VEGETATIVE GROWTH, MORPHOGENESIS AND CARBOHYDRATE CONTENT OF THE ONION PLANT AS A FUNCTION OF LIGHT AND TEMPERATURE UNDER FIELD- AND CONTROLLED CONDITIONS

A. M. BUTT

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Dit proefschrift met stellingen van

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De Rector Magnificus van de Landbouwhogeschool,
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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
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OP GEZAG VAN DE RECTOR MAGNIFICUS, DR. IR. F. HELLINGA,
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VAN EEN COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP DONDERDAG 27 JUNI 1968, TE 16.00 UUR

DOOR

A. M. BUTT

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VEGETATIVE GROWTH, MORPHOGENESIS AND CARBOHYDRATE CONTENT OF THE ONION PLANT AS A FUNCTION OF LIGHT AND TEMPERATURE UNDER FIELD- AND CONTROLLED CONDITIONS

THESIS

IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF AGRICULTURAL SCIENCES
AT THE AGRICULTURAL UNIVERSITY,
WAGENINGEN, THE NETHERLANDS
ON THURSDAY, 27 JUNE, 1968, AT 16 O'CLOCK

BY

A. M. BUTT

B.SC. (AGR.) AND M.SC. (HORTICULTURE),
AIN SHAMS UNIVERSITY, EGYPT, U.A.R.

THEOREMS

I

Carbohydrate by itself does not appear to be a causal factor for tuberization in general and bulb development in the onion plant in particular.

This thesis

II

The growth of the onion plant under the environmental conditions prevailing in the Netherlands is curtailed by factors other than light intensity.

This thesis

III

The formative effects of light on different plant organs suggest that within the plant an adaptive regulation exists which may well be influenced by the energy balance, but not merely through an overflow mechanism.

This thesis

IV

Onion cultivars are more likely to be adapted to different districts in the same latitude than to districts of similar climate in different latitudes.

JONES and MANN, 1963: Onions and their allies.

V

Improvement of field crop yields is more likely to be achieved by increasing the photosynthetic capacity rather than the photosynthetic efficiency.

VI

In order to evaluate leaf-morphology as a character of taxanomic importance, it is necessary to assess by experimental research, the variability of the leaf in the taxon under study.

VII

The formation of tubers and bulbs has several interesting analogies to the flower and fruiting activities of plants.

LEOPOLD, 1964; Plant growth and development.

A. M. BUTT
Wageningen, 27th June, 1968.

VIII

The beneficial effects of maintaining night temperature lower than day temperature must be considered cautiously.

CALVERT, 1965: Symposium on vegetable growing under glass, The Hague, 1965.

IX

Artificially induced mutations offer the plant breeder a tool to break through the limitations of presently known variability in plants.

SIGURBJÖRNSSON, 1968: Hereditas, 59 (2–3).

X

Extension of farm mechanisation should only take place because of shortage of labour.

XI

It is not justified to assess the true digistibility of protein diet through determining faecal nitrogen and food nitrogen.

To the memory of my mother in law
To the memory of my father
To my mother
To my wife in much gratitude

This thesis is also published as Mededelingen Landbouwhogeschool Wageningen 68–10 (1968)
(Communications Agricultural University Wageningen, The Netherlands)

FOREWORD

This study could not have been completed without the help of a large number of people. In the first place I wish to record my wholehearted gratitude and appreciation to my promotor, Professor Dr. E. C. WASSINK, for his hospitality, encouragement and deep interest in the study.

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Finally, I wish to express my appreciation to my wife who devoted herself to make my life easy and quiet.

CONTENTS

CHAPTER 1

INTRODUCTION

A. GROWTH AND DEVELOPMENT

One of the most outstanding distinguishing characters of living matter is growth. The simplest definition, commonly used by botanists, for growth is an increase in cellular mass (size, dry weight), though there are some instances which are considered as growth without any accompanied increase in weight (germination of seeds and sprouting of potato tubers). Increase in size and weight, however, although its most obvious aspect, is only one feature of growth.

