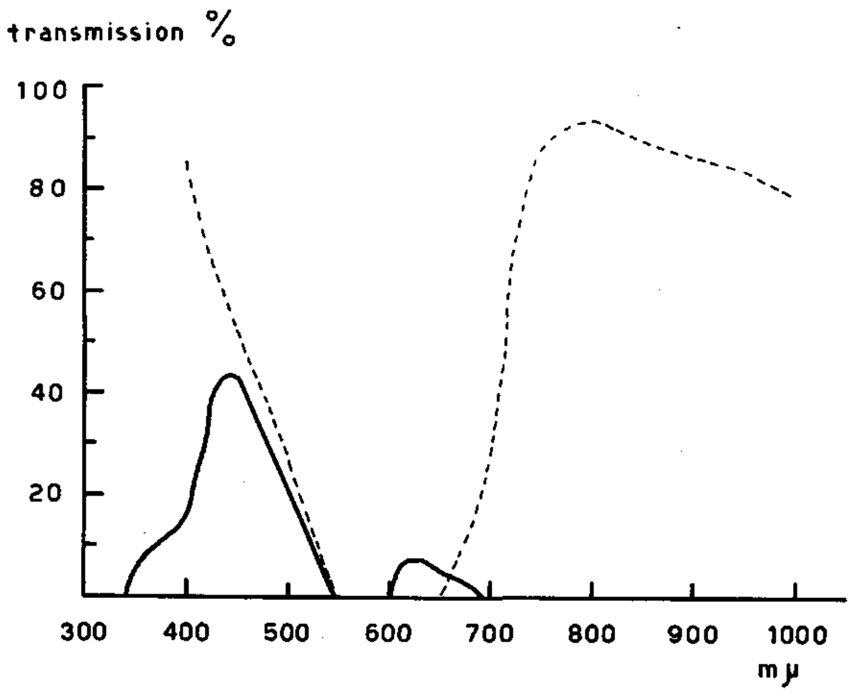


FIG. 4. Transmission curves of two blue filters. Broken lines: blue 21; full-drawn lines: perspex old blue 27.

[1] The author wishes to thank Ir. P. GAASTRA for the help he offered while carrying out these measurements.

for 1 hr. Records were made every 10 minutes during this period. Incandescent lamps have been used as light source.

In order to study the effect of the different light intensities on the growth and development of the plant, three different equipments were set up. The high light intensity equipment was provided with 38 fluorescent tubes (40 W"daylight"); divided into four groups, one group of 15 lamps above the plants, two groups of 8 lamps on each side and the last group of 7 lamps behind the plants. The medium light intensity equipment was provided with 19 lamps, 11 above the plants and 4 on each side. The low light intensity equipment was provided with only 7 lamps above the plants. Glass plates of 0.3 cm thickness were fitted either under or besides the fluorescent lamps, and the hot air produced during the daily illumination was driven out by fans.

In the experiments with different regions of the spectrum two types of equipment were used: the first for high light intensity and the second for low light intensity. The latter was only used for supplementary light. These equipments are almost the same as used and fully described by WASSINK and VAN DER SCHEER (1950) and WASSINK and STOLWIJK (1952). Recently some extensions of the high light intensity equipment have been made which are included in the description given by STOLWIJK (1954). In this connection it is worth mentioning that in the blue light compartment of high light intensity the blue glass filter

TABLE I

General data about light equipments and light measurements

Treatments	Sort of light	Type of measurement	Light intensity Flat meter and thermopile: ergs/cm²sec Spherical meter: ergo/sec/cm² ø sphere
Photoperiodism (indoors)			
basic illumination	natural day		
supplementary illumination	white	flat meter	4800 and 780
		spherical meter	11000 and 1370
Photoperiodism and vernalization (outdoors)			
basic illumination	natural day		
supplementary illumination	white	flat meter	367
Light intensity (indoors)	white	flat meter	41700 – 28500 – 14400
		spherical meter	135000 – 80000 – 31000
Light quality (indoors)			
basic illumination	white	spherical meter	25600
	coloured	thermopile*	25600*
supplementary illumination	white	spherical meter	535
	coloured	thermopile*	535*
Night temperature and High temperature (indoors)	white	flat meter	16700
		spherical meter	32200
Nutrition (indoors)	white	flat meter	16700 and 41700
		spherical meter	32200 and 135000

* Average of readings from 4 directions.

"nr. 21" was replaced by a perspex "Old Blue 27" filter which yields a blue light of higher purity, especially when infrared rays are concerned. This is shown in Fig. 4. Some general data about the measurements of the light intensities applied are given in Table 1.

If not mentioned in the text, the photoperiod used had a duration of 16 hrs.

All light measurements were carried out by the methods mentioned by STOLWIJK (1954). In the treatment in which the plants received the light energy from various directions, the spherical light meter, described by WASSINK and VAN DER SCHEER (1951), is more suitable than the flat light meter.

4. NUTRIENT SOLUTIONS

The influence of mineral nutrition on plant growth and development was studied with pure sand cultures which were supplied, weekly with nutrient solutions. Most of the media used were prepared on the basis of SHIVE's solution (1915). The ratio between different concentrations of the ion was (1:2:4). In all cases the normal standard solution was considered to contain the concentrations required for optimal growth and is presented by the central number of each series. Differences in the osmotic pressure are compensated by adding other salts, such as $CaCl_2$ to raise it to the level of the highest concentration used. For this reason it seems inadvisable to use solutions with very large differences in concentration. The solutions used are given in Table II.

TABLE II

Composition of nutrient solutions-concentration in grams per liter

Concentration	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4.7H_2O$	Salts added
Shive nor. sol.	0.860	1.960	2.418	
0.25 × N	0.215	1.960	2.418	$CaSO_4.2H_2O$
0.50 × N	0.430	1 960	2 418	$CaSO_4.2H_2O$
2.00 × N	1.720	1.960	2.418	
4.00 × N	3.440	1.960	2.418	
0.25 × (K+P)	0.860	0.490	2.418	$CaCl_2$
0.50 × (K+P)	0.860	0.245	2.418	$CaCl_2$
2.00 × (K+P)	0.860	3.920	2.418	
4.00 × (K+P)	0.860	7.840	2.418	

*) Micronutrients were added in all cases

5. PLANT DISSECTION AND OTHER RECORDS

In this work, microdissection studies were carried out for spike initiation and spike development, along with the various treatments. In each treatment, samples were chosen at random, when 50 % of the plants had reached the physiological age required for dissection. Five to ten plants were dissected from each treatment. The technique used for dissecting the plants was the same as described by LUYTEN and VERSLUYS (1921). The plant material was fixed in alcohol 96 %. and transferred to alcohol 50 % before dissection. After removal of both developed and undeveloped leaves, the vegetation points were placed in petri dishes filled with water and alcohol 50 % before examination under the binocular microscope. Just before examination, the vegetation points were rinsed in a strong solution of iodine and potassium iodide, which makes it easier to distinguish details. Iodine also proved to be more convenient than fuchsin and glycerin which easily produce light reflections when microphotographs are made. In order to keep the vegetation points in the desired positions, they were fitted in small blocks of plasticine, paying attention that they always remained under the liquid. The vegetation points were illuminated during their examination by means of lamp concentrating the light on one spot.

For microphotographs a Zeiss Optan stereo-microscope with attached Zeiss Winkel camera 6.5 $\times$ 9 cm was used, allowing magnifications of 6, 10, 16, 25 and 40 times. Just before photographing, the vegetation point is stained with iodine as mentioned before and then washed softly in water for some moments after which it is transferred to another petri dish, containing distilled water. This dish is placed on a piece of black velvet covering the table of the microscope in order to insure a dark background. The vegetation point is then illuminated by a strong, focussed light which passes through a green filter. Two kinds of photographic plates were used; Isochrome ($^{18}/_{10}$ °Din.) and Gevachrome 32 ($^{21}/_{10}$ °Din.) which both proved satisfactory. The second plate was found to be more sensitive and to give more details. The developmental stages in the shoot apex of wheat are shown in Plate 1 to which reference is made in the experiments.

With respect to the vegetative growth, stem length, tiller number, leaf area and leaf number have been recorded. The root/top ratio being of significance in the growth of higher plants, was also studied. Dry weight determinations were also made to have a clear idea about the distribution of the metabolic products and how they are directed within the plant under certain conditions. Chemical analyses for plant materials were carried out with the aid of the Laboratory of Soil Testing and Plant Analysis at Oosterbeek-Netherlands. In all cases sampling, drying, grinding and preserving of plant material were done according to the standard methods described by LOOMIS and SHULL (1937).

The leaf ratio (length/breadth) was calculated for the 2nd or 3rd well developed leaf from the top, as the average of 5–10 leaves.

CHAPTER III

TEMPERATURE

1. GROWTH AND DEVELOPMENT AS INFLUENCED BY TEMPERATURE

The effect of temperature on the vegetative growth and the development of wheat must be primarily due to changes in the pattern of the biochemical reactions within the plant. As a result, the balance between various processes of growth and development, which is most sensitive to these changes is influenced by changes of temperature. So, e.g., early heading of wheat was found to be generally favoured at relatively high temperatures, but results in rather poor ears and small shrunken seeds. This is largely due to the fact that tissues of the plants growing at high temperatures rather soon reach maturity and turn to senescence. This results in a significant reduction of photosynthetic products, so that the substrate required for supporting the development of ears becomes limiting. In such a case, it is not surprising that during the growing period, the different stages of growth and development may compete with each other. This, in some way, makes the antagonism between the different stages of growth and development more apparent, especially under the environmental conditions favouring the limitation of synthesis.

The results presented in Table III and graphically illustrated in Fig. 5 indicate that, concerning the vegetative growth, 20 °C seems to be an optimal temperature for stem elongation in both Hindi and Heine VII varieties, while stem elongation was suppressed when the temperature was increased to about 30 °C, or when it was decreased to 10 °C. However, the suppressing effect of high temperature was more apparent in the Hindi variety. In this respect, it is interesting to note that, just after germination, stem elongation proceeded faster at 30 °C than at 20 °C, which phenomenon somewhat later was reversed; the plants grown at 20 °C showed more progress and finally exceeded those of 30 °C. In this connection, one must keep in mind, that although stem elongation was suppressed by either low or high temperatures, the cause of this suppression seems to be quite different in these two cases. In the former case the rate of photo-

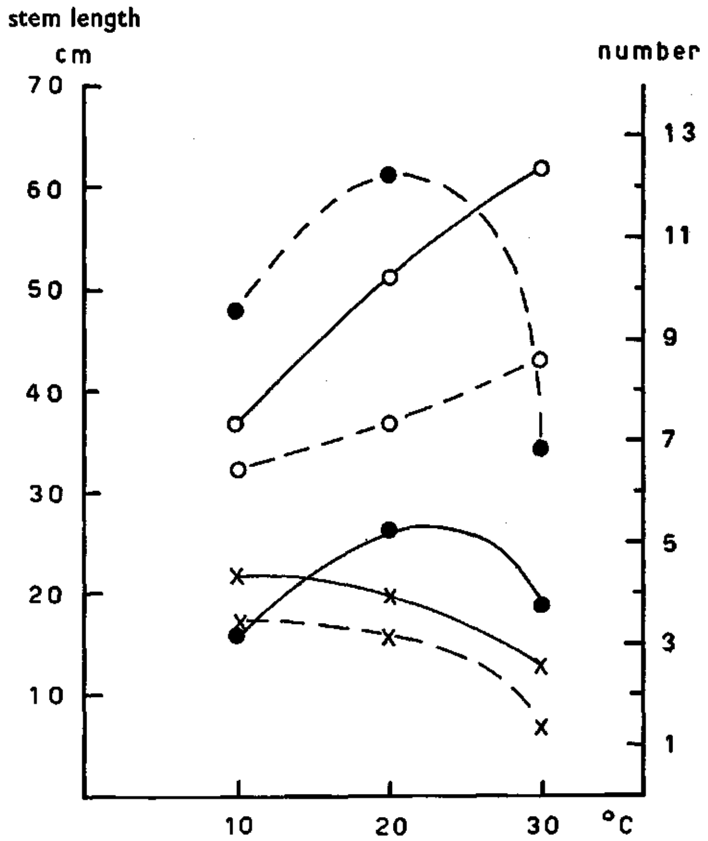


FIG. 5. Different aspects of vegetative growth in wheat as influenced by constant temperature conditions; Hindi and Heine VII varieties, after 105 days treatment.
Dotted lines: Hindi var., Full-drawn lines: Heine VII var. • stem length, o leaf number, × tillers number.

synthesis per unit time may be suppressed by the low temperature, while in the latter case, the rate of dissimilation may be accelerated as light intensity may be limiting the rate of photosynthesis, so that also then a decrease in the net rate of synthesis results. In the two cases one may expect a relatively poor growth.

TABLE III

Different aspects of vegetative growth in wheat as influenced by different temperatures under constant conditions. Hindi and Heine VII varieties, after 105 days treatment

Temp. °C	Heine VII var.			Hindi var.		
	Stem length (cm)	Leaf number	Tiller number	Stem length (cm)	Leaf number	Tiller number
10	15.9 ± 0.15	7.4 ± 0.25	4.4 ± 0.25	47.9 ± 2.06	6.5 ± 0.35	3.5 ± 0.29
20	26.1 ± 0.63	10.3 ± 0.60	4.0 ± 0.00	61.6 ± 2.25	7.4 ± 0.25	3.2 ± 0.20
30	19.4 ± 0.52	12.4 ± 0.40	2.6 ± 0.24	34.3 ± 1.35	8.7 ± 0.25	1.4 ± 0.25

Concerning the influence of temperature on the formation of the leaves and tillers in wheat, the data presented indicate that in both varieties a negative correlation exists between these two aspects of growth, which means an antagonism between these vegetative growth stages. The higher the temperature, the smaller the number of tillers and the larger the number of leaves. A difference between the two varieties used is that stem elongation was much more pronounced in Hindi than in Heine VII. On the other hand, the number of leaves and tillers produced per plant in Heine VII were always higher than that of those produced in the Hindi variety. This is a rather good indication that stem elongation under the conditions of our experiments generally proceeds in competition with other vegetative growth stages, such as tillering and leaf formation.

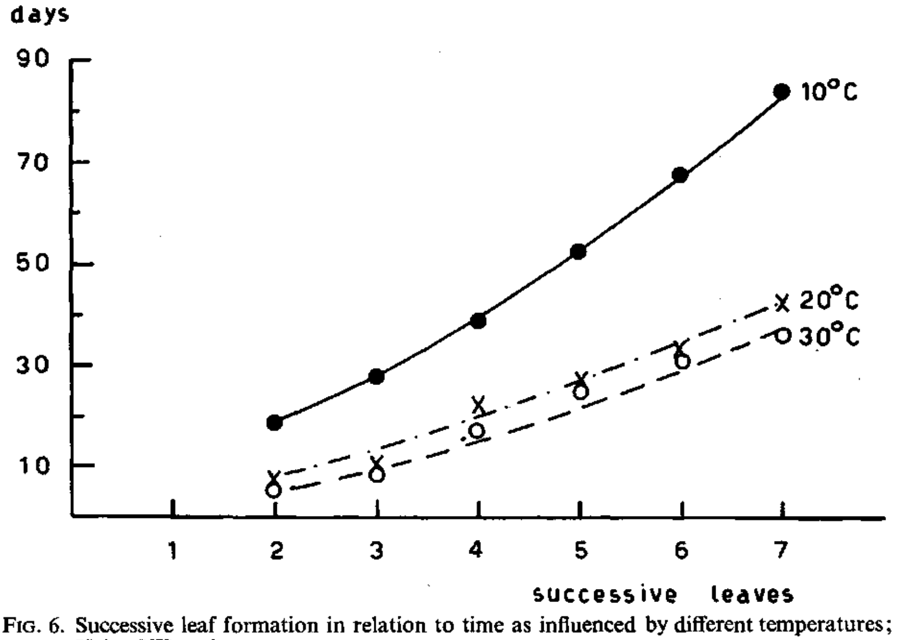


FIG. 6. Successive leaf formation in relation to time as influenced by different temperatures; Heine VII variety.

The data presented in Table IV and graphically illustrated in Fig. 6 show that the time required for the emergence of successive leaves is decreased significantly by increasing the temperature within the range of 10° to 30 °C; i.e. the time required for the emergence of the 7th leaf was 84, 42, and 36 days at 10°, 20°, and 30 °C respectively. A similar relation was found with all preceding leaves. In this connection, it is worth mentioning that a linear relationship seems to exist between the number of leaves and the length of the vegetative growth period. The differences between different temperature treatments are quantitative differences in the leaf number, while the linear relation mentioned above remains, resulting in different slopes of the various curves.

TABLE IV

Successive leaf formation in relation to time as influenced by different temperatures under constant conditions. Heine VII variety

Temp. °C	Time in days required for leaf formation up to the 7th leaf					
	2nd	3rd	4th	5th	6th	7th leaf
10	19	28	39	53	68	84
20	8	11	22	28	33	42
30	5	9	18	25	31	36

Concerning the influence of temperature on the dry matter production in the plant, both light intensity and light quality should be considered as significant factors. In our experiments plants were grown under "daylight" fluorescent tubes at an average intensity of 32 200 ergs/sec./cm² ø sph. From the results presented in Table V, and graphically illustrated in Fig. 7, the following can be concluded.

1. The absolute dry weight per plant reached its maximum at 20 °C, and was relatively higher at 30 °C than at 10 °C. When the dry weight production of either roots and shoots was determined separately, the same result was obtained.

2. When the root/top ratio is considered, a reversed relationship is found to exist between this ratio and temperature; namely the higher the temperature, the lower this ratio will be.