The development of a plant from the fertilized egg is not simply an increase in the weight and size of the fertilized egg; otherwise a mature plant would be only an enlarged egg and not a highly specialized individual. Therefore, it is believed by some workers that development which precedes, accompanies and follows cell division and enlargement, is another aspect of growth.

On the other hand, many authors distinguish sharply between growth, development and differentiation. In their sense, growth merely implies cell division and cell enlargement processes, while the sequence of structural and functional changes that occur during the life cycle of an organism is regarded as development. This involves progression of the organism from small and simple to large and complex. According to these authors, differentiation is the acquisition of a determined structure and function in the course of development; it is only a component of development though often used as a synonym (NICKERSON and BARTNICKI-GARCIA, 1964 and quoted by ZEEVAART, 1965).

Whether development is regarded as a separate phenomenon or as un aspect of growth, the facts of developmental plant physiology clearly show that the course of development can be altered by environmental factors. The means by which such an effect can occur should reside in an alteration of the nucleic acid instructions – not permanent in the heritable manner, but metastable or temporarily fixed. A similar alteration in instructions should occur with changes in developmental sequences, such as the changes from juvenility to maturity, and from maturity to senescence (LEOPOLD, 1964).

The most general environmental factors that influence plant growth and development are light and temperature. With the onions, changes in these factors often express themselves in organ formation and growth.

Onion seeds of a given cultivar, from the same source, grown under different conditions of light and temperature can give us scallions, sets, large normal, doubled or split bulbs, or bolting plants.

Bulb development in the onion plant which is the swelling of leaf bases (sheaths) and formation of scales only begins in response to the stimulus of long days (GARNER and ALLARD, 1923; MCCLELLAND, 1928), although the cultivars may greatly differ in daylength requirement, e.g., from 12 to 16 hours light a day (MAGRUDER and ALLARD, 1937). Moreover, there is an interaction between daylength and temperature. For a given daylength, high temperatures accelerate bulb formation, while at lower temperatures longer days are needed to obtain the same effect (THOMPSON and SMITH, 1938; HEATH and HOLDSWORTH, 1943).

Bulb formation is generally accompanied by carbohydrate accumulation. This accumulation obviously indicates an excess of carbohydrate over current consumption. The question may arise whether accumulation of carbohydrate is due to increased photosynthetic activity under long day conditions or rather to the inability on the part of the plant to utilize the carbohydrate as rapidly as it is formed, in promoting growth, so that the material is stored for its own subsequent use or for the nutrition of its sexually or vegetatively produced progeny.

According to WILSON (1934), the onset of bulbing results from the accumulation of sugars in all parts of the plant; large quantities of soil nitrates tend to delay bulb formation and reduce yields. It was found also that onion plants grown from sets under short day conditions (8 hrs.) developed bulbs when feeded with sugars (HEATH and HOLLIES, 1963). Moreover, as pointed out by COCKSHULL and HEATH (1962), the finding of HEATH and HOLDSWORTH (1948) that defoliation (removal of the leaf blades) delayed bulbing until after the emergence of new leaves, could be interpreted as showing the need for a continuous sugar supply.

To some investigators, on the other hand, carbohydrate supply is not generally accepted as an important factor in morphogenesis, and it seems unlikely that accumulation of carbohydrate would by itself be sufficient to cause the complex growth associated with bulb formation (CLARK and HEATH 1962). Thus, the duration of the light period on bulb formation exercises a regulatory action on internal processes of the plant other than those which merely determine the total quantity of carbohydrate produced.

Investigations into the developmental physiology and the morphological and histological changes that occur during bulb development led to the speculation of the existance of a bulbing hormone (HEATH and HOLDSWORTH, 1948). It was suggested that bulbing was controlled by a growth substance originating in either the leaves or the stem apex as a result of long day conditions. Following a new and modified bio-assay for detection of a substance causing bulbing, in extracts of induced and non-induced onion plants, CLARK and HEATH (1962) were able to observe an increase in IAA-content to a very high level during the first week following induction, but this fell off rapidly after 5–7 days and eventually falls below the level found in the non-induced plants. The IAA-content as found by the afore mentioned authors, however, failed to fully account for the behaviour of the onion plant as grown under all the different conditions so far explored.

B. SCOPE OF THE PRESENT INVESTIGATION

Although a certain amount of work has been carried out on the development of the onion plant in relation to duration and intensity of illumination, and temperature, it seems that detailed information on the changes in growth and growth correlations that happen during the life history of the plant, still is of interest. Furthermore, no consideration, so far, has been given to the influence of intensity, duration, and quality of the supplementary light applied to extend the main photoperiod.

Morphogenesis and carbohydrate accumulation are the general features of bulb development, and may be altered by light intensity, duration and temperature and interrelations of these factors.

For these reasons, the growth, morphogenesis and carbohydrate metabolism of onions *(Allium cepa L.*, for further specification see Ch. III) as a function of light and temperature has been chosen as the object of the present study.

Moreover, we have studied the effect of plant density on bulb development, because variations in density of population also produce variations in morphogenesis and growth. In addition, seedstalk development as influenced by light intensity, duration and quality as well as plant density was investigated. The results of these parts of our studies will be published elsewhere.

CHAPTER II

REVIEW OF LITERATURE

A. LIGHT

While the genetic constitution of a given organism sets definite ultimate limits to the types of development and the reactions of which that organism is capable, the environmental factors, an important one of which is light, exert a profound influence upon the expression of its heredity (MEYER, 1965). Thus, the growth and development can be strongly affected by light: intensity, duration and quality, which will be considered in some detail.