TABLE V

Dry matter production(g) and root/top ratio as influenced by different temperatures under constant conditions. Hindi variety, after 77 days treatment

Temperature °C	Entire plant	Root	Top	Root/top ratio
10	2.420	0.604	1.816	0.332
20	3.935	0.686	3.149	0.214
30	2.623	0.375	2.248	0.166

These results obtained for the root/top ratio were of importance, especially in interpreting the injurious effect of relatively high temperatures on the growth of some higher plants. It is generally accepted that a temperature of about 30 °C cannot be considered as a directly injurious factor. It has been found however, that this temperature checks the wheat growth especially under low light conditions. This means that such a temperature might affect the growth indirectly,

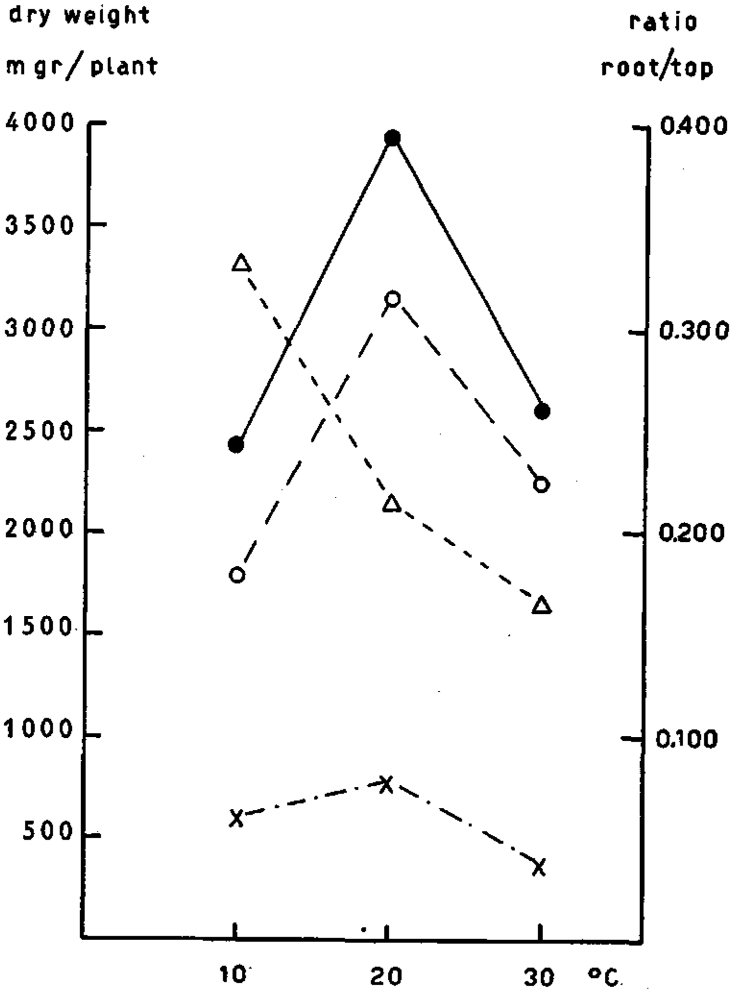


Fig. 7. Dry weight and root/top ratio as affected by different treatments of temperature; Hindi variety, after 11 weeks treatment.
• entire plant, o top, × root, △ root/top ratio.

e.g. by unfavourably changing the root/top ratio, which in fact represents the balance between two different growth aspects.

In almost all cases examined, it has been found that the roots of plants which had been grown at relatively high temperatures were proportionally weak if compared with the roots produced at lower temperatures. This was supposed to be due to shortage of oxygen which is of major importance for root growth and function. This was verified experimentally by growing two groups of wheat plants (Hindi variety) at 30 °C in the oxygen box described in Chapter II. One of these groups was supplied with excessive oxygen, while the other was left as a control without any external supply of the gas. The result shows that the first group within 10 days had produced more vigorously extending roots than the second one. This progress in root growth was favourable in inducing stronger and more healthy tops than that of the control. It is interesting to note that, when this experiment was repeated at a temperature of 10°C, no significant difference was observed. This may indicate that oxygen requirement for root growth increases with increasing temperature. In this connection, it seems interesting to note, that excessive leaf elongation caused by high temperature becomes dangerous, especially when the roots are too weak to supply the elongated leaves with sufficient water to keep their turgidity. In severe cases they usually break. A rather successful method to avoid this is to cut the upper parts of the leaves, a treatment which proved to be very useful in keeping the turgidity of the leaves. With this treatment, the dry weight production was expected to decrease, but this was not the case. The average dry weight per plant (calculated from 10 plants grown in 5 pots) with treated leaves was 2.84 and 3.02 grams for sand and clay soil respectively, while the average for untreated plants was 2.59 and 2.96 grams.

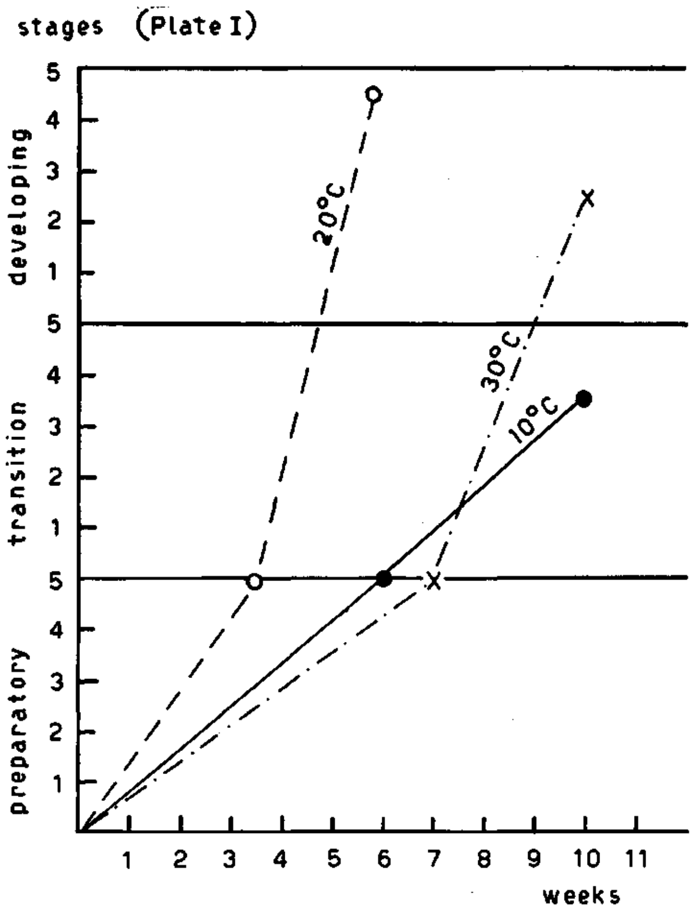


FIG. 8. The development of wheat (Hindi var.) in relation to different conditions of constant temperature.

Concerning the effect of temperature on the development of wheat, the results obtained show that Heine VII, a typical winter variety, remained in the rosette stage under the range of temperatures (from 10–30 °C). This has been further emphasized by dissecting plants from different temperature treatments. Not one plant was found to enter the transition stage. On the other hand, the Egyptian varieties reached reproductive stage in all the treatments, except under conditions of high temperature combined with relatively low light intensity, where especially the Baladi variety failed to reach the heading stage. However, when these plants were dissected, it was noticed that spike initiation had occurred although further development of the spikes was checked under the mentioned conditions.

The data presented graphically in Fig. 8 indicate that at 20 °C both spike initiation and spike development were significantly earlier than at 10 °C or 30 °C. Concerning flower initiation, the difference was 24 and 17 days respectively. It was observed also, that, although the difference between 10 °C and 30 °C did not exceed one week, the development of the spike during the latter treatment was obviously earlier than during the former one, i.e., the plants grown at 30 °C reached the third developmental phase ten weeks after planting, while the plants grown at 10 °C were still in the fourth transition stage.

2. FROST RESISTANCE AND COLD REQUIREMENT DURING THE EARLY STAGES OF GROWTH

The imported subtropical wheat varieties were grown in a field experiment alongside two local varieties, of which one is a typical winter variety and the other is a typical spring variety. These varieties were sown either in winter or in spring; in the latter case they were grown either from vernalized or non-vernalized seeds. The chilling of the seeds had been carried out during 45 days at 1 °C in vernalization boxes as described in Chapter II.

Concerning the frost resistance in different varieties sown in winter either in October or December, the imported varieties, being always grown under subtropical conditions, were expected to perish during severe frost in winter time. However, only Baladi was killed during the frost in February 1954. In the Hindi variety about 32 percent of the plants escaped from frost and later produced healthy ears. It is worth mentioning that when the plants were examined, it was observed that in almost all cases, the roots were ruptured. The local varieties showed more resistance to frost, especially Heine VII. In this connection it was observed that during the severe frost period, the colour of the leaves of the subtropical varieties changed to brown-red, while in Heine VII variety it was dark green. In general, plants grown (with the aid of the wooden cabinets outdoors) under short-day conditions were found to be more sensitive to frost than those grown under comparable long-day conditions.

During the different treatments of spring sowings (20th March) all the varieties, with the exception of Heine VII, flowered whether grown from vernalized or non-vernalized seeds. Heine VII, however, if grown from non-vernalized seed, remained in the rosette stage. This clearly indicates that the quotum of low temperature needed for inducing flowering in winter varieties is not necessary for subtropical wheat varieties which headed freely with or without any cold treatment. From the data presented in Table VI and Fig. 9 it appears, that if earliness in flowering is considered, Hindi is a neutral variety.

Baladi on the other hand, proved to be influenced more by day length. In this experiment, after the plants have developed the fourth leaf, some pots were transferred from the short-day to the long-day conditions, and some other pots from the long-day to the short-day conditions. Both the Baladi and Hindi varieties having had long-day and long-short-day treatments produced their ears 80 days after planting while those having had short-day and short-long-day treatments produced their ears after 93 and 105 days respectively (see Table VI). It seems important to note that in both cases, varieties grown under natural conditions of day-length were relatively earlier than those grown under the wooden cabinets. The winter wheat variety, Heine VII, seems to be very late in comparison with the subtropical varieties. This was proved to be true with the two sowing dates used.

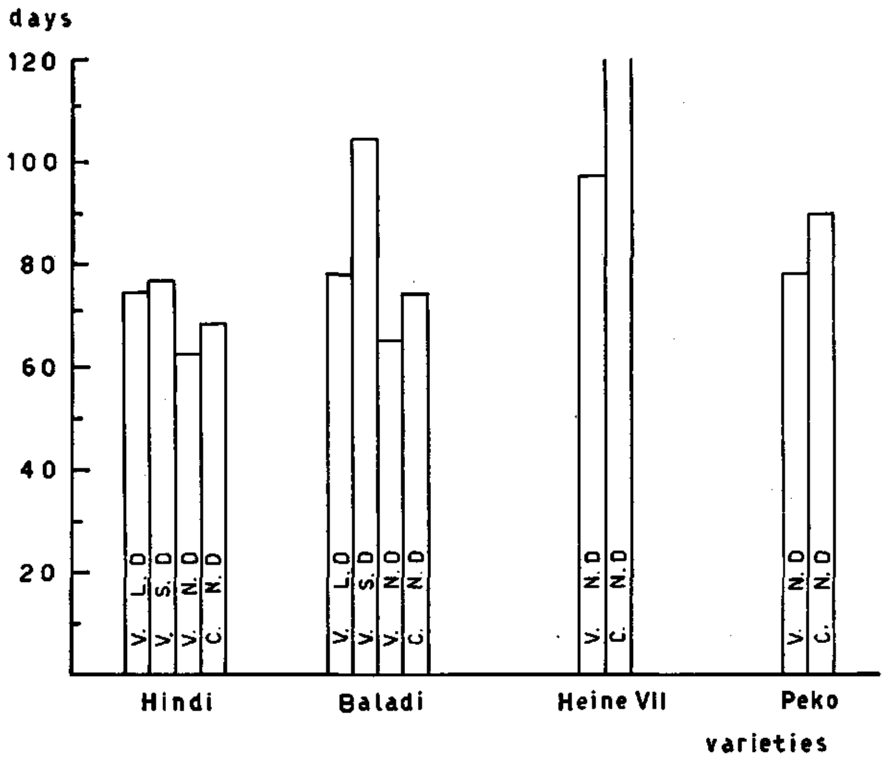


FIG. 9. Time of spike emergence in four different wheat varieties sown in spring (20th March) as influenced by vernalization and day-length. Experiment conducted outdoors.
v: vernalized, c: non-vernalized, L.D.: Long-day (10+6 hrs), S.D.: short-day (10+0 hrs).

Dissections were made of the late (non-shooting) varieties 100 days after planting in order to examine the vegetation points. The data presented in Table VII indicate that plants from vernalized Baladi under short-day conditions had already produced well developed ears, while in Heine VII only two rows of inflorescences were formed. Under long-day conditions, the development was more pronounced, except when the long-day was followed by short-day con-

TABLE VI

Heading time (in days) in four wheat varieties as influenced by vernalization under different conditions of day length

Variety	45 days vernalization					Control non-ver.
	L.day	S.day	L–S.day	S–L.day	Natural D.	
Hindi	75	77	75	79	63	69
Heine VII	late	late	late	late	98	rosette
Baladi	79	105	80	93	66	75
Peko	–	–	–	–	79	90

ditions; then the plants remained physiologically young and no further development could be observed. Concerning this it is interesting to observe that some samples from non-vernalized Heine VII produced the double ridge structure, which indicates that the plants already have passed the vernalizing stage. This could only be possible, if we suggest that the relatively cold nights of early spring had fulfilled the cold requirements of this stage.

TABLE VII

Physiological development of the vegetation points in the non-shooting plants from the spring sowing treatments. Dissected on 29-7-1954

Variety	Chilling period (days)	Day-length treatm.	Degree of development
Heine VII	45	L.D.	Some tips with bracts on both sides Some tips with well developed flowers
Heine VII	45	S.D.	Some tips with 2 bracts Some tips with 2 rows of inflorescences
Heine VII	45	L.S.D.	All very young, no further development
Heine VII	45	S.L.D.	Some tips with bracts Some tips with 2 rows of flowers Some tips good development
Heine VII	0	Nat. D.	Some tips double ridged Some tips with bracts
Baladi	45	S.D.	All well developed ears

3. GROWTH AND DEVELOPMENT AS INFLUENCED BY DIFFERENT NIGHT TEMPERATURE

In order to study the influence of different night temperatures on the growth and development of higher plants, some precautions must be taken to avoid misleading results. If plants are transferred from low temperature rooms, in order to receive their daily illumination at relatively higher temperatures, the shoot system of the plant reaches the room temperature within a short time. On the other hand, the root system remains cool for a much longer time, until the soil around it reaches the level of the room temperature. This was found to have an injurious or even fatal effect in some cases. This is because transpiration under such conditions exceeds the supply of water by the roots, which remain cool during the first part of the day. This period, in fact could be considered as an extension of the temperature conditions prevailing during the preceding night. As a result turgor pressure in the cells of the plants is reduced or even lost, thus the rate of photosynthesis is decreased significantly and in severe cases the wilting point is reached. This phenomenon becomes more apparent if the difference between day and night temperature is relatively large. In the light of these results, some precautions must be taken in experiments dealing with the effect of night temperature:

a. When the plants are transferred, at the end of the dark period, to receive their daily photoperiod, the temperature of the soil around the roots must be altered until it reaches, as near as possible, the temperature surrounding the roots. A quick and easy way to achieve this is to allow a slow current of water of the required temperature to pass through the soil for some minutes.

b. Control plants must receive the same treatment in order to avoid differences in growth which may occur as a result of the different moisture content of the soil.

A satisfactory system to move the plants must be used, in order to avoid damage from shocks that may occur to the roots. If small trolleys are used for this purpose they must be moved slowly and cautiously.

In the experiments conducted to study the influence of different night temperatures on the growth and development of wheat, an optimal day-temperature of about 22° ± 1.2°C was used during the daily photoperiod. The plants received a 16 hrs photoperiod, and were then transferred to receive a dark period of 8 hrs at different temperatures (2°, 10°, 20° and 27°C).

The results of the effect of night temperature on vegetative growth indicate some differences which could be considered fundamentally the same as those produced at various temperatures which are kept constant throughout the daily cycle. The data presented in Table VIII and Fig. 10 show that, concerning the stem elongation, the most favourable night temperature was between 10° and 20°C. On the other hand, it was observed that outside this range, both lower (2°C) and higher (27°C) temperatures suppress stem elongation; this suppression was more significant at the former than at the latter temperature. As to the effect of the night temperature on the number of leaves and tillers produced per plant, it has been demonstrated that the higher the night temperature, the smaller the number of tillers but the greater the number of leaves. A correlation between the absolute dry weight formed by the plant and stem elongation can be observed in Table IX and Fig. 11. A similar correlation was found to exist between dry weight and the "multiplied leaf ratio" (length × breadth) which may be considered as an indicator for the leaf area.

TABLE VIII

Different aspects of vegetative growth in wheat as influenced by different night temperatures. Hindi variety, after 70 days treatment

Night temp. °C	Stem length (cm)	Tiller number	Leaf number
2	38.4 ± 1.70	2.8 ± 0.20	6.2 ± 0.20
10	61.9 ± 2.37	2.2 ± 0.20	6.75 ± 0.22
20	57.6 ± 2.53	1.8 ± 0.20	7.4 ± 0.25
27	50.2 ± 1.21	1.25 ± 0.18	8.3 ± 0.19

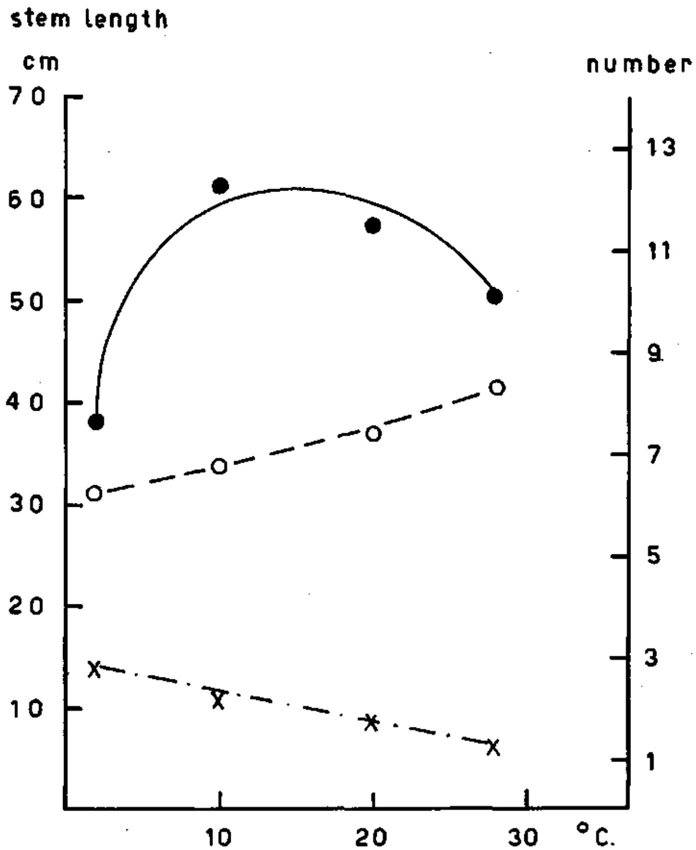


FIG. 10. Effects of various night temperatures on growth of wheat (Hindi var.). Measurements after 70 days treatment.
• stem length, o leaf number, × tillers number.

Dry weight determinations have been carried out for different treatments. From the data presented in Table X and graphically illustrated in Fig. 12 two conclusions arise.

TABLE IX

Stem length and leaf area in relation to dry matter production as influenced by different night temperatures. Hindi variety, after 70 days treatment

Night temp. °C	Dry weight (g)	Stem length (cm)	Leaf ratio l/br (average)	Multiplied ratio (l × br) cm²
2	1.64	38.4 ± 1.70	45/0.8	36.00
10	2.80	61.9 ± 2.37	36/1.4	50.40
20	2.76	57.6 ± 2.53	40/1.2	48.00
27	2.60	50.2 ± 1.21	41/1.1	45.10

Multiplied ratio = leaf length × leaf breadth.