1. *Light intensity effects*

a. Growth and development

The growth and development of plants as a function of light intensity has for long been a subject of interest. As early as 1923, GARNER and ALLARD, working with the silver skin onion cultivar, showed that the plants, grown under one-third the intensity of sunlight (3500 ft.c.), developed bulbs in substantially the same way as those grown in full sunlight (10500 ft.c.). At most, dying of the tops of the shaded plants was delayed one week, while the bulbs were about the same size as those in the control. They concluded, that there is no evidence that bulb formation in the onions is due to excessive intensity of sunlight in the summer. On the other hand, MAXIMOV (1923), with bean, reported that root and shoot dry weight, root/top ratio, and leaf area increased as the light intensity increased. Similarly, MILTHORPE (1945) pointed out that shading decreased dry weight, leaf area, height and net assimilation rate of the flax plant. Studying the light intensity effects on the root growth rate of some tree seedlings, WASSINK and RICHARDSON (1951) found the root growth rate of *Acer pseudoplanatus* seedlings to be determined rather directly by conditions for photosynthesis, while that of *Quercus borealis* did not differ at the light intensities used, for the period of the experiments, so that in this case root growth seems to rely upon storage material rather than upon direct photosynthesis. Plotting the root growth rate of *Acer pseudoplanatus* against light intensity, a curve strongly reminding of that for photosynthesis was obtained. WASSINK (1952) working with bulbous *Iris*, was able to show that plants which have initiated flowers may stop development of the complete flower stalk, unless a definite minimum amount of light energy is supplied. The data obtained by WAGENAAR (1954), working with spinach show a dry matter and leaf area increase with increasing light intensity. The increase was relatively greater from 22000 to 57000 ergs/cm^2/sec than from 57000 to 114000 ergs/cm^2/sec. BENSINK (1958, 1960), with lettuce, pointed out a morphogenetic effect on leaf growth caused by light intensity. Under conditions of low light intensity, long and narrow leaves, indicated by high length/width ratio, are formed. Root/top ratio was found to increase at low nitrogen concentration at all light intensities. He, therefore, suggested that differences in root/top ratio are affected primarily by a still unknown formative mechanism in the plant that distributes dry matter production over shoot and root system, and is affected by light intensity, temperature, nitrogen concentration and still other factors. In young tomato plants, ABD EL RAHMAN et al., (1959) stated that the transpiration rate and the total amount of water transpired in the course of the experiment increased linearly with light intensity. The same was true for fresh and dry weight. According to KAMEL (1959), shading of barley plants increased leaf length, relative leaf length (length/width), leaf area ratio, and the length of the vegetation period, while it decreased shoot and leaf number, leaf width and thickness, root/top ratio, dry weights of the various plant organs, and the ratio of non-photosynthetic tissues over photosynthetic tissues (C/F). The daily growth rate and the total green leaf area increased with increasing light intensity up to a certain stage, whereas the reverse was true at the late stages. The quantitative studies of EVANS et al. (1961) on the effect of shading on morphogenesis and growth of the wood land annual *Impatiens parviflora* showed that the rate of increase of dry weight per unit leaf area is practically proportional to the mean total radiation up to about 100 cal/cm^2/day, and almost independent above 300 cal/cm^2/day. In contrast, the leaf weight ratio (leaf dry weight/plant dry weight) is practically independent of the mean daily total radiation. Comparison of data for the growth of young plants of *Impatiens parviflora* and *Helianthus annuus* showed that the former responds to shading by a marked increase in the leaf area ratio (total green leaf area/total plant dry weight), while the rate of dry weight increase per unit leaf area decreases much less for a given degree of shading than in the case of *Helianthus annuus*. In 'Marquis' wheat, FRIEND et al. (1962) found that increasing light intensity in the range from 200 to 2500 ft.c. resulted in higher rates of leaf initation, emergence, expansion and increase in width and thickness; leaf length, however, decreased. Both absolute and relative growth rates increased with light intensity up to 2500 ft.c. KUIPER (1962) working with sugar beet plants grown under different light intensities, concluded that, at low light intensities, the rate of leaf expansion is determined by the rate of input of light quanta. Moreover, the dry weight of roots is reduced, presumably because under these conditions the photosynthetic products are mainly used for the growth of new leaves, while only a small amount of sugars is transported to the roots. Plotting total dry weight against light intensity, a linear relationship was obtained. Similarly, MATCHES et al. (1962) with Alfalfa seedlings pointed out that root dry weight accumulation was more sensitive to shading than top dry weight accumulation. From his experiment with *Allium cepa*, grown at artificial light, PARIBOK (1962) found that changes in the power used for lighting had practically no effect on the times when the bulbs were formed, but did affect the productivity of the plants. On the contrary, HEATH and HOLLIES (1963) in their investigations into the effect of shading on bulb development in the onion plant, found that 50% reduction of summer light delayed the start of swelling and reduced the number of scales formed. In a further experiment, onion plants were grown at full daylight, or only approximately 25% or 15% daylight, though due to the season and the structure of the greenhouse, even the full daylight treatment received only a comparatively low intensity. They found, however, that all plants grown at full daylight bulbed. The growth at 15% light was so poor that the plants died 2½ week earlier as compared with the others, though the plants which survived ultimately bulbed. Briefly, shading delayed bulb development but did not prevent it. With clover, STEM (1963) reported that the leaf area index increased with increasing level of radiation, and thus also the level of radiation required for maximum growth rate. In *Gladiolus*, KOSUGI (1962) stated that all plants produced from small corms (10 g) when grown at 35% of natural summer light, became blind. ALBERDA (1965), working with *Lolium perenne* plants grown under different light intensities, viz., 5.0, 3.5, and 2.0×10^4 ergs/cm^2/sec, and in darkness, found an increase in dry matter production as the light intensity increased. Correcting for the loss of dry weight as a result of respiration, he found the increase to be in the ratio of 5.0: 3.5: 2.0, which is almost exactly the ratio of the light intensities used.