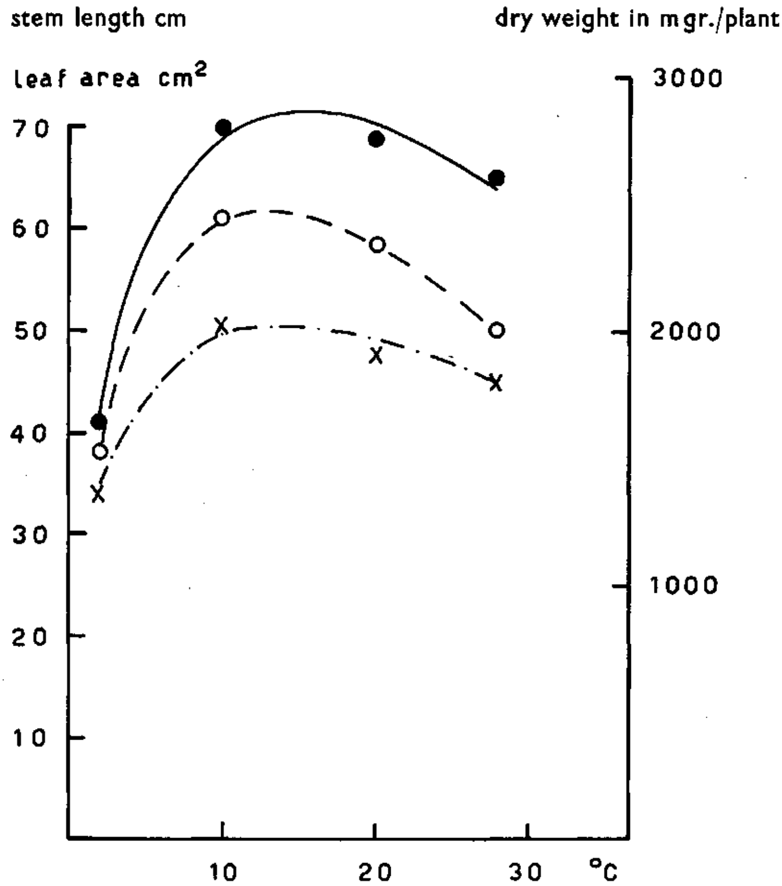


FIG. 11. Curves showing the correlation between stem length (o), leaf area (multiplied ratio) (×) and dry matter production (•) as influenced by various night temperatures; Hindi var. after 70 days treatment.

a. Lowering the night temperature from 27 °C to 10 °C results in the production of maximum dry weight per plant. Further decrease of the night temperature to 2 °C results in an abrupt decrease in the dry matter yield per plant. This

TABLE X

Dry matter production (g) and root/top ratio as influenced by different night temperatures. Hindi variety, after 70 days treatment

Night temp. °C	Entire plant			Root			Top			Root/top ratio
	Fresh	Dry	%	Fresh	Dry	%	Fresh	Dry	%	
2	14.58	1.64	11.24	3.72	0.386	10.37	10.86	1.254	11.54	0.307
10	21.68	2.80	12.91	6.56	0.918	13.84	15.12	1.882	12.44	0.478
20	20.82	2.76	13.25	4.46	0.750	16.90	16.36	2.010	12.25	0.373
27	22.12	2.60	11.75	4.86	0.562	11.56	17.26	2.038	11.80	0.275

was nearly the same case with the root dry weight and also when the root/top ratio was considered.

b. When the growth of the tops is considered, the case is quite different, and we find that the higher the night temperature, the higher the dry weight production is.

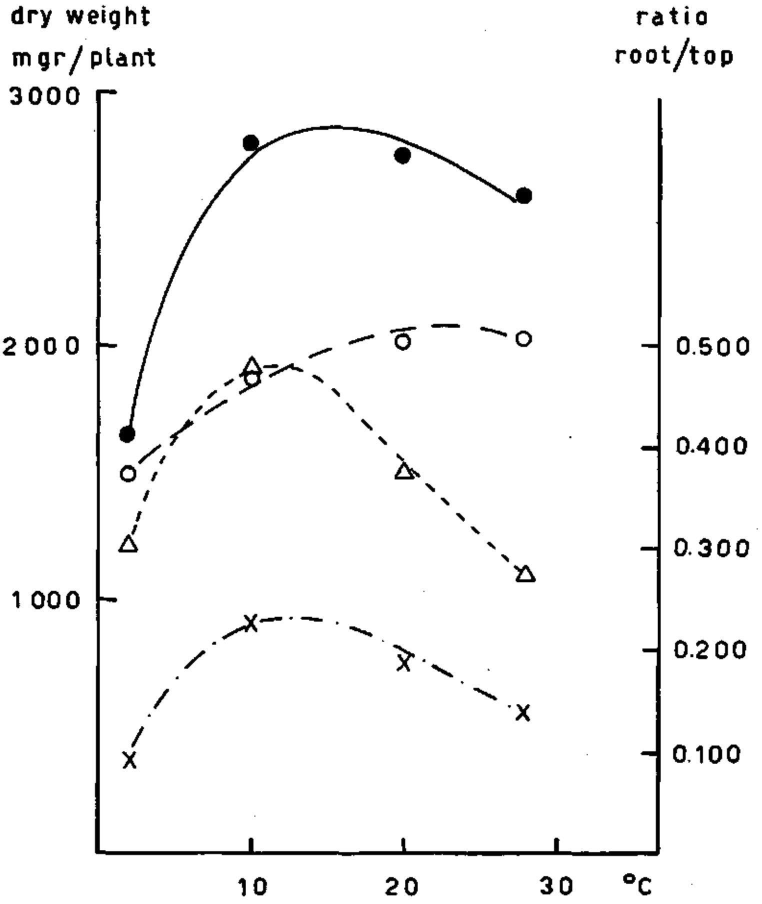


FIG. 12. Dry weight production and root/top ratio as influenced by various night temperatures; Hindi var. after 70 days treatment.
• entire plant, o top, × root, △ root/top ratio.

Concerning the effect of night temperature on the development of wheat, it was noticed that 20 °C is the most favourable night temperature for both the intiation and the development of the spikes. From Fig. 13, it is apparent that lowering the night temperature to 10 °C or increasing it to 27 °C retarded the initiation by one or two weeks respectively. If the temperature is further decreased to 2 °C, both initiation and development were retarded more significantly than in all other cases. It seems that during the development of wheat, a night temperature of 10 °C induced earliness in both initiation and development of the spikes more so than 27 °C. This result is rather different from that produced in plants grown under constant temperature conditions. In the latter case, as has been stated above, although initiation was favoured at 10 °C, yet the development proceeded more quickly at 30 °C than at 10 °C (see Fig. 13).

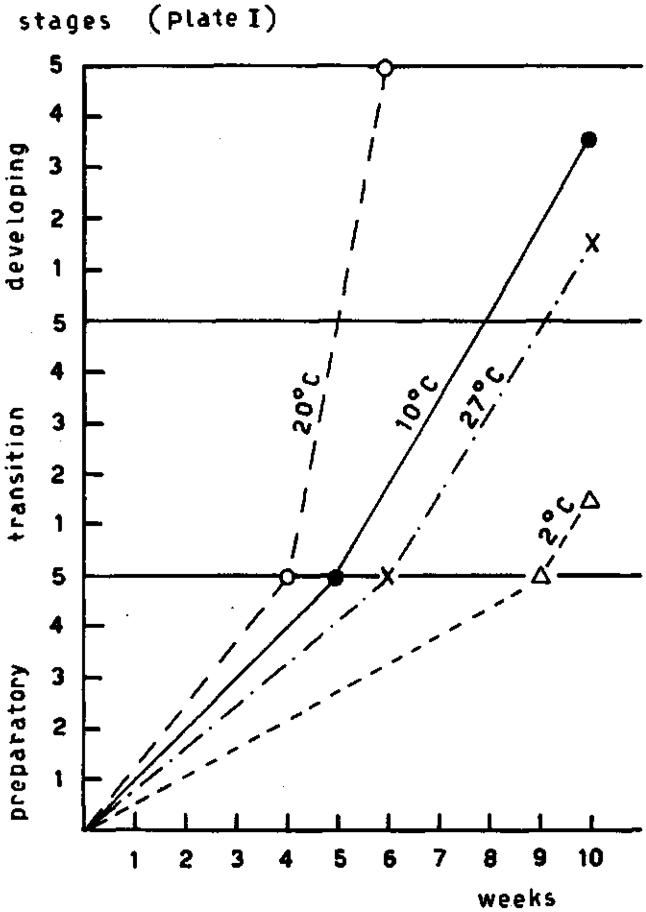


FIG. 13. The development of wheat (Hindi var.) in relation to different conditions of night temperature.

4. DISCUSSION

Before discussing the influence of temperature on the growth and development of the wheat plant, it seems important to draw attention to the fact that this influence could be altered by changing the prevailing environmental factors, especially those connected with light. However, in some cases it is difficult to isolate the effect of temperature as a pure factor influencing a certain process. This is largely due to the interference of other factors which may arise from the main factor itself.

The effects of night temperature may be discussed in relation to the results obtained at constant temperature in order to examine whether the fundamental effect of temperature is the same in both cases. The pattern of leaf formation and tiller production was similarly influenced in the two types of temperature treatment. And so were stem elongation and dry weight production. This does not mean that the dry weight production per plant reaches the maximum at the same temperature in the different types of experiments. At constant temperature the maximum dry weight production was reached at 20 °C, while with different night temperatures, the highest dry weight production was reached when the night temperature was decreased to 10 °C. This seems reasonable, because if the day temperature is further decreased to 10 °C, the rate of photosynthesis will be significantly decreased. On the other hand, decreasing the night temperature to 10 °C will suppress the dissimilation process, and a more favourable balance between synthetic processes and dissimilation is obtained. In this connection, it has been shown that further decrease in the night temperature to 2 °C strongly suppressed the dry weight. This could be explained in the following way:

a. It is probable that some processes which may take place during the night, are suppressed at such a low temperature. In this connection it may be mentioned that WASSINK and WASSINK (1952), concluded that some synthetic processes, perhaps connected with protein synthesis, go on during the night.

b. It is also probable that such low a night temperature (2 °C) affects also the metabolic processes during the day via its suppressing effect on the metabolic enzymatic system during the dark period. This of course could be reasonable only if we suggest that this enzymatic system requires some time in order to resume its full activity after the cold treatment during the preceding night.

We may conclude that lowering the night temperature is favourable, provided that it does not exceed a certain limit according to the plant in question. In this respect, it has been reported by ROBBINS (1946), that the recommended difference between day and night temperature is about 6–11 °C. This difference is about the same as found by WENT (1944), who observed that the maximum growth of tomatoes was obtained by maintaining the day temperature at 26.5 °C and allowing the night temperature to fall to 17–20 °C. In the light of our results, it appears that the difference in dissimilation is not the chief effect of different night temperatures, especially after we have seen that lowering the night temperature to 2 °C (suppressing the dissimilation process) decreased the dry weight production within the plant.

The effect of various night temperatures on the root/top ratio proved to be nearly the same as that of various constant temperatures. However, it seems that this ratio in relation to temperature is controlled by other environmental conditions, such as light intensity, mineral nutrition, and oxygen concentration around the roots. The first two factors will be discussed in the following chapters.

Concerning spike initiation and spike development in wheat, night temperature seems to have an accelerating effect up to 20 °C. This effect was most significant in inducing development when other factors such as day length and light intensity are optimal. This may be the chief cause of the relatively lower production of dry matter at 20 °C than at 10 °C. At the former temperature the vegetative growth period is shortened; thus the total energy received is decreased. On the other hand, when the night temperature was further increased to 27 °C, the development was retarded once more. This of course may refer to the depletion of the carbohydrates at high night temperature, leaving only a small reserve to support development. At 2 °C night temperature, the development also proceeds rather slowly, due to the suppressive effect of this low temperature on the whole metabolic processes as mentioned above.

CHAPTER IV

LIGHT

1. VEGETATIVE GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY PHOTOPERIODISM

The nature of the photoperiodic reaction has not yet been revealed. This may in part be due to the fact that most of the photostimulus processes proceed at relatively low light intensity. Whether a linear relationship exists between light intensity and the response of the organism, is not yet established. However, until now, the ultimate response is fairly the only approach we have towards explaining the process.

In this study, the photoperiodic response of the wheat plant was quantitatively examined with special reference to its vegetative growth and development. During the course of the experiment, the plants daily received 8 hrs natural illumination in the greenhouse, after which they were divided into 5 groups.

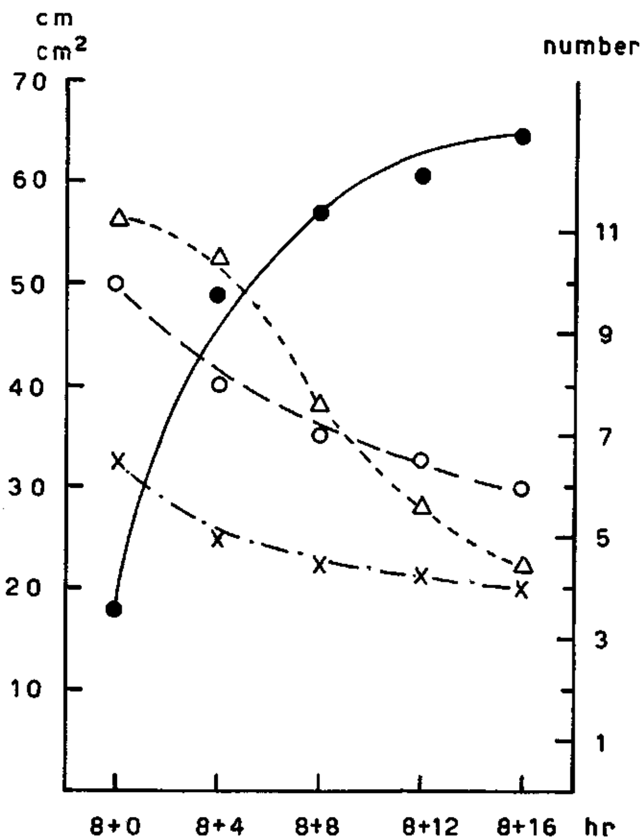


FIG. 14. Effects of different photoperiods on growth of wheat (Hindi var.). Measurements after 45 days treatment.
● stem length, ○ leaf number, × tillers number, △ „multiplied ratio".

These groups were then transferred to five different equipments, in order to supply the plants with supplementary light of a certain intensity (see Table 1), for different periods ranging from 0 to 16 hrs, with 4 hrs difference between the successive treatments.

The data presented in Table XI and graphically illustrated in Fig. 14 indicate that in Hindi the influence of photoperiod on stem elongation is contrary to its influence on the production of leaves or tillers. This means that gradually increasing the day-length to 24 hrs resulted in a gradual increase of the stem length, and at the same time suppressed the other two aspects of growth. Concerning the leaf area, the "multiplied ratio" (l × br) presented in Table XI also proved a gradual decrease in leaf area as the photoperiod is increased.

TABLE XI

Vegetative growth in wheat as influenced by different photoperiodic treatments Hindi variety, after 45 days treatment

Photoperiod hrs	Stem length (cm)	Tiller number	Leaf number	Leaf ratio l/br	Multiplied ratio (l × br, cm²)
8+ 0	17.7 ± 0.60	6.5 ± 0.34	10.0 ± 0.32	40.1/1.4	56.14
8+ 4	48.9 ± 1.46	5.0 ± 0.32	8.0 ± 0.29	37.8/1.4	52.92
8+ 8	56.8 ± 1.74	4.5 ± 0.29	7.0 ± 0.00	28.2/1.3	36.66
8+12	60.8 ± 1.74	4.3 ± 0.29	6.5 ± 0.34	22.0/1.2	26.64
8+16	64.7 ± 2.01	4.0 ± 0.32	6.0 ± 0.32	22.5/1.0	22.50

When the dry weight determinations had been obtained, it was found that increasing the photoperiod up to 20 hrs gave maximum total production. When the photoperiod was further increased to 24 hrs, the total dry weight per plant decreased once more. This was nearly the same when determinations were made of the shoots only. Concerning dry weight production within the roots, no significant differences were obtained between the different photoperiodic treatments. However, when the root/top ratio was considered, it was observed that this ratio reached its maximum (0.500) under photoperiods ranging from 8 to 16 hrs daily. Increasing the photoperiods to 20 or 24 hrs caused a sudden decrease in the ratio to reach a minimum of about 0.350, see Table XII and Fig. 15.

TABLE XII

The production of dry matter (g) and the root/top ratio in wheat as influenced by different photoperiodic treatments. Hindi variety, after 50 days treatment

Photo-period hrs	Entire plant			Root			Top			Root/top ratio
	Fresh	Dry	%	Fresh	Dry	%	Fresh	Dry	%	
8+ 0	26.10	3.270	12.53	9.90	1.090	11.01	16.20	2.18	13.46	0.500
8+ 4	25.15	4.010	15.94	7.15	1.335	18.67	18.00	2.675	14.86	0.495
8+ 8	27.65	4.695	16.99	9.15	1.560	17.05	18.50	3.135	16.94	0.497
8+12	22.25	4.520	20.31	5.75	1.175	20.43	16.50	3.35	20.30	0.354
8+16	20.20	4.040	20.10	5.25	1.065	20.29	14.85	2.975	20.03	0.357

Concerning the photoperiodic effect on the development of wheat, a strong relationship exists between the daylength and the physiological development of

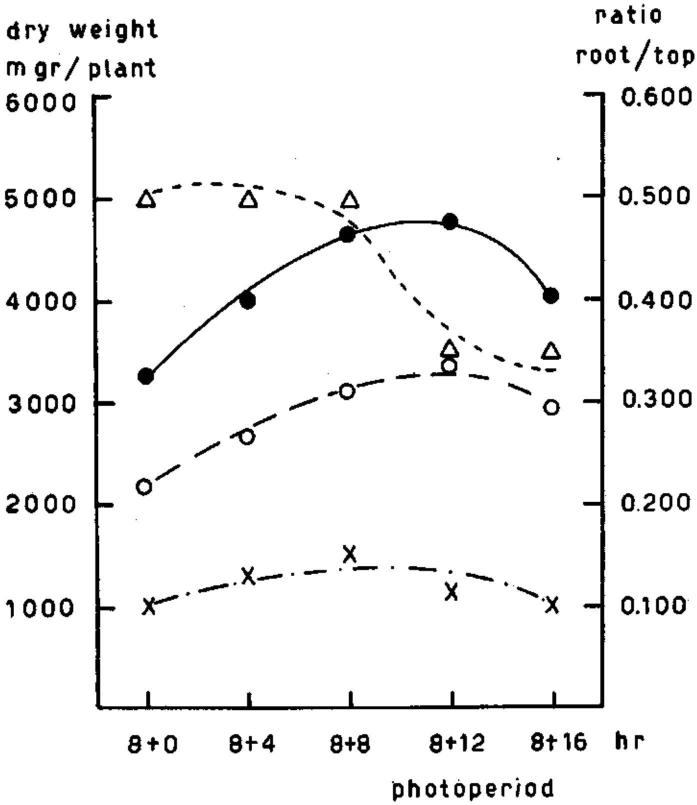


FIG. 15. Dry weight production and root/top ratio in wheat (Hindi var.) as influenced by various photoperiods. After 50 days treatment.
• entire plant, o top, × root, △ root/top.

the plant. In almost all the experiments conducted, a photoperiod of 8 hrs was found insufficient to induce spike initiation even after 6 weeks of treatment. On the other hand, 3 weeks treatment with 20 or 24 hrs photoperiod was sufficient to induce well developed spikes. In this respect, it is interesting to note that the response of the plants gradually increased when the photoperiod was increased from 8 to 24 hrs, see Fig. 16.

In the light of these results, the following conclusions can be drawn:

a. A positive relationship exists between stem elongation and photoperiod. Contrary to this, when the formation of leaves and tillers is considered, a negative relationship is observed.

b. The development of wheat seems to be quantitatively affected by day-length, which means that the longer the day-length, the earlier is the development of the plant.

c. A correlation between stem elongation and development towards reproduction is probable, when photoperiodic reaction is considered.

In another experiment conducted in the field under controlled conditions of

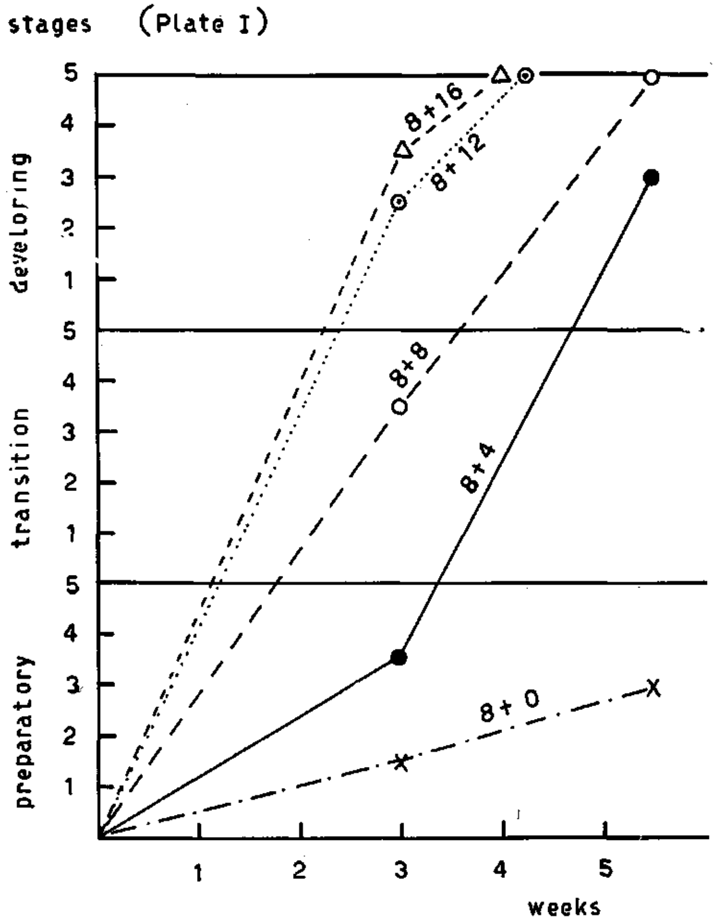


FIG. 16. The influence of different photoperiods on the development of wheat (Hindi var.).

day-length (10 + 0 and 10 + 6 hrs), both Hindi and Peko varieties were sown as winter wheats (in October). Records were made of the stem length at two different dates, time of heading and for dry weight production of ears in relation to that of the stems. The data presented in Table XIII show that during the first 50 days, no significant differences were observed between the two varieties under either day-length treatment. On the other hand, 210 days after planting, Hindi var. was significantly taller than Peko var. in both day-length treatments.

In addition, it was also observed that in both varieties, plants grown under long-day conditions were relatively taller than plants grown under short-day conditions. Concerning heading, Hindi var. was earlier by 46 and 32 days under long-day and short-day respectively than Peko. In this respect, it is interesting to note that in Hindi variety the difference between long and short-day treatments does not exceed 9 days, while in Peko this difference reaches more than 3 weeks. Concerning the production of dry matter per plant, the figures given in Table XIV show that, in general, more dry matter is produced in Hindi. The ratio of dry matter in the ears to that in the stems indicates that Hindi variety also produces high ratios. In both varieties, the dry matter of the ears is higher under the long-day treatment.

TABLE XIII

Photoperiodic reaction under natural conditions of temperature during winter time Hindi and Peko varieties, measurements after 50 and 210 days treatments

Variety	Age in days	10+0 hrs photoperiod		10+6 hrs photoperiod	
		Stem length (cm)	Days up to heading	Stem length (cm)	Days up to heading
Hindi	50	2.4 ± 0.06	–	2.9 ± 0.08	–
Peko	50	2.2 ± 0.09	–	2.4 ± 0.09	–
Hindi	210	33.6 ± 1.16	234	41.3 ± 1.60	225
Peko	210	20.4 ± 0.28	280	26.4 ± 1.30	256

TABLE XIV

The production of dry matter(g) as influenced by photoperiod under natural conditions of temperature in winter time. The determinations were carried out when the mealy stage was reached.

Variety	10+0 hrs photoperiod			10+6 hrs photoperiod		
	Stem+leaves	Ears	%	Stem+leaves	Ears	%
Peko	71.6	11.2	15.6	83.8	32.4	38.6
Hindi	98.5	24.2	24.5	76.0	35.3	46.4

2. VEGETATIVE GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY SUPPLEMENTARY LIGHT OF DIFFERENT INTENSITIES

In the previous section, all photoperiodic treatments were receiving their supplementary illumination at a certain constant level of light intensity. Thus, the differences produced were related primarily to the differences in the duration of the supplementary light. The question arises as to what extent the intensity of the supplementary light affects the growth and development of wheat. This question leads to another experiment in which three equipments with different light intensities (0, 1300, and 11 000 ergs/sec./cm^2 ø sph.) were used for supplementary illumination. The plants were divided into three groups.

These groups were subjected 8 hrs daily to natural illumination in the green house (from 10 a.m. to 6 p.m.); each group then is transferred to one of the light equipments mentioned before, to receive supplementary illumination until the next morning.

Concerning the vegetative growth, the data presented in Table XV and graphically illustrated in Fig. 17 show that increasing the intensity of the supplementary light from 0 to 11 000 ergs/sec./cm^2 ø sph. caused a subsequent increase in stem elongation from about 17.5 to 59 cm. On the other hand, the number of both leaves and tillers was decreased by increasing the supplementary light intensity within the same range. When the leaf area was calculated, it was found that the "multiplied ratio" increases with decreasing intensity of the supplementary light.

TABLE XV

Vegetative growth in wheat as influenced by different intensities of supplementary light; Hindi variety, after 45 days treatment

Suppl. light int. ergs/sec./cm² ø sph.	Stem length (cm)	Tiller number	Leaf number	Leaf ratio l/br	Multiplied ratio (l × br) cm²
0	17.5 ± 1.28	11 ± 0.14	9 ± 0.14	41/1.5	61.5
1 370	34 ± 1.69	8 ± 0.32	7.5 ± 0.4	37/1.5	55.5
11 000	59.5 ± 2.13	5.5 ± 0.34	6.5 ± 0.22	32/1.1	35.2

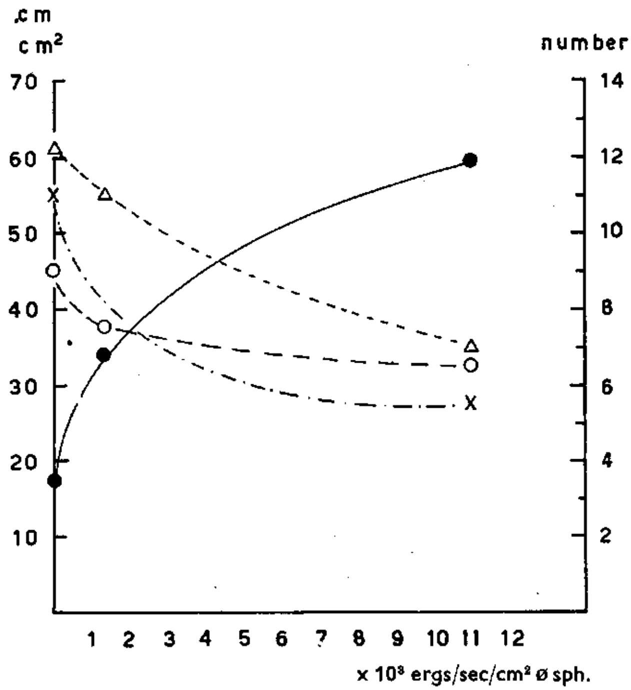


FIG. 17. Effects of supplementary light at different intensities on growth of wheat (Hindi var.), after 45 days treatment.
• stem length, o leaf number, × tillers number, △ multiplied ratio.

This becomes reasonable if we suggest that the excessive energy (of the supplementary light) is primarily used in speeding up the developmental growth at the expense of other vegetative growth processes.

The influence of supplementary light was also studied in relation to the dry matter production. The results given in Table XVI and graphically illustrated in Fig. 18, show no significant differences in dry weight, neither for the whole plant, nor for the roots and tops separately. When the root/top ratio was concerned, it was found that this ratio increased when the supplementary light intensity was increased from 0 to 1370 ergs/sec./cm² ø sph. With a further increase of up to 11 000 ergs/sec./cm² ø sph. the case was reversed and the root/top ratio decreased once more. However all these differences were not quite significant, and could equally well be attributed to differences in development or to sampling error.

TABLE XVI

Dry weight (g), and root/top ratio in wheat as influenced by different intensities of supplementary light; Hindi variety, after 45 days treatment

Suppl. light int. ergs/sec./cm² ø sph.	Entire plant			Root			Top			Root/top ratio
	fresh	dry	%	fresh	dry	%	fresh	dry	%	
0	27.3	3.05	11.2	9.2	1.0	10.8	18.1	2.05	11.3	0.487
1 370	26.2	3.15	12.0	9.1	1.05	11.5	17.1	2.10	12.2	0.500
11 000	25.9	3.7	14.1	8.4	1.2	14.2	17.5	2.50	14.2	0.480

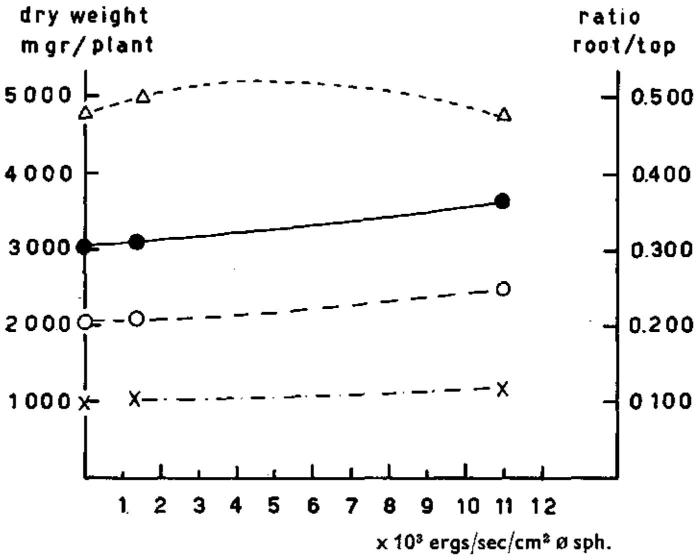


FIG. 18. Dry weight production and root/top ratio as influenced by different intensities of supplementary illumination. After 45 days treatment.
• entire plant, o top, × root, △ root/top.

Concerning the influence of the supplementary light on the physiological development, it is obvious from Fig. 19, that the higher the light intensity, the quicker the progress towards reproduction will be. This proved to be true when both initiation and development of the spike were considered. After 3 weeks of treatment, the plants receiving 1370 and 11 000 ergs/sec./cm² ø sph., reached the second and fifth transition stages respectively, while the plants of the third (dark) series, were backward and most of them failed to develop further than the second preparatory stage. The ratio of development of the different treatments remained nearly constant, and after 6 weeks the plants were in the fifth developmental, the first developmental, and the fourth preparatory stages respectively.

3. VEGETATIVE GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY LIGHT INTENSITY DURING THE DAY

Up to the saturation point, a linear relationship exists between the rate of photosynthesis and the light intensity. This relationship continues provided other limiting processes are absent, which of course practically cannot occur ultimately (see fig. 20).

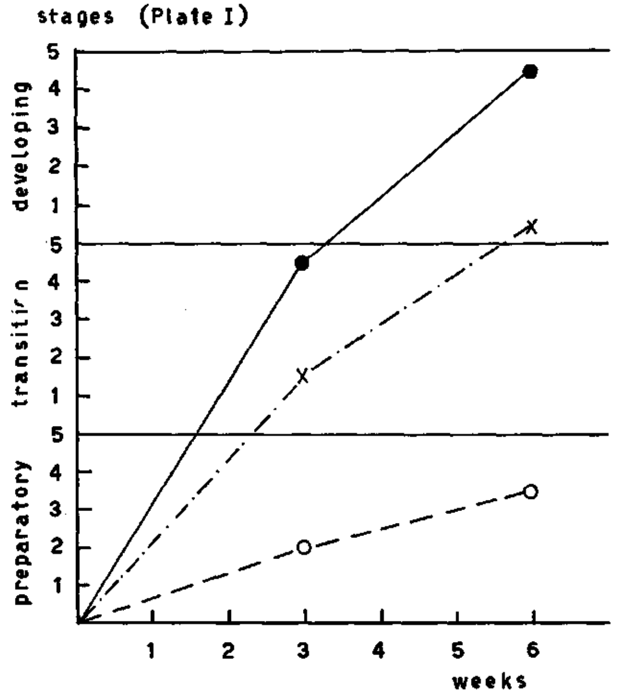


FIG. 19. The development of wheat (Hindi var.) as affected by different intensities of supplementary illumination.

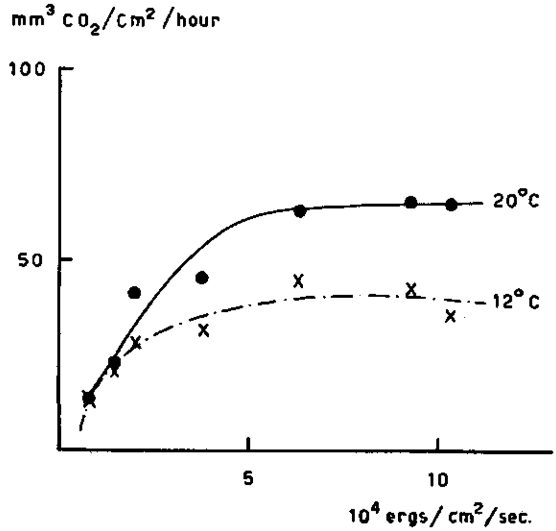
• 11 000 ergs/sec/cm² ø sph., × 1370 erg/sec./cm² ø sph., o dark.

Concerning the growth of higher plants, the function of light is rather complicated. This is largely due to the fact that light does not only act as a source of energy, but also as a factor regulating various morphological characteristics in the plant. When stem elongation is considered, light intensities ranging from 31 000 to 135 000 ergs/sec./cm² ø sph. at 22 °C (average temperature), were found to exert a suppressive effect on stem elongation. The figures presented in Table XVII, and graphically illustrated in Fig. 21 indicate that within the range mentioned, the higher the light intensity, the shorter will be the plants produced. However, the suppressive effect of light intensity is more obvious between 31 000 and 80 000 ergs/sec./cm² ø sph. It is interesting to notice that stem elongation in the control plants (in the greenhouse) was significantly greater than in plants grown constantly in the artificial light treatments. It is possible that differences in light intensity and also in light quality are responsible for the early development of the control plants and subsequently for the significantly greater elongation of their stems.

TABLE XVII

Vegetative growth in wheat as influenced by different intensities of light; Hindi variety, after 58 days treatment

Light intensity ergs/sec./cm² ø sph.	Stem length (cm)	Tiller number	Leaf number	Leaf ratio l/br	Multiplied ratio (l×br) cm²
135 000	27 ± 1.41	22.2 ± 1.24	9.5 ± 0.40	28/1.2	33.6
80 000	30.5 ± 2.22	13.1 ± 0.59	8.3 ± 0.33	26/1.0	26.0
31 000	47.5 ± 1.70	5 ± 0.32	6.6 ± 0.25	30/0.8	24.0
control	7.25 ± 3.09	8.1 ± 0.60	6.5 ± 0.22	23/0.9	20.7



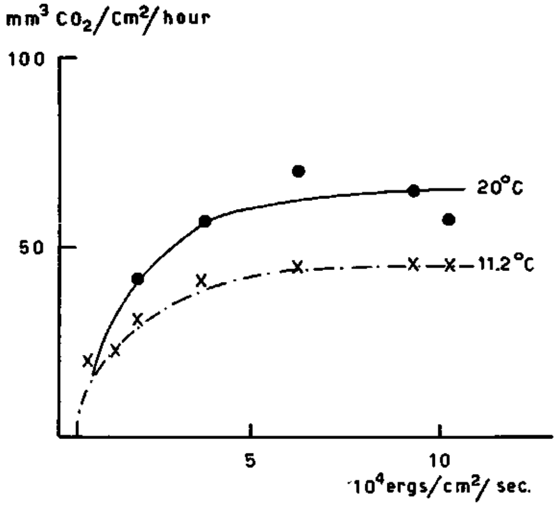


FIG. 20. CO_2-consumption per unit leaf area as influenced by different light intensities. Measurements were made on leaves from 10 °C.-room (above) and 20 °C.-room (below). Heine VII var.