b. Light intensity and the chlorophyll system

That light is one of the requisites for chlorophyll formation in Angiosperms is well established. On the other hand, the relation between chlorophyll concentration and light intensity was not clearly understood. Thus, the concept of chlorophyll constancy in adult leaves has been claimed by WILLSTÄTTER and STOLL (1918). This was generally held till the results of many investigators (HENRICI, 1919; BUKATSCH, 1940 and WENDEL, 1940) confirmed the existence of variation in the chlorophyll content of leaves during the day. The reaction of light intensity on the chlorophyll system in plants was demonstrated by MONTFORT (1941) who distinguished two types of plants: the photostable type which increases its chlorophyll content with increasing light intensity and vice versa, and the photolabile type, reacting upon increasing intensity of the light by decreasing its chlorophyll content. Several authors as, e.g., WARBURG and NEGELEIN (1922) have shown that the concentration of chlorophyll / dry matter in *Chlorella vulgaris* decreases with increasing light intensity. Similarly, in *Acer pseudoplanatus*, WASSINK et al. (1956) reported a decline in the chlorophyll content of leaves as the light intensity increased. Working with seedlings of *Larix decidua* and *Picea excelsa*, LAUDI (1964) found no correlation between fresh weight and chlorophyll content variations for plants grown under different light intensities ranging from 90 to 4000 lux. The chlorophyll content of *Larix* leaves per gram fresh weight of plants grown at 90 lux was 40% less than the average of all plots. In a study of the kinetics of chlorophyll bleaching, OSIPOVA (1964) came to the conclusion that there are at least three forms of chlorophyll α in maize leaves which differ in their photostability. The photostability of chlorophyll α depends on the illumination conditions prevailing during growth of the plants, being high for plants grown under high light intensity. Furthermore, a direct relationship between the photostability of chlorophyll and the intensity of photosynthesis is established.

It should of course be kept in mind that since the fundamental studies of Willstätter and Stoll (1913), numerous investigators have studied various aspects and properties of chlorophyllous pigments in the living cells, in aqueous systems, and in organic extracts. An extensive survey of this whole field has been given fairly recently by Smith and Benitez (1955). More recently, much evidence has accumulated – for which there were already some early indications by work of Lubimenko and his associates – that, not only in purple bacteria but also in green plant cells, chlorophyll occurs in various modifications, the rôle of which in photosynthesis is not yet definitely established (see, e.g., French, 1961).

That chlorophyll content of the plants may also be affected by the daily duration of illumination and by light quality has been shown. Shul'gin (1964) followed the chlorophyll composition in radish leaves growing at different photoperiods, viz., 12, 17 and 24-hour. For the 24 hrs. day, 12 hrs. of natural light was supplemented with 12 hrs. of blue or red light, while in case of 12 hrs. and 17 hrs., illumination consisted entirely of natural light. Shul'gin found the chlorophyll content to increase with increasing light intensity. Moreover, it increased with the length of the photoperiod for the cotelydons and was somewhat higher with supplementary blue light than with red. The chlorophyll content of the 2nd and 3rd leaves (20 days old plants) increased with increasing length of the photoperiod, and was approximately the same for the 17 hrs. and 24 hrs. photoperiods with either blue or red light. For the 4th to 5th leaves (30 days old plants), the chlorophyll content reached a maximum at a 24-hour photoperiod and was higher with blue at low light intensity and higher with red light (during 50% of the 24-hrs. photoperiod) when illumination was carried out at high light intensities. With the onion plant, Kakhnovich (1963) found the optimum light intensity for the development of the chloroplast apparatus to vary in the range of 16000–50000 ergs/cm^2/sec, depending on the spectral composition of the light. At the same light intensity (45000 ergs/cm^2/sec), the maximum number of chloroplasts developed in white, red, or yellow light and the minimum in green light. The amount of chlorophyll a + b increased with light intensity up to 20000–25000 ergs/cm^2/sec. Red light was more effective than blue-violet light in producing accumulation of chlorophyll a + b at low light intensities; at high light intensities (30000–40000 ergs/cm^2/sec), the effect of the spectral composition practically disappeared.

c. Light intensity and photosynthesis

The photosynthetic rate can be measured either directly by estimating the CO_2 input or the O_2 output per unit leaf area and time, or indirectly by determining the dry weight increase. For the latter purpose Gregory (1917) introduced the concept of the 'net assimilation rate' which was defined as the rate of increase in total plant dry weight per unit of assimilating material per unit time. At various times, different units of 'assimilating material' have been used. Bongers (1958), working with algae, brought forward that the reference unit applied may greatly affect the result. Williams (1936) replaced leaf area by dry weight and later (1939) by leaf protein. Watson (1952) stressed the use of leaf area for the sake of uniformity, which later has been substituted by the leaf area index (WATSON, 1958) which for calculations of NAR essentially makes no difference.