On the other hand, a positive relationship was found to exist between tillering and light intensity; this relationship as made clear in Fig. 21, is of the linear type. In the plants grown under natural illumination in the greenhouse the number of tillers produced per plant was relatively higher than that produced with low

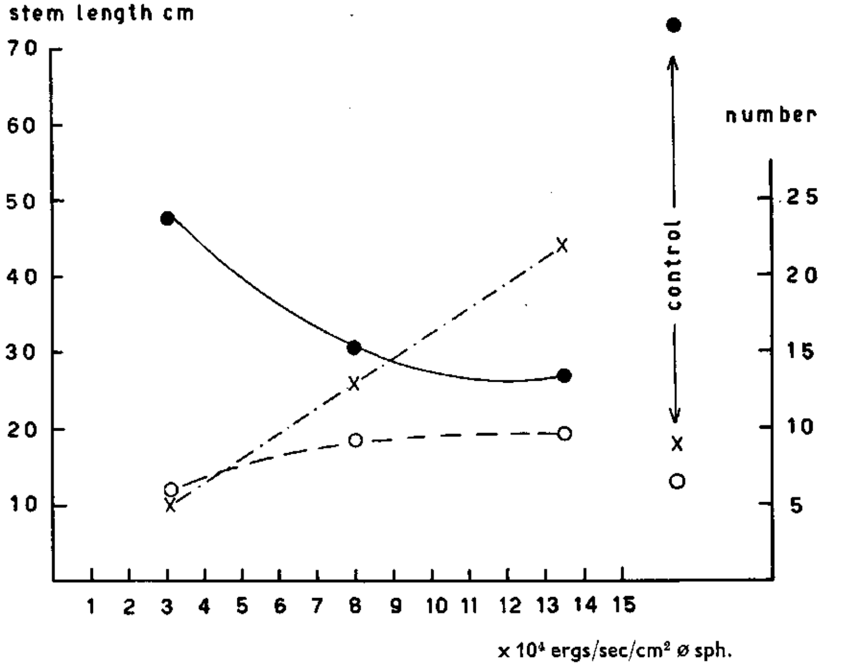


FIG. 21. Effects of various light intensities on growth of wheat (Hindi var.). After 58 days treatment.
● stem length, ○ leaf number, × tillers number.

light intensity (31 000 ergs/sec./cm^2 ø sph.), while with higher intensities (80 000 and 135000 ergs/sec./cm^2 ø sph.) the number of tillers produced was significantly higher than that of the control plants.

Concerning the number of leaves, the differences which have been observed cannot be considered of significant importance, especially within the range from 80000 to 135000 ergs/sec./cm^2 ø sph. The plants in the greenhouse on the other hand, formed a relatively smaller number of leaves than the plants grown under artificial light of high intensity. So these plants show still more the "long-day" aspect which can be related anyhow to the differences in temperature and day length under the greenhouse conditions.

When dry weight determinations were carried out on plants of the different light treatments, it was found that the dry matter production exactly corresponds with the absolute amount of light energy given to the plant. The data presented in Table XVIII, and graphically illustrated in Fig. 22 show that this was true for the entire plant as well as for the roots and tops seperately. This means that below the saturation point, the dry matter production in both roots and tops increased about linearly with the light intensity. Concerning the root/top ratio, it was found that although this ratio was increased by increasing the light intensity from 31 000 to 80 000 ergs/sec./cm² ø sph., a further increase to 135 000 ergs/sec./cm² ø sph., was without effect. The yield of dry matter from the plants grown in the greenhouse was obviously smaller than that from the plants grown under high light intensity. This probably is connected with more pronounced "long-day" type so that the cycle is more quickly completed. This experiment was conducted in July during which the temperature is relatively high and the day-length including the twilight is about 17 hrs.

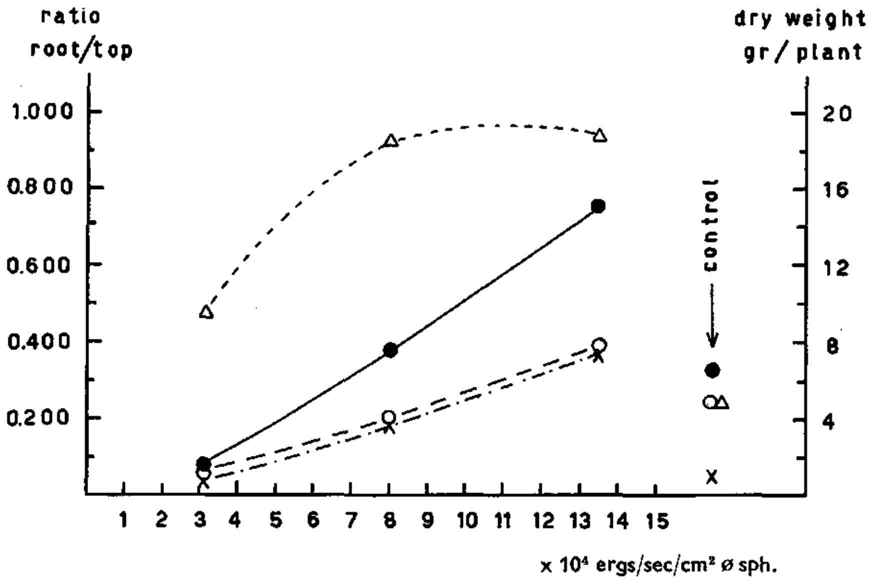


FIG. 22. Dry weight production and root/top ratio as affected by different light intensities. Hindi var., after 58 days treatment.
● entire plant, ○ top, × root, △ root/top.

TABLE XVIII

The production of dry matter (g), and the root/top ratio in wheat as influenced by different light intensities. Hindi variety after 58 days treatment

Light intensity ergs/sec./cm² ø sph.	Entire plant			Root			Top			Root/top ratio
	fresh	dry	%	fresh	dry	%	fresh	dry	%	
135 000	81.1	15.0	18.5	49.7	7.3	14.7	37.4	7.7	20.6	0.948
80 000	46.8	7.7	16.5	24.8	3.7	14.9	22.0	4.0	18.2	0.925
31 000	9.7	1.633	16.8	2.0	0.533	26.7	7.7	1.1	14.3	0.484
Control	22.7	6.078	26.8	9.3	1.178	12.7	13.4	4.9	36.6	0.240

The influence of light intensity on the development is graphically shown in Fig. 23. It is obvious that when spike initiation is considered, increasing the light intensity from 31000 to 80000 ergs/sec./cm² ø sph. induced earlier flowering. When the light intensity was increased further to 135000 ergs/sec./cm² ø sph. the initation of the spike was significantly retarded. After 3 weeks of treatment, when the vegetation points were examined, they were found to reach the third, the fifth, and the second preparatory stages in the three different treatments respectively. After 6 weeks treatment, the development, however, was found to be more favoured at high light intensity (135 000 ergs/sec./cm^2 ø sph.). The plants in the greenhouse were much earlier in spike initiation and emergence than any of the other treatments.

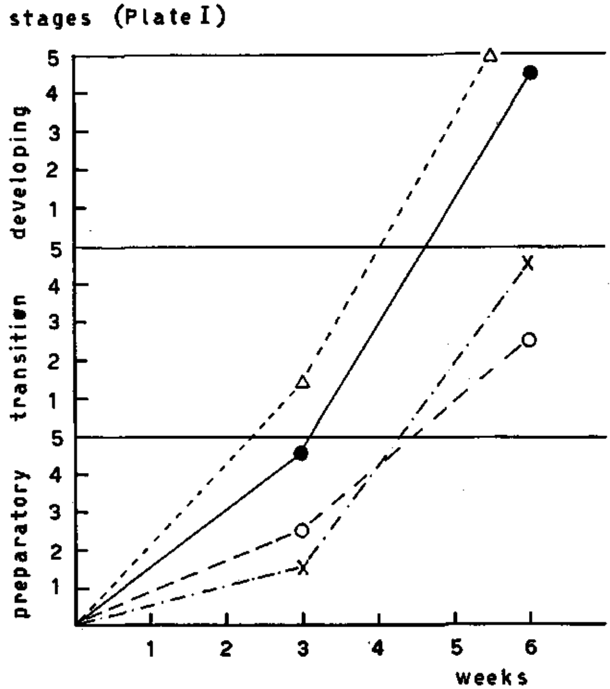


FIG. 23. The development of wheat (Hindi var.) as influenced by different light intensities. o low, • moderate, × high light intensities, △ plants grown in the greenhouse.

4. VEGETATIVE GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY DIFFERENT SPECTRAL REGIONS OF LIGHT

A considerable amount of work concerning the influence of light from different spectral regions on the growth of plants has been conducted by many investigators. In this study, however, a trial is made to investigate the differences which may exist between the effect of various spectral regions when they are given to the plant as supplementary light (at low intensity) and their effect when given as exclusive illumination at equal high intensity.

Before treatment, the plants were kept for one week in the greenhouse with an 8 hrs photoperiod. They were then divided into two main groups, the first received 16 hrs of high intensity in the coloured light cabinets, while the second group received 10 hrs daily in the greenhouse followed by 6 hrs of supplementary spectral light at relatively low intensity. The spectral regions used in this experiment were blue, red and infrared, with white as a control. In order to avoid the injurious influence resulting from exclusive infrared irradiation in this case, a combination of infrared and green was used (8 hrs of each, cf. p. 53).

From the data presented in Table XIX, and graphically illustrated in Fig. 24 it is clear that stem elongation was slightly increased by supplementary irradiation in the red and the infrared spectral regions as compared with the controls; with blue supplementary irradiation, the stems were relatively shorter than in the control plants. At high light intensity, the plants in the red and infrared light were significantly taller than the control plants in the white light cabinet. It is interesting to note that the suppressive effect of the blue light was also observed under constant irradiation at high light intensity. From the figures offered in Tables XIX and XX, it is clear that plants grown under a high intensity of spectral light were significantly taller than those grown under supplementary light conditions. In the first case, the average length of the stem after 3 weeks was about 24 cm, while in the second case after the same period it was only 11 cm. It is probable that this depends on differences in temperature and absolute light intensity. In this experiment however, it was not the intention to compare speed differences in both cases. It should be noted, however, that the leaf number is quite of the same order of magnitude in both series (see below).

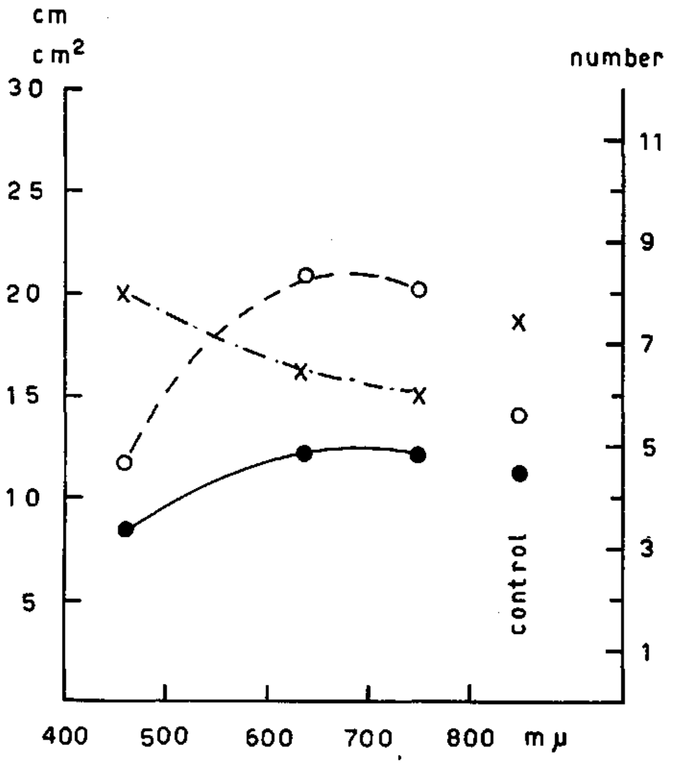


FIG. 24. Growth of wheat (Hindi var.) as affected by a 10+6 hours treatment with various spectral regions at low intensity.
• stem length, × leaf number, o multiplied ratio.

TABLE XIX

Vegetative growth in wheat as influenced by different spectral regions given as supplementary irradiation at low intensity; Hindi variety, after 3 weeks treatment

Spectral region	Stem length (cm)	Leaf number	Leaf ratio l/br	Multiplied ratio (l × br) cm²
Blue	8.4 ± 0.34	8.0 ± 0.14	18.4/0.6	11.04
Red	12.3 ± 0.48	6.6 ± 0.20	26.2/0.8	20.96
Infrared	12.0 ± 0.65	6.1 ± 0.17	27.2/0.75	20.4
Control	11.3 ± 0.35	7.4 ± 0.25	23.2/0.6	13.92

TABLE XX

Vegetative growth in wheat as influenced by different spectral regions given constantly at high intensity; Hindi variety, after 3 weeks treatment

Spectral region	Stem length (cm)	Leaf number	Leaf ratio l/br	Multiplied ratio (l × br) cm²
Blue	13.0 ± 1.66	8.4 ± 0.30	25 /0.4	10.00
Red	31.3 ± 1.86	6.0 ± 0.32	39.7/0.55	22.83
Infrared+Green	30.6 ± 0.94	7.5 ± 0.53	33.2/0.45	14.94
Control	21.3 ± 1.15	7.0 ± 0.29	34.5/0.6	20.70

When the leaf number per plant was counted after 3 weeks treatment, the data show that in both cases of light treatment, the blue light produced the highest number when compared with other regions. When the average number of leaves produced in each of the two cases was calculated, no significant differences were observed (7.03 for the supplementary light and 7.20 for the exclusive light). The differences in leaf area, however, were significant. The figures of the "multiplied ratio" which are given in the last column of table XIX and XX indicate that red light, given either supplementary or as constantly irradiation, increases the leaf area. The main difference in the two cases is that in the first case the leaf area increases in breadth and in the second case in length. This generally is the case with different spectral regions.

Concerning the physiological development of wheat as influenced by different spectral regions, it is obvious from Fig. 25 that three weeks treatment under white and red supplementary irradiation were sufficient to induce earliness in spike initation while, under infrared and blue light, the plants were only in the preparatory stages. However, somewhat later, the different effect of red and infrared disappeared, while the plants grown under blue light remained backward.

This happened after the plants were transferred to the greenhouse for the rest of their life. The excessive elongation of the plants especially in the high light intensity cabinets was a difficulty for which the plants were transferred to the greenhouse after 3 weeks treatment and kept there for further observations.

Under high light intensity, the development of the plants was found to be more favoured by red irradiation than by any other spectral colour used. From Fig. 26 it is obvious that after 3 weeks of treatment with infrared (infrared and green), white and red spectral lights, the vegetation points were in the 1st, 2nd and 4th developmental stages respectively. In the blue light (at high intensity), although spike initiation was reached, the vegetation points showed no further development than to the first transition stage. It is important to note that with high light intensity, the spectral regions used were significantly more effective in speeding up the initiation of the spike, than with supplementary light at low

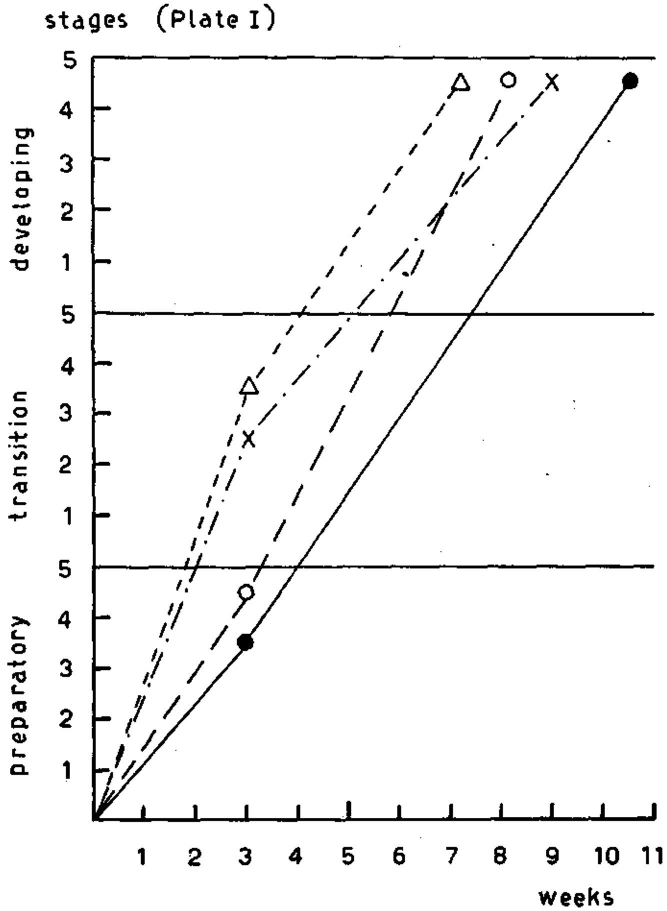


FIG. 25. The development of wheat (Hindi var.) as affected by a 10 + 6 hours treatment with various spectral regions at low intensity.
• blue, ○ infra-red, × red, △ white.

intensity. In the first case, the plants in the red light, after three weeks treatment, reached the fourth developmental stage, while in the second case, the plants were only in the third transition stage. The temperature inside the cabinets, being of major importance, was kept constantly at 20°–22 °C. As to the light intensity, see Table I.

5. DISCUSSION

Although the nature of the reaction preceding flower initiation is obscure, the response of a certain plant to different photoperiodic conditions indicates that flowering is entirely dependent on a chain of reactions which are sensitive to any change in the environmental factors. The photoperiodic reaction, however, is too complicated to relate it to one stimulating factor, and its pattern is modified or the reaction even prevented by other factors, such as temperature, light intensity, CO_2-concentration, and the form in which energy is supplied to the

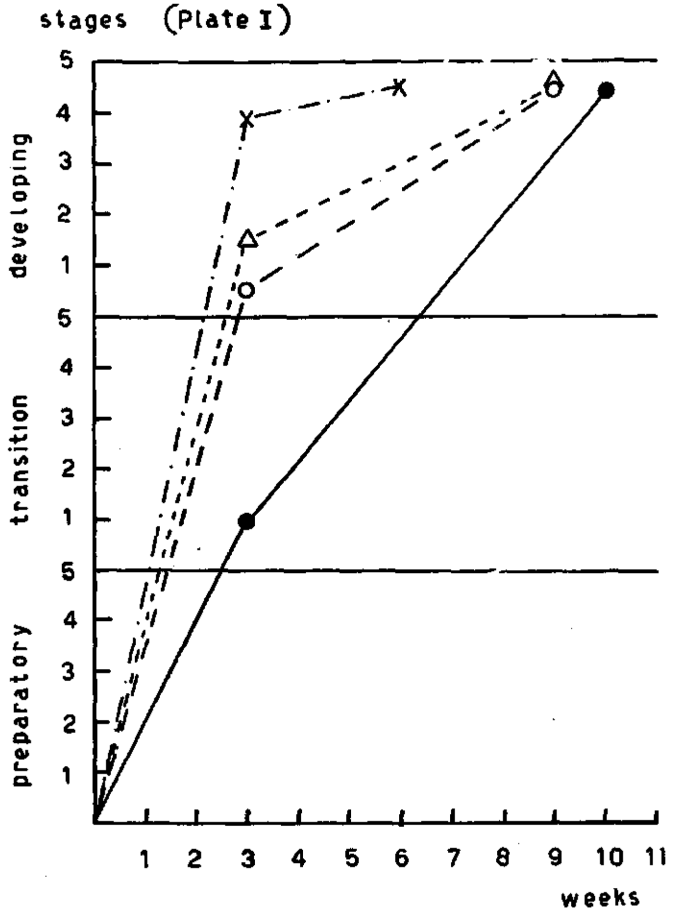


FIG. 26. Effects of various spectral regions at high intensity on the development of wheat (Hindi var.); 16 hrs photoperiod.
× red, o infra-red + green (8 + 8 hrs), • blue, Δ white.

organism. Some of these factors have been previously studied by various investigators. The main point which will be primarily considered in this discussion is the role of the energy utilized by the wheat plant, in relation to the photoperiodic reaction.

The evidence presented in the previous sections of this chapter suggests some modifying effects of different light intensities on the photoperiodic responses of the plants. These modifying effects were found to differ according to the conditions of the experiment. It has been demonstrated, e.g., that increasing the light intensity beyond a certain level during the high light intensity period resulted in a significant retardation of the transition from the vegetative to the reproductive stage. On the contrary, during the supplementary illumination period, increase of the light intensity was significantly favourable in inducing earliness both in initiation and development of the spike. In this respect one must note that in the first case the range of light intensity used was much higher than in the second case (Table I). Thus, it can be assumed that light energy, which is known to influence the rate of photosynthesis in a linear relationship, could not be eliminated as it is an important factor affecting the photoperiodic reactions in the plant. However, the influence seems to be positive at relatively low light intensities. In her studies of the metabolic processes in relation to the photoperiodic reaction in spinach, WAGENAAR (1954) showed that there was no difference in flowering between plants grown at high and low light intensities. This result should be considered cautiously, especially when we know that two different sources of light have been used in her experiments. In such a case, it is quite likely that the responses produced, resulted from spectral differences, as well as from differences in light intensity. The importance of this factor was also reported by WAGENAAR who stated that the spectral composition of the two types of lamps used might be more decisive for the reactions of the plants. In the present investigation, a wide range of light intensities was produced by using only "daylight" fluorescent tubes as a source of light.

Although a definite relationship between the photoperiodic reaction and the products of photosynthesis has not yet been established, there are many reasons to suggest that the distribution of these products within the plant is significantly influenced by the photoperiodic treatment given. This influence, as shown in the different responses of the plant, seems to be of a hormonal nature. This means that the distribution of the photosynthetic products during the different aspects of growth is mainly controlled by the production of a hormone-like substance which, probably, is sensitive to differences in the photoperiod. In almost all the cases examined, it was found that after the reproductive stage was reached, the area of the extending leaves produced was relatively smaller than that of the leaves produced before this stage. Moreover, the tiller formation ceased. Thus it seems quite likely that the energy provided for the plant after the transition stage is reached is used for the spike formation and perhaps for inducing stem elongation. In this respect, it is important to note, that the elongation of the stem coincides with spike formation. This phenomenon was recently reported by BERNARD (1955), who stated that elongation of the internodes of the vegetative axis commences when the spike starts to form. More anatomical studies are required, however, to demonstrate the exact time at which elongation of the stem begins (prior, during or after the spike begins to form).

Turning to the antagonism of spike formation and the production of new tillers, it is quite possible that the hormone-like substance which was suggested before inhibits the formation of new tillers and leaves. In such a case, the energy is utilized by the plant for growth of the bud initials in the axils of the undeveloped leaves. There is another possibility that, after the induction occurs, the differentiated bud initials may inhibit the formation of new tillers and leaves by means of another hormone, different from that which caused the induction itself. It is interesting to note that, after the transition from the vegetative to the reproductive stage, the leaf initials fail to develop, and the number of leaves which expand is restricted. Moreover, the leaf area of the late expanding leaves becomes relatively small. It is not known whether this phenomenon refers to a hormone effect or to the shortage of energy within the plant. It is also found that even under high light intensities no tillers are formed in the axils of these late leaves. This makes the first suggestion more probable.

Under favourable photoperiodic conditions (16 hrs), spike initiation in wheat was found to be retarded by increasing the light intensity beyond a certain limit. This could be interpreted by suggesting that high light intensities are destructive for the hormone, or at least limit its formation. This destructive effect was suggested previously to explain the influence of the light interrupting the dark period in suppressing flowering in short-day plants. The fact that the wheat plants under high intensities initiate the spike later than under moderate light intensities supports the idea that light is not a destructive factor in the first case but only limiting for the induction process. In this respect, it has been observed that the light energy was mostly used in increasing the number of tillers which reached a maximum under high light conditions, see Fig. 21. On the other hand, during the supplementary illumination, earliness is favoured by increasing light intensities within the range used, which intensities really are much lower than the maximum for optimal induction.

Another important observation is that the maximum response to different photoperiodic treatments was induced when the day-length was increased to 24 hrs, while the dry matter production reached a maximum under a 16–20 hrs treatment. This could indicate the independence – in principle – of the photoperiodic reaction from the photosynthetic process. This evidence, however, is not conclusive, especially because the biochemical reactions within the plant depend more on the activities of enzymes connected with carbohydrate metabolism than on the absolute amount of the photosynthetic products. For this reason, increasing the light intensity beyond a certain limit, although it increased the dry weight production, had no effect in speeding up spike initiation, but rather retarded it.

In another experiment which was conducted outdoors under two different conditions of day-length (10 + 0 and 10 + 6 hrs), during the first 50 days there was no significant difference between the two treatments. Later in summer, after 210 days, these treatments showed obvious differences. This can only be understood if day-length, as a factor controlling plant growth and development, is highly dependent on the temperature conditions. Obviously, the photoperiodic reaction was limited by the low temperature during the first growth period, while during the summer the temperature was sufficiently high to give a more pronounced photoperiodic response. It is also very probable that the rate of development of the plant is of major importance in inducing such differences as mentioned above.

As to the influence of spectral light on the growth and development of wheat, the results under supplementary light were significantly different from those obtained in high light intensity conditions. The only constant influence was observed when the blue light (through perspex "Old Blue 27" filter) was used. In both cases, the blue light showed an inhibitory effect on both initiation and development of the spike. In this connection, it is worth mentioning that, in a previous experiment, in which the blue filter nr. 21 was used in the high intensity light cabinet, the blue light showed no inhibitory effect on the development of the plants. This seems surprising, but as seen from Fig. 4 this may be due to transmission of some violet and infrared through this type of screen. In this respect, ÅBERG (1943–1946), using high pressure mercury lamps, showed that the violet-blue region did not suppress elongation of tomato plants.

As to the influence of the red light, it seems justified to emphasize its favourable effect on the development of wheat especially at high intensity. This indicates the importance of both light energy and quality in inducing growth and development of plants. In this respect STOLWIJK (1954), discussing the work of BORTHWICK *et al.* (1952), stated that their concept of the photochemical equilibrium implies that the light response is independent of light intensity. This however does not mean that the absolute amount of light energy absorbed by any of the pigments is of no importance.

In our experiments in the high light intensity cabinets, infrared was used together with green light (8 hrs from each). Thus a comparison with other spectral regions is not reliable because of the differences in the photosynthetically active light.

CHAPTER V

NITROGEN

Ever since it has been claimed that the C/N ratio, with temperature and photoperiod, is a decisive factor in flowering, many controversies have existed among the results of different investigators. Some of these results are quoted in the review of literature (Chapter I) concerning this point. The aim was to see whether N concentration influences vegetative growth proceeding towards development, and whether this can be expressed quantitatively in some way or other. For this reason, the development of the wheat plant was studied in relation to N supply under three different environmental conditions of light intensity, photoperiod, and temperature, while also the C/N ratio has been taken into consideration.

1. VEGETATIVE GROWTH AND DEVELOPMENT OF WHEAT AS INFLUENCED BY NITROGEN CONCENTRATION IN RELATION TO LIGHT AND TEMPERATURE

Concerning the vegetative growth of wheat, the results given in Table XXI and graphically illustrated in Fig. 27, indicate that at high nitrogen concentration, tillering, leaf formation, and leaf area increase with increasing light intensity. With the exception of the leaf area, this was also true for low nitrogen concentration. Increasing the light intensity did not increase leaf area when the nitrogen supply was restricted.

With both nitrogen concentrations used, stem elongation decreased upon increasing the light intensity up to 135 000 ergs/sec./cm^2 ø sph. It seems important to note that when tiller number and leaf area are considered, the quantitative differences between the two nitrogen treatments were very obvious.

The influence of nitrogen concentration on the leaf number is presented in Table XXI. Under different light treatments, the leaf number was decreased by decreasing nitrogen concentration. It was also found that the average reduction over the three light treatments was 1.3 leaves. Another important observation is that the difference in leaf number between low and high nitrogen treatments increases by increasing the light intensity.

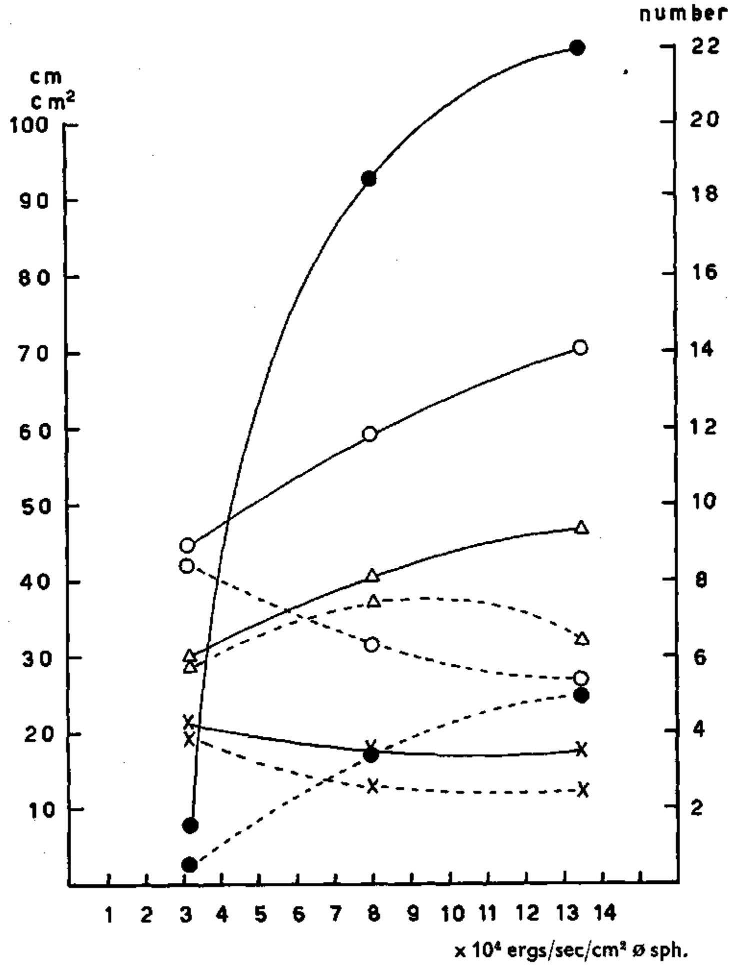


FIG. 27. The influence of various nitrogen concentrations on the growth of wheat (Hindi var.) af different light intensities. Full-drawn lines: +N, broken lines: –N.
× stem length, △ leaf number, ● tillers number, o multiplied ratio.

TABLE XXI

Vegetative growth in wheat in relation to nitrogen concentration at different light intensities; Hindi variety, after 42 days treatment

Light intensity ergs/sec./cm² ø sph.	Nitrogen concen-tration	Stem length (cm)	Tiller number	Leaf number	Leaf ratio (l/br)	Multiplied ratio (l x br)
135 000	+N	18.5 ± 0.92	22.1 ± 1.03	9.2 ± 0.37	47.5/1.5	71.25
	–N	12.0 ± 0.94	5.0 ± 0.22	6.5 ± 0.37	29/0.8	23.2
80 000	+N	18.6 ± 1.14	18.6 ± 0.40	8.2 ± 0.37	46/1.3	59.8
	–N	12.7 ± 1.04	3.5 ± 0.22	7.5 ± 0.22	35/0.9	31.5
31 000	+N	21.7 ± 1.62	1.6 ± 0.40	6.0 ± 0.0	49.7/0.9	44.7
	–N	20.0 ± 1.05	0.5 ± 0.22	5.8 ± 0.20	49/0.9	44.1

When the dry matter production of the wheat plant was determined, it was found that with both nitrogen treatments, the dry weight had gradually increased by increasing light intensity (Table XXII and Fig. 28). The only difference observed between the two treatments was that the dry matter production was much greater in plants grown at a high than at a low nitrogen concentration. This difference, however, corresponds with the absolute amount of light energy which means that the higher the light intensity applied, the larger will be the differences between the two treatments. Another important observation is that the root/top ratio was favoured by low nitrogen concentration. This generally was true under different light intensities. This clearly indicates that the growth of the roots is relatively promoted by low nitrogen concentration.

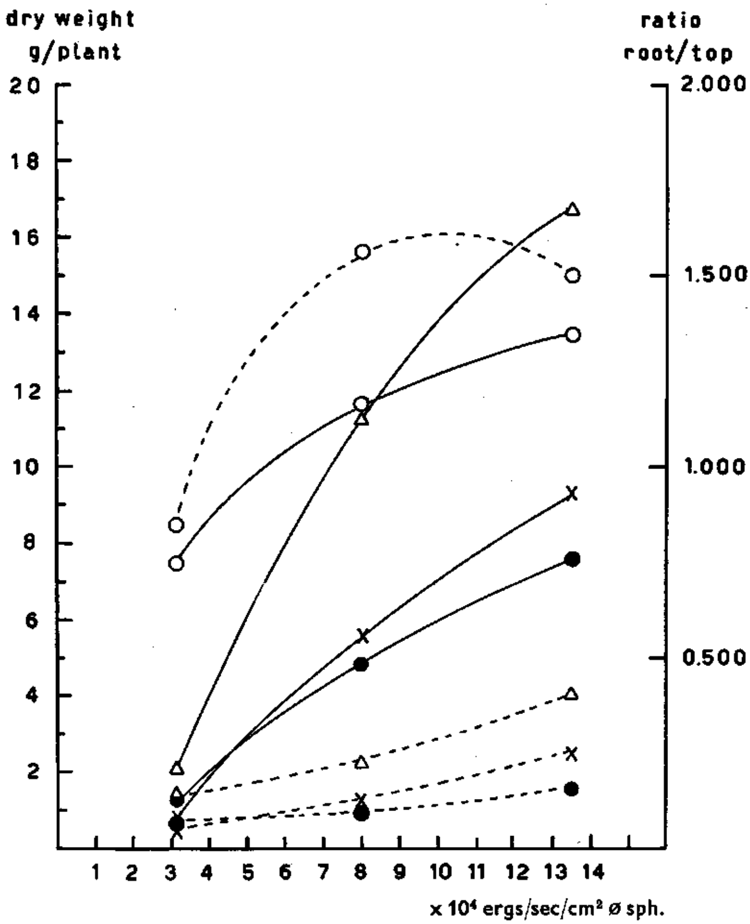


FIG. 28. Effects of various nitrogen concentrations on the dry weight production and root/top ratio in wheat plants grown at different light intensities.
Full-drawn lines: +N. Broken lines: –N
• root, × top, △ entire plant, o root/top ratio.

TABLE XXII

The influence of nitrogen concentration on dry weight (g) production and on the root/top ratio of wheat under different conditions of light intensity; Hindi variety, after 45 days treatment

Light intensity ergs/sec./cm² ø sph.	Nitrogen concentration	Entire plant		Root		Top		Root/top ratio
		fresh	dry	fresh	dry	fresh	dry	
135 000	+N	69.9	16.9	24.7	9.3	45.2	7.6	1.223
	−N	16.1	4.1	9.0	2.5	7.1	1.6	1.500
80 000	+N	42.1	10.4	10.9	5.6	31.2	4.8	1.166
	−N	13.6	2.3	8.1	1.4	5.5	0.9	1.555
31 000	+N	6.0	2.1	1.4	0.9	4.6	1.2	0.750
	−N	4.9	1.3	1.2	0.6	3.7	0.7	0.857

The influence of nitrogen concentration in relation to temperature on the dry matter production in wheat was also studied. The data presented in Table XXIII and graphically illustrated in Fig. 29, show that the differences in dry weight between different nitrogen treatments become more apparent by decreasing the temperature. The stem growth, however, was more sensitive to changes in nitrogen concentration at 20 °C, than at 10° or 27 °C.

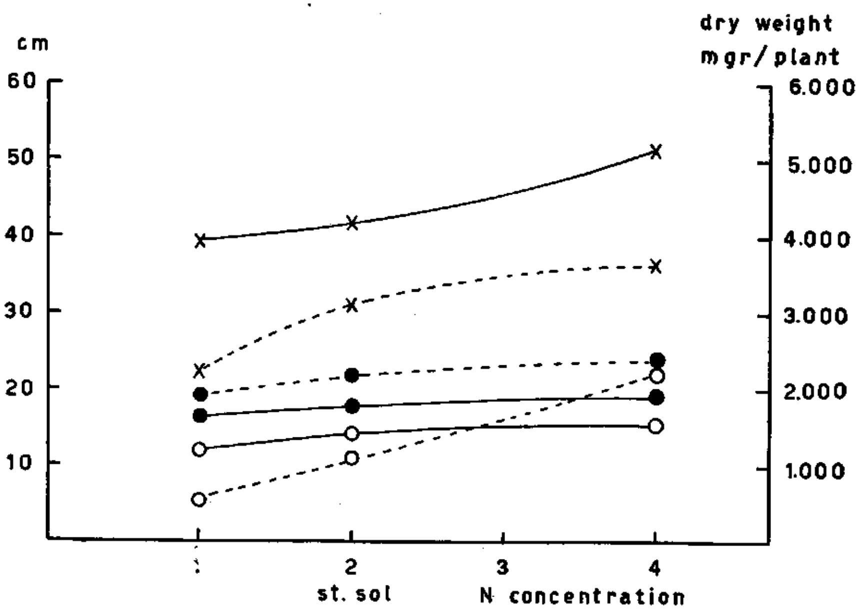


FIG. 29. Stem length and dry weight production as affected by nitrogen concentration under different temperature conditions; Hindi var., after 8 weeks treatment.
Full-drawn lines: stem length, broken lines: dry weight. o 10 °C, × 20 °C, • 27 ° C.