As to the influence of the intensity of light upon the rate of photosynthesis, much of the experimental work in this regard previous to 1905 is of reduced value, since factors other than light intensity often were not given due consideration (MILLER, 1938). BLACKMAN and MATTHAEI (1905), considering the importance of the other factors and working under well controlled conditions, came to the conclusion that when CO_2 concentration and temperature are not limiting, the photosynthetic rate is proportional to the intensity of the incident light. Recently, GAASTRA (1959), in some field crops, determined light intensity curves of photosynthesis at different leaf temperatures and normal and increased CO_2 concentrations. Briefly, when the CO_2 concentration was non-limiting, the photosynthetic rate increased with light intensity till a temperature sensitive light saturation is reached. In the Bermuda grass community, ALEXANDER et al. (1962) found the CO_2 uptake and, ultimately dry matter production to involve the summation of many diverse effects determining the degree to which the total leaf volume approaches light saturation during the growth period. Determining the rate of photosynthesis in clonal leaves of the lowbush blueberry as a function of light intensity at 0.4% CO_2, FORSYTH (1965) obtained a higher rate at the light intensity of 1000ft.c. than of 650 ft.c. The young and middle-aged leaves had a higher rate of apparent photosynthesis than the older leaves.

Light saturation, compensation point, and maximum rate of photosynthesis differ with the plant species and the conditions under which they had previously grown. BOYSEN-JENSEN and MÜLLER (1929) compared the light responses of peach trees, grown in full sunlight, with those grown in the shade, and found that the intensity at which photosynthesis was saturated was much lower in the shade leaves than in the sun leaves. BÖHNING et al. (1956), investigating the relationship between light intensity and apparent photosynthesis in leaves of sun and shade plants, stated that at a light intensity of 100–150ft.c. photosynthesis was zero in the leaves of sun plants. Light saturation was reached in the range of 2000–2500ft.c. In the shade plants apparent photosynthesis was not zero until a light intensity as low as 50ft.c. was reached. Light saturation also occurred at a relatively low intensity, being in the range of 500–1000ft.c. The compensation point of the sun leaves was 100–150ft.c. and 50 ft.c. foı the shade leaves. Similarly, WASSINK et al. (1956) have shown that photosynthesis of detached leaves of *Acer pseudoplatanus* which had previously grown at low light intensity, showed light saturation at a lower light intensity than those previously grown at high light intensity.

Concerning the net assimilation rate in relation to light intensity, the investigations carried out by BRIGGS, KIDD and WEST (1920) on maize, GREGORY (1926) on barley, GOODALL (1945) on tomatoes, WATSON (1947) on wheat, sugar beet and potatoes, BLACKMAN, BLACK and KEMP (1955) on sunflower, have shown for barley, tomatoes and sunflower a significant and positive effect of light on the net assimilation rate, while for no species a significant negative effect has been observed. In *Gladiolus*, WASSINK (1960) demonstrated a fairly linear relationship between light intensity and NAR calculated over the entire season. BLACKMAN and WILSON (1951a) on several plant species found the NAR to be proportional to the logarithm of light intensity over the range of 0.10 to full daylight.

That photosynthesis and growth rate may be inhibited by excessive light intensities (solarization) is well known. STEEMANN-NIELSEN (1952) with *Cladophora* showed a decline in the photosynthetic rate in high light intensities which continued even when the plants were returned to low light intensity. The inhibition was proportional to the duration of excess light as well as to the intensity applied. He concluded that both the light and dark reactions of photosynthesis were damaged by excessive light. JOHNSON and WAYNE (1955) pointed out that high light intensities affected both growth and fruiting of the tomato plant by limiting stem elongation and by inducing a type of dormancy in the fertilized and non-fertilized young fruits. As quoted by LEOPOLD (1964), SIRONVAL and KANDLER (1958), examining the light inhibition effects, were able to distinguish between an initial 'induction effect', in which photosynthesis was inhibited without chlorophyll bleaching and a subsequent bleaching effect on chlorophyll itself.

d. Light intensity and carbohydrate content

The first evident synthetic product that is formed by the green plant from the simple inorganic compounds obtained from the air and the soil, under conditions of illumination, in any appreciable quantity is carbohydrate. Carbohydrates are the most abundant compounds in the plant and make up the bulk of its dry weight. As the energy stored by green plants in the molecules of carbohydrates during photosynthesis