TABLE XXIII

Stem length and dry weight production in wheat as influenced by nitrogen concentration under different conditions of temperature; Hindi variety, after 56 days treatment

Nitrogen concentration	27 °C		20 °C		10 °C	
	Stem length (cm)	Dry weight (gr)	Stem length (cm)	Dry weight (gr)	Stem length (cm)	Dry weight (gr)
−N	16.50 ±1.03	1.95	39.4 ±1.16	2.25	12 ±0.90	0.55
N	16.7 ±0.98	2.20	42.2 ±1.98	3.15	14.4 ±0.64	1.15
+N	16.90 ±1.10	2.40	51.5 ±1.24	3.65	15.2 ±0.77	2.20

Concerning the development of wheat, there is much evidence that low nitrogen concentrations have a favourable influence in inducing early spike initiation. This was also found at the two light intensities used, although it was more significant at high than at low intensity. When the plants were dissected 45

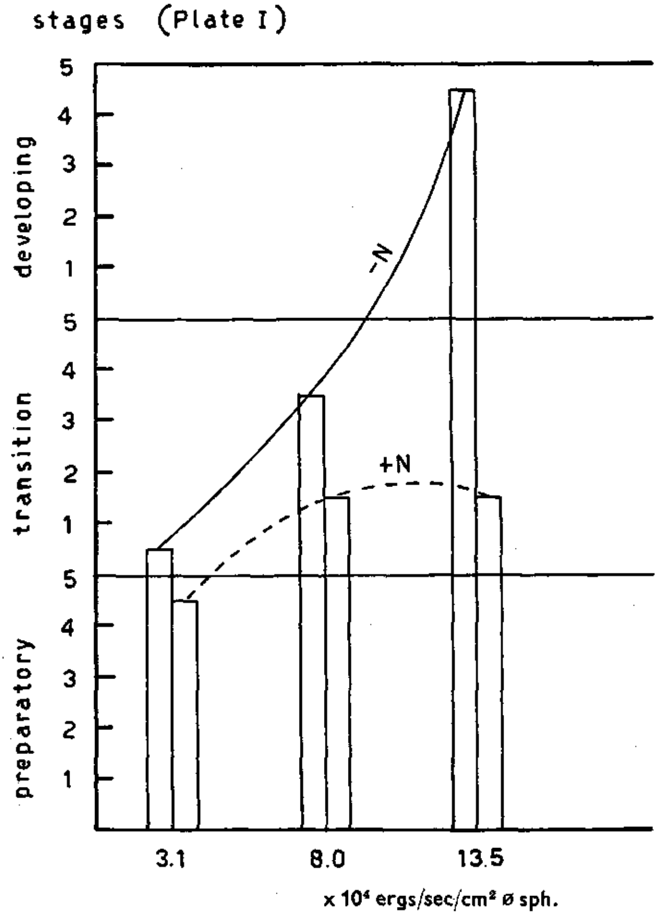


FIG. 30. Effects of various nitrogen concentrations on the development of wheat (Hindi var.) under different conditions of light intensity.

days after planting, it was found that the plants grown under combined conditions of high nitrogen concentration and high light intensity had only reached the second transition stage, while those grown at low nitrogen concentration had already reached the fifth developmental stage. This big difference was not noticed with the plants grown under low light conditions. In the last case the difference produced between the two nitrogen treatments did not exceed one stage on the scale. The data concerning the development of the wheat plant under different conditions of light and nitrogen is graphically given in Fig. 30.

2. C/N RATIO AS INFLUENCED BY LIGHT INTENSITY, PHOTOPERIODISM, AND NIGHT TEMPERATURE

In order to study more accurately the interrelation of the metabolic processes within the plant and its development, some chemical analyses have been carried out in order to estimate the ratio between the total sugars and soluble nitrogen compounds (C/N ratio). The figures given in Tables XXIV, XXV and XXVI are obtained by analysis of plants grown under the different environmental conditions mentioned above. The analyses were carried out with the aid of the "Laboratory for Soil Testing and Plant Analysis", Oosterbeek/Holland. The author wishes to thank Ir. W. Domingo for his kind cooperation in this matter.

The results presented in Table XXIV indicate that, under both high and low light intensities, C/N ratio was always favoured by low nitrogen treatments. With high light intensity, however, the differences in this ratio were relatively larger than those produced with low light intensity. From the last two columns of Table XXIV it is also obvious that the difference in the C/N ratio coincides with the difference in the physiological development of the plant.

TABLE XXIV

C/N ratio at different light intensities in relation to the development of wheat (at two different levels of N concentration)

Light intensities ergs/sec./cm² ø sph.	Nitrogen concentration	Soluble N compounds	Total sugars	C/N	Development on the scale (plate 1)
31 000	−N	0.027	4.92	182	First transition stage
	+N	0.044	4.95	112	Fourth preparatory stage
135 000	−N	0.056	18.61	332	Fifth developmental stage
	+N	0.044	6.74	153	Second transition stage

When the photoperiodic influence was considered, the results given in Table XXV indicate that, with the exception of the first treatment (8 + 0), there was a gradual increase in the C/N ratio by increasing the day-length treatment up to 24 hrs. Moreover, it was found that this increase in the ratio coincides with the rate of development reached by the plant. Whether the C/N ratio, under certain conditions, is a result or a cause of the development of the plant, will be discussed later in this chapter.

TABLE XXV

C/N ratio in relation to photoperiod as influencing the development of wheat

Photoperiod hrs	Soluble N compounds %	Total sugars %	C/N	Development on the scale (plate 1)
8+ 0	0.066	7.76	117	Third preparatory stage
8+ 4	0.057	6.37	111	Third developmental stage
8+ 8	0.053	6.41	120	Fifth developmental stage
8+12	0.037	10.00	270	Full heading
8+16	0.027	10.20	377	Full heading

The data presented in Table XXVI show that the influence of night temperature on the development of the plant also coincides with its influence on the C/N ratio. At 2°C, however, the development was relatively slow even with higher C/N ratio. This is largely due to the fact that at such a low temperature, the whole of metabolic processes within the plant proceed at a low rate, which, however, still may be sensibly different for various single processes.

TABLE XXVI

C/N ratio in relation to night temperature as influencing the development of wheat

Night temperature °C	Soluble N compounds %	Total sugars %	C/N	Development on the scale (plate 1)
2°	0.033	2.08	63	Second transition stage
10°	0.041	1.78	43	Fourth transition stage
20°	0.038	2.68	70	Full heading
27°	0.049	2.70	55	Second developmental stage

The ratio between the dry matter content of ears and that of stems + leaves as influenced by different nitrogen concentrations was studied. An experiment was conducted outdoors (December 1954) under controlled conditions of daylength (10 + 0 and 10 + 6 hrs). The results given in Table XXVII indicate that the higher the nitrogen concentration, the lower was the ratio. This was found to be true under both photoperiods. On the contrary the absolute dry matter of either ears or stems was found to be favoured at high nitrogen concentrations. Under short-day conditions the dry matter production, especially that of the ears was relatively lower than under long-day conditions. This is not astonishing, because at the time of sampling (8 July), the plants from the short-day treatment were relatively less ripened than those from the long-day treatment.

TABLE XXVII

Dry matter content of ears, and stems as influenced by nitrogen concentration

Nitrogen treatment	Day-length (hrs)	Fresh weight (gr)	Dry weight (gr)			Ears / stems+leaves
			entire weight	ears	stems+leaves	
+N	10+6	29.0	20.87	8.28	12.59	65.7
N	10+6	25.4	17.33	7.42	9.91	74.8
−N	10+6	16.3	10.25	4.78	5.47	87.3
+N	10+0	22.7	13.14	3.30	9.84	33.5
N	10+0	20.4	12.02	4.23	7.79	54.3
−N	10+0	18.0	10.67	3.62	7.05	51.3

3. DISCUSSION

There has always been a considerable controversy, as to whether nitrogen plays an important role in the flowering process of higher plants. If it does, plants might be expected to flower only under certain conditions of nitrogen concentration. It was found in this investigation that the transition from the vegetative to the reproductive stage in wheat was possible under a wide range of nitrogen concentrations. Earliness in flowering however, was found to be influenced by the nitrogen concentration, especially at high light intensity. Thus, it becomes clear that the difference in the rate of development of a certain plant grown under certain nitrogen conditions is partly dependent on the light intensity. The figures given in Table XXIV clearly show, that at low nitrogen concentrations the percentage of the soluble nitrogen compounds was significantly increased (about twice) by increasing the light intensity, while the sugars were much more increased. In this way, the C/N ratio is considerably influenced by light intensity especially at low nitrogen level. The influence of light intensity on the nitrogen content in *Chlorella* was also found by AACH (1952).

Returning to the interrelation of nitrogen concentration and rate of development, it seems justified to state that low nitrogen supply does not always mean a corresponding decrease in the nitrogen content of the plant. When the C/N ratio was calculated, a direct correlation was found to exist between this ratio and the rate of development under the two light intensities used. The question that arises is, whether this ratio is a cause or a result of the transition process from the vegetative to the reproductive stage. The results produced, prove beyond doubt that the C/N ratio is sensitive to changes in other factors (light intensity, photoperiod and night temperature), as well as to nitrogen concentration.

A positive correlation was found to exist between the rate of development and the C/N ratio as influenced by the different photoperiods. Only one exception was noticed; the ratio in the 8 + 0 hrs was a little higher than in the 8 + 4 hrs treatment, while the development in the latter case was more advanced. When the night temperature was considered, it was also demonstrated that a correlation exists between the rate of development and the C/N ratio at 10°C, 20°C, 27°C. At 2°C, on the other hand, development was relatively slower in spite of the relatively high C/N ratio produced. If development is really a result of this ratio, the plants grown at 2°C night temperature should be expected to be more developed than those grown at 10° or 27°C.

It is, however, quite possible that the high C/N ratio produced at such low temperature (2°C), has no relation to development, because most of the biochemical processes are inhibited at low temperatures. Anyhow, the concept that the plant could be shifted from vegetative growth to reproduction by increasing the C/N ratio, cannot be generally accepted because under certain conditions the ratio could be increased without causing any subsequent development. In the light of these results, the following can be concluded:

a. The C/N ratio is not a decisive factor in flowering, as it has been demonstrated that the transition from vegetative growth to reproduction can take place under a wide range of this ratio.

b. On the other hand, when earliness in flowering is considered, the correlation between the rate of development and the C/N ratio may indicate a significant influence of this ratio. However, even now, it is not easy to state whether this influence comes before or after the physiological transition from the vegetative to the reproductive stage.

c. The C/N ratio can be altered by various external factors, such as light intensity and night temperature, as well as by nitrogen concentration.

There is good evidence that at relatively low temperatures, the influence of nitrogen upon dry matter production is greater than at higher temperatures. This may be explained by assuming an influence of the nitrogen level on photosynthesis (cf. PIRSON, 1937). This influence may be more pronounced at light saturation than at limiting light intensities. At low temperature, light saturation may have been reached, even at the moderate light intensity used (cf. fig. 20). An increase in nitrogen level may then be accompanied by an increase in photosynthesis, relatively greater at low temperature than at high temperature.

CHAPTER VI

GENERAL DISCUSSION

THE INTERRELATION BETWEEN GROWTH AND DEVELOPMENT

As it was difficult to eliminate the growth responses of the plant from its development, the interrelation between these processes remained obscure. Whether these two processes are independent from each other or not was considered long ago by some investigators. LYSENKO (1928, 1935, 1954) claimed that the developmental phases of a plant proceed in a strict sequence quite independent of the vegetative growth. On the contrary it is generally accepted that the interrelation between growth and development renders the plant unable to enter the reproductive stage before a certain growth is reached. Before supporting the opinion of any of those workers, it is appropriate to refer to some results concerning the following:

a. The possibility of producing pure vegetative growth without flower induction.

b. The possibility of inducing the physiological development of the plant without the necessity of growth.

It has been proven beyond doubt, that the first type of growth can be easily produced under certain conditions. In this respect GARNER and ALLARD (1931) were able to suppress the flowering of three species of long-day plants for periods of 8 or 9 years, by continually exposing them to short-day conditions. LYSENKO (1931) showed also that maize (a short-day plant) produced only vigorous vegetative growth, when grown under long-day conditions. It has been demonstrated in the previous chapters that different photoperiodic treatments fail to produce pure vegetative growth in wheat when the plants are previously vernalized. Pure vegetative growth was only produced when the annual variety Heine VII was grown in spring from unvernalized seeds. From these results it seems justified to state that these plants, under certain conditions, can grow vegetatively without any morphological indication of development.

As to the question whether it is possible to induce the plant's development while arresting vegetative growth, we must consider especially two factors, temperature and day-length, which have a decisive effect on development. Seed vernalization of winter annuals and biennials is a good example of inducing the development of the plant, even before any growth is recognized. One should observe that the seeds must be slightly germinated, before they can respond to the low temperature treatment. This, however, need not mean that growth, in a quantitative sense is required for development, but only that the embryo must be activated before it can respond to vernalization. Moreover, it has already been demonstrated by GREGORY and PURVIS (1936), that it is possible to vernalize the seeds while on the mother plant during a certain stage of ripening. This clearly indicates that it is a certain state of activity rather than growth which is needed for the embryo in order to be successfully vernalized. If on the other hand, the seeds are fully ripened and have entered the stage of dormancy, the low temperature will be without effect till the dormancy is broken. Furthermore, the results produced (Fig. 1) show that the loss in dry matter during the very early stages of germination is too small to induce a significant growth, but is only important for activation of the embryo. Thus, if growth is considered as an increase in dimensions or weight, it can be concluded from these facts that, at least in this very young stage, a plant can undergo a physiological development without any observable relation to growth.

When the photoperiodic reaction is considered, the interrelation between growth and development seems to be more complicated. It is generally accepted that the development of the plant as a result of the photoperiodic reaction is not possible before a certain level of growth is reached, which differs according to the prevailing conditions. In this respect, KOPETZ (1936, 1937) suggested that a period of pure vegetative growth (V_r) must elapse before the plant can respond to photoperiodic treatment. This, however, may only indicate the age of tissues as an important factor in the photoperiodic reactions. On the other hand, this is no striking proof that both growth and development processes cannot proceed independently from each other. As long as the induction phase could be fulfilled within the plant without any morphological indication, the limits of a purely vegetative period as mentioned by KOPETZ, cannot be practically recognized. For this reason, it has been cited by some investigators that the progress of the plant towards reproduction can be divided into two or more separate stages, which may require different environmental conditions. EGUCHI (1937) mentioned two stages; the stage which leads to flower bud differentiation, and the flowering stage. SAPEGIN (1940) divided the photophase into preparatory and executive stages. He further mentioned that during the preparatory stage, the growing points show no morphological changes, but the conditions then prevailing determine the number of spikelets. These stages are similar to those postulated previously by KLEBS (1918): the ripeness-to-flower and the development of the flower primordia to form the inflorescence.

In cereals, the transition from the vegetative to the reproductive condition is first recognized by the formation of the double ridge (PURVIS (1934) and PURVIS and GREGORY (1937)). This however, seems to be of importance only from the morphological side, because the appearence of the double ridges takes place after the induction phase is complete, and when the transition from the vegetative to the reproductive conditions has taken place.

In the light of the previous facts, a rather simple explanation for the interrelation between the two processes of growth and development can be put forward as follows:

1. Before the induction is brought about by any favourable photoperiodic treatment, some substances must be produced alongside the photosynthetic

products. The latter are used partly as building material, especially in vegetative growth and partly as a source of energy in all energy requiring processes that cannot make use of the light energy directly.

2. The production of the inducing substances, which are still unknown, is primarily controlled by two decisive factors: temperature and photoperiod. The vegetative growth, on the other hand, is likely to be influenced by all environmental factors.

3. When the induction of the flowering stage is complete, both the amounts and distribution of the food materials become significant in promoting the growth of the flower primordia, and also in supplying the energy required for other stages of vegetative growth.

4. The amount of food materials synthesized by the plant, is primarily dependent on light intensity, while the distribution of these materials seems to be partly controlled by hormones which are produced by the flowering organs themselves, under certain environmental conditions.

A point of special interest, is that, at relatively low light intensity, although the initiation of the wheat spike was relatively early, the growth of the spike proceeded very slowly. This strongly supports other evidence that the amount of light energy is of minor importance during induction but of much more importance during the further development. In this respect it has also been observed that, in almost all cases studied, tillering, leaf formation and leaf area were all suppressed as soon as the spike development had started. This apparently indicates an antagonism between growth and development. Since however, this phenomenon is observed always after the induction phase is complete, it is more reasonable to speak about an antagonism between different types of vegetative growth. In such a case, the competition between these different types for food material especially at low light intensity is regarded as the main reason for this antagonistic phenomenon. This does not mean that supplying the plants with excessive energy will entirely prevent this competition, because the movement and distribution of food materials may well be considered to be controlled in part by hormone-like substances. This was strongly supported by STUART (1938) who showed that the local application of indole-acetic acid to certain regions of bean stems induced marked accumulation of food in those regions. CHOULDHRI (1948) dealing with *Phaseolus vulgaris*, also proved that the application of dichlorophenoxyacetic acid (2,4-D) can greatly depress transport of food from the cotyledons, and prevent their abscission.

Considering these facts, it becomes clear that vegetative growth and development can proceed quite independently during the induction phase. On the other hand, after the induction phase is complete, and the growth of the spike primordia begins, the interrelation between this growth and other types of vegetative growth appears through their competition for food energy. Before this stage is reached, the function of a photoperiodic treatment is to produce some kind of hormones in the mature leaves, which play the most important part in the flowering process. The possibility of regulating flowering by interrupting the dark period by light for only a very short time, is strong evidence that the induction phase can be brought about quite independent of growth. On the other hand, the growth of the flower buds was significantly depressed at relatively low light intensity, which means that this process proceeds at the expense of the photosynthetic products.

Nitrogen concentration was also found to be of significant importance in the course of growth and development of wheat. It is interesting to note that the influence of nitrogen becomes more marked by increasing the light intensity under which the plants are grown. Thus, it can be suggested that the role of nitrogen within the plant is entirely dependent on the prevailing light conditions. According to CURTIS (1950), KLEBS has already mentioned that light and other factors were of some importance in relation to nitrogen supply. When different conditions of nitrogen concentration and light intensity were studied, the results of the present investigation were conclusive in showing that:

a. The wheat plants grown in long days under conditions of high nitrogen and high light intensity produced very strong vegetative growth with moderate reproductive development. The plants were of similar appearance to those grown under short day conditions.

b. The plants grown under conditions of high nitrogen concentration and low light intensity produced weak vegetative growth without reproductive development.

c. The plants grown under conditions of low nitrogen concentration with low light intensity produced very weak vegetative growth with moderate reproductive development.

d. The plants grown under conditions of low nitrogen concentration with high light intensity produced weak vegetative growth while reproductive development was significantly earlier than in other treatments.

These results are similar to those produced by KRAUS and KRAYBILL (1918). The only difference is that they gave more considiration to the rate of flowering and fruiting, while in this study more attention was given to earliness in flowering.

The analysis of the plant material showed that earliness in flowering under different conditions was mostly accompanied by high C/N ratio. Whether this high ratio is a cause or a result of early flowering or a consequence of conditions which also favour flowering is difficult to decide. This is largely due to the fact that the limits of the induction phase are difficult to recognize. A point of special interest is that although earliness in flowering was accompanied by high C/N ratio, the reverse was not always true. This means that flowering, in some cases may be relatively late even with a high C/N ratio. In such cases other factors, such as temperature and light intensity, may have caused an alteration in the metabolic pattern, or changed the ratio sugars/soluble N directly, by influencing some process of hydrolysis.

SUMMARY

The aim of this investigation was to obtain more information about the subtropical wheat varieties Hindi and Baladi, concerning the relationship between growth and development as influenced by temperature, light and nitrogen.

Most experiments were made with Hindi. In some experiments the local varieties Heine VII (a typical winter wheat) and Peko (a typical spring wheat) were used for comparison.

A. *The influence of temperature* (Chapter III).

From the experiments conducted indoors under controlled conditions the following results were obtained:

1. The time required for the emergence of successive leaves is decreased significantly by increasing the temperature within the range of 10°–30°C. The number of leaves formed on the plant showed a linear relationship with the length of the vegetative growth period (Table IV, Fig. 6).
2. The higher the temperature the lower the root/top ratio was. A fairly high oxygen supply around the roots seemed to be necessary for optimal growth especially at higher temperatures (Table V, Fig. 7).
3. Concerning the influence of different night temperatures on the growth and development of wheat, the importance of regulating the root temperature at the beginning of the light period to reach the room temperature as quickly as possible was demonstrated.
4. The most favourable night temperature for stem elongation was between 10° and 20°C under the conditions of the present experiments. The higher the night temperature, the smaller the number of tillers and the greater the number of leaves (Table VIII, Fig. 10).
5. At different night temperatures, there was a positive correlation between the dry matter production per plant and both stem length and leaf area.
6. At 10°C night temperature, the development of the spike was earlier than at 27°C; the reverse was true under constant temperature conditions.

From the experiments conducted outdoors under natural conditions of temperature and controlled day-length it has been found that:

1. The subtropical varieties of wheat, although they are grown in Egypt as winter varieties, belong to the spring type (Table VI, Fig. 9).
2. Although the vernalization process had no influence on the development of the subtropical varieties, the yield of grains was found to be generally favoured by this process.

B. *The influence of light* (Chapter IV).

From the experiments conducted indoors under controlled conditions the following results were obtained:

1. A gradual increase of the day-length from 8 to 24 hrs resulted in a gradual increase in the stem length, and suppressed tiller number, leaf number and leaf area (Table XI, Fig. XIV).
2. The highest production of dry weight per plant was obtained under 16 and 20 hrs photoperiod. With continuous illumination dry weight decreased once more as a result of reduction in the vegetative growth period (Table XII, Fig. 15).
3. A strong relationship existed between the day-length and the rate of development towards reproduction (Fig. 16).
4. When a basic illumination in the greenhouse was followed by a supplementary illumination of different intensities, a higher intensity of supplementary light caused an increase in stem elongation and a decrease in tillering, leaf formation and leaf area (Table XV, Fig. 17).
5. The progress of the plant towards reproduction was also favoured by increasing the intensity of the supplementary light (Fig. 19).
6. Increase of the intensity of the basic illumination suppressed stem elongation but both tillers and leaf number were significantly increased (Table XVII, Fig. 21).

7. Light intensity favoured flowering up to 80 000 ergs/sec./cm² ø sph. Although the spike initiation was relatively slow under high light intensities, the developmental growth of the reproductive organs was significantly faster (Fig. 23).
8. Concerning the influence of different spectral regions, three weeks treatment under white and red supplementary irradiation were sufficient to induce early flowering, while under infrared and blue light, the plants had only reached the preparatory stages (Table XIX, Fig. 24).
   With an illumination of 16 hrs red light of high intensity spike initiation was accelerated, with blue light it was retarded, when compared with the development in white light (Table XX).
9. Concerning the root/top ratio, it was found that this ratio was greater at higher than at lower light intensities (Fig. 22).

C. *The influence of nitrogen* (Chapter V).

1. It has been demonstrated that the influence of nitrogen is obviously dependent on light intensity (Tables XXI and XXII).
2. The C/N ratio of the plant was found to be sensitive not only to changes in nitrogen concentration, but also to changes in other factors such as photoperiod and night temperature (Tables XXIV, XXV, XXVI).
3. The chemical analysis (soluble C – and N – compounds) of the plant material showed that earliness in flowering, obtained under different environmental conditions, was mostly accompanied by high C/N ratio.
4. In some cases, however, although the C/N ratio was relatively high, flowering was late. It is possible that other factors. such as temperature and light intensity, have caused an alteration in the metabolic pattern or changed the ratio directly by influencing some processes of hydrolysis.
5. The ratio between dry matter content of ears, and that of stems + leaves as influenced by different nitrogen concentrations was studied. It has been demonstrated that the higher the nitrogen concentration, the lower was the ratio. This was true under short and long-day conditions. On the contrary, the absolute amount of dry matter of either ears or stems was found to be favoured by high nitrogen concentration, and was generally less under short-day than under long-day conditions (Table XXVII).
6. It has been demonstrated that the root/top ratio was generally favoured by low nitrogen concentration under different conditions of light intensity used (Table XXII, Fig. 28).

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HET VERBAND TUSSEN GROEI EN ONTWIKKELING VAN TARWE, ONDER INVLOED VAN TEMPERATUUR, LICHT EN STIKSTOF

SAMENVATTING

Het doel van dit onderzoek was om bij de subtropische tarwerassen Hindi en Baladi meer inzicht te verkrijgen in het verband tussen groei en ontwikkeling onder invloed van temperatuur, licht en stikstof.

De meeste proeven werden gedaan met het ras Hindi. In enkele proeven werden de inheemse rassen Heine VII (een typisch winterras) en Peko (een typisch zomerras) ter vergelijking gebruikt.

A. *De invloed van de temperatuur.*

Met laboratoriumproeven uitgevoerd onder constant gehouden omstandigheden werden de volgende resultaten verkegen:

1. De tijd nodig voor het verschijnen van opeenvolgende bladeren nam belangrijk af door de temperatuur binnen het gebied van 10–30°C te verhogen. Het aantal bladeren aan de plant vertoonde een lineair verband met de lengte van de periode van vegetatieve groei.
2. Hoe hoger de temperatuur, des te lager was de verhouding wortel/spruit. Speciaal bij hogere temperaturen scheen een goede zuurstofvoorziening van de wortels nodig te zijn voor optimale groei.
3. Wat betreft de invloed van verschillende nachttemperaturen op de groei en ontwikkeling van tarwe, werd aangetoond, dat het belangrijk was om de temperatuur van de wortels bij het begin van de lichtperiode te regelen ten einde deze zo spoedig mogelijk de temperatuur van de kamer te doen bereiken.
4. Onder de gekozen proefomstandigheden lag de gunstigste nachttemperatuur voor de lengtegroei van de stengel tussen 10° en 20°C. Hoe hoger de nachttemperatuur, des te kleiner was het aantal zijspruiten en des te groter het aantal bladeren.
5. Bij verschillende nachttemperaturen was er een positieve correlatie zowel tussen de productie van droge stof per plant en de lengte van de stengel als tussen de productie van droge stof per plant en het bladoppervlak.
6. Bij een nachttemperatuur van 10°C kwam de aar vroeger tot ontwikkeling dan bij 27°C; het omgekeerde was het geval bij continu constante temperatuur (20 °C).

Op grond van veldproeven bij natuurlijke temperatuursomstandigheden en constante daglengte is aangetoond dat:

1. De subtropische tarwerassen, hoewel ze in Egypte als winterrassen verbouwd worden, tot het zomertype behoren.
2. Hoewel vernalisatie geen invloed had op de reproductieve ontwikkeling van de subtropische rassen, de opbrengst aan korrels in het algemeen door deze behandeling bevorderd wordt.

B. *De invloed van het licht.*

In laboratoriumproeven, uitgevoerd onder constante omstandigheden, werden de volgende resultaten verkregen.

1. Een geleidelijke toename van de daglengte van 8 to 24 uur leidde tot een geleidelijke toename in de stengellengte, en deed het aantal zijspruiten, het aantal bladeren en het bladoppervlak afnemen.
2. De hoogste productie van droge stof per plant werd verkregen bij een photoperiode van 16–20 uur. Bij continue belichting nam het drooggewicht opnieuw af als gevolg van het bekorten van de periode van vegetatieve groei.
3. Er bestond een sterk verband tussen de daglengte en de snelheid van de reproductieve ontwikkeling.
4. Wanneer hoofdbelichting in de kas gevolgd werd door aanvullende belichting van verschillende intensiteiten, veroorzaakte een hogere intensiteit van het aanvullende licht een toename van de lengtegroei van de stengel en een afname in uitstoelen, bladvorming en bladoppervlak.
5. Ook het bereiken van het reproductieve stadium werd bevorderd door de intensiteit van het aanvullende licht te vergroten.
6. Vergroting van de intensiteit van de hoofdbelichting deed de lengtegroei van de stengel afnemen; zowel het aantal zijspruiten als het aantal bladeren werd echter belangrijk vergroot.
7. Tot een waarde van 80 000 ergs/sec/cm^2 Ø bol werd de bloei door toenemende lichtintensiteit bevorderd. Hoewel de aar bij hoge lichtintensiteiten betrekkelijk langzaam aangelegd werd, werd de groei van de reproductieve organen belangrijk versneld.
8. Wat betreft de invloed van verschillende spectrale gebieden was drie weken bestraling met wit en rood aanvullend licht voldoende om vroege bloei te induceren, terwijl met infrarood en blauw aanvullend licht de planten slechts de voorbereidende stadia hadden bereikt. Een belichting van 16 uur met rood licht van hoge intensiteit versnelde de aanleg van de aar, een belichting van 16 uur met blauw licht vertraagde deze, vergeleken met de ontwikkeling in wit licht.
9. De verhouding wortel/spruit bleek bij hoge lichtintensiteit groter te zijn dan bij lage.

C. *De invloed van stikstof.*

1. Aangetoond is, dat de invloed van stikstof afhankelijk is van de lichtintensiteit.
2. De C/N verhouding van de plant bleek niet alleen afhankelijk te zijn van de stikstofconcentratie, maar ook van andere factoren, zoals photoperiode en nachttemperatuur.
3. Chemische analyse van het plantenmateriaal (betreffende oplosbare C- en N-verbindingen) toonde aan dat vroege bloei, bij verschillende omstandigheden verkregen, meestal gepaard ging met een hoge C/N-verhouding.
4. In enkele gevallen was echter de bloei laat, hoewel de C/N verhouding betrekkelijk hoog was. Het is mogelijk, dat andere factoren, zoals temperatuur en lichtintensiteit, een verandering in het stofwisselingspatroon veroorzaken, of rechtstreeks de C/N verhouding veranderen door invloed te oefenen op een of ander hydrolyse proces.

5. De invloed van verschillende stikstofconcentraties op de verhouding tussen de droge-stofproductie van de aren en die van stengels + bladeren werd onderzocht. Aangetoond is dat deze verhouding des te lager was naarmate de stikstofconcentratie hoger was. Dit was het geval zowel bij korte als bij lange dag. De absolute hoeveelheid droge stof van aren of stengels daarentegen bleek door hoge stikstofconcentratie vermeerderd te worden, en was in het algemeen kleiner bij korte dag dan bij lage dag.
6. Aangetoond is, dat een lage stikstofconcentratie bij de verschillende toegepaste lichtintensiteiten tot een vergroting van de verhouding wortel/spruit leidde.

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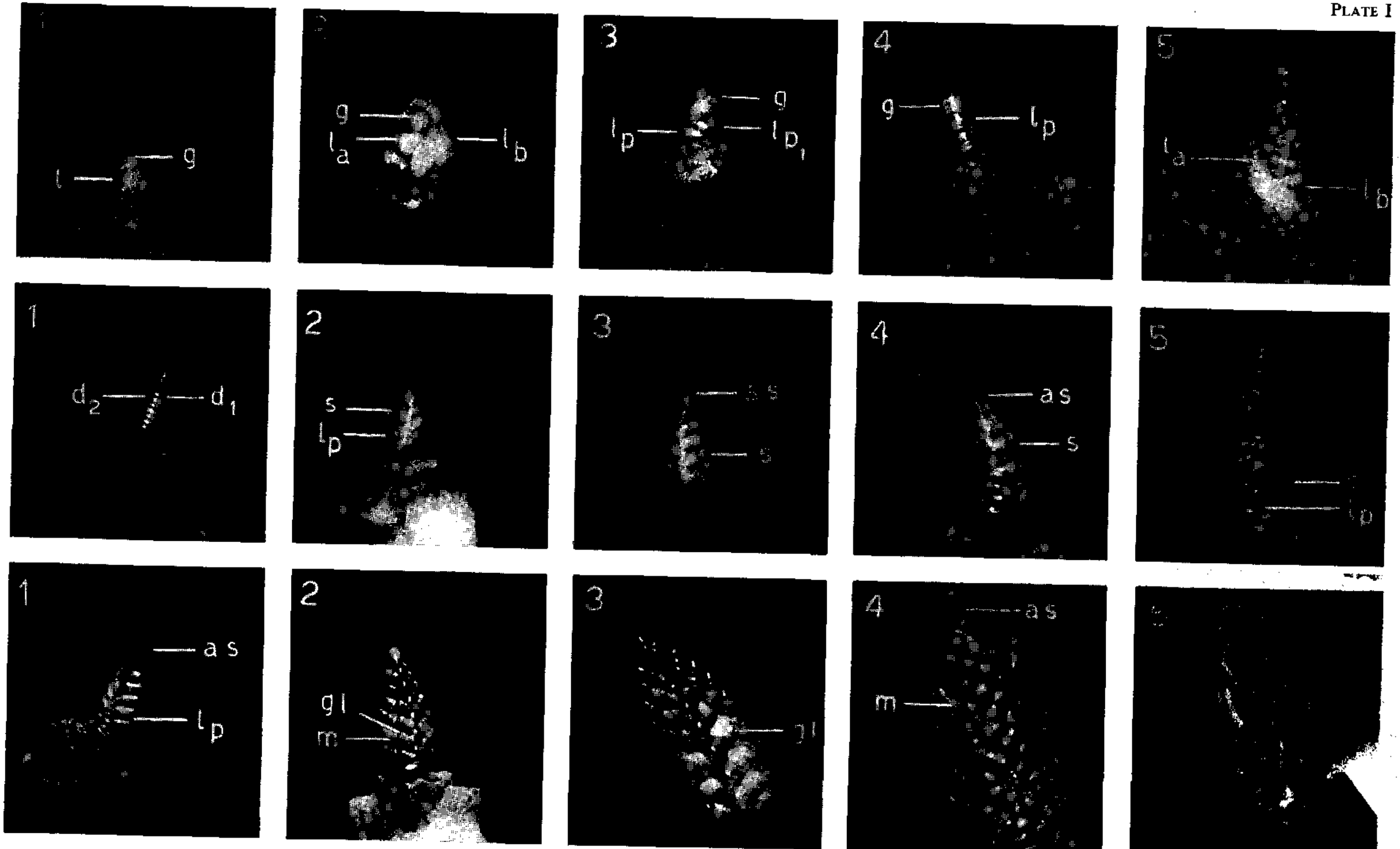
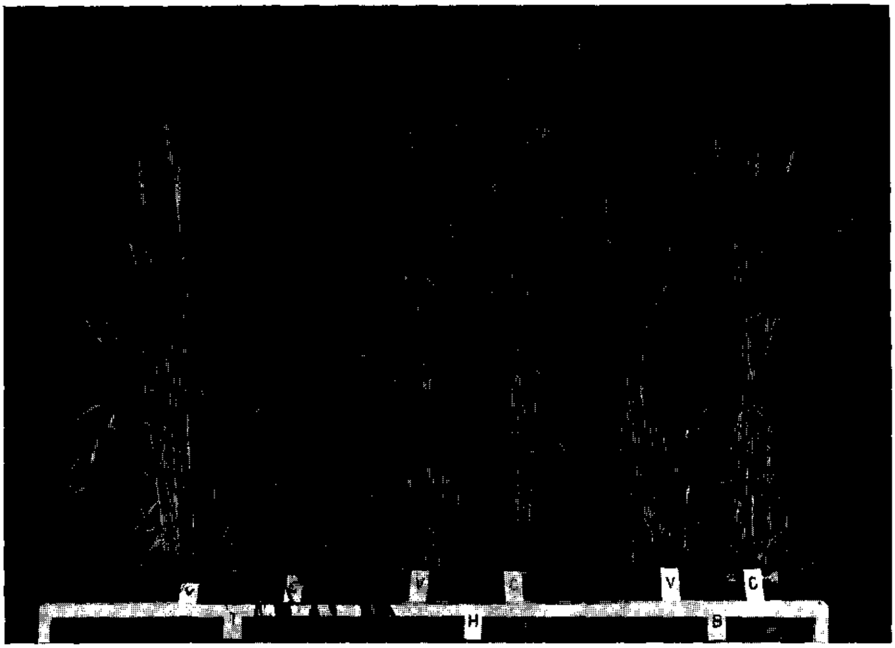
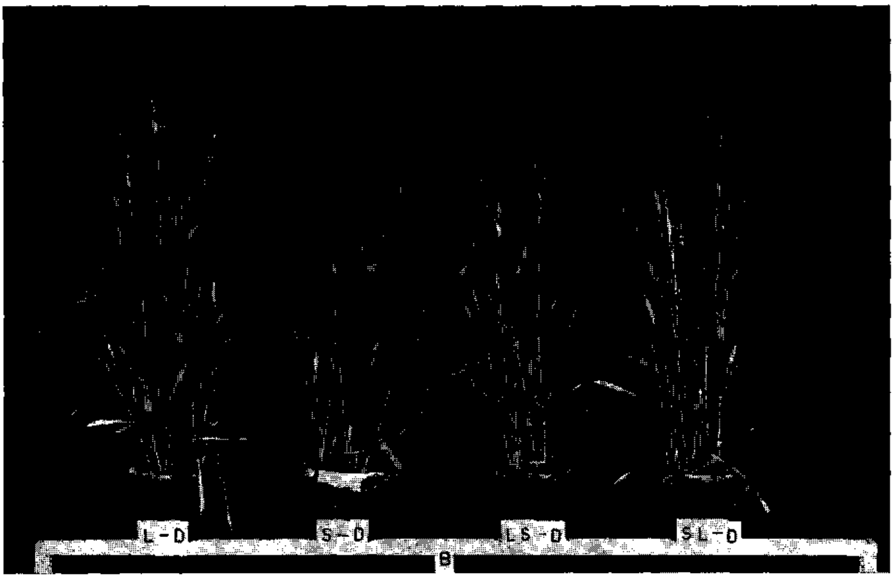
PLATE I



Morphological development of the wheat apex: g, growing point; lp, lp_1, leaf primordia; l, la, lb, undeveloped leaves; d_1, d_2, double ridges; s, spikelet primordium; as, apical spikelet primordium; gl, glume; m, lemma; o, own (beard)
Preparatory stage, 1–5 above. Transition stages, 1–5 middle. Developing stages, 1–5 below.

PLATE II





Above: vernalization effect on the development of 3 wheat varieties sown in spring (20 March 1954), outdoors. v: vernalized 45 days, c: non-vernalized, T: Heine VII, H: Hindi, B: Baladi.
Below: the development of Baladi var. (B) as influenced by different day-length treatments under natural conditions of temperature (sown 20 March 1954). L.D.: Long-day, S.D.: short-day, LS.D.: transferred from long to short-day after the 4th leaf emergence. S.L.D. transferred from short to long-day after the 4th leaf emergence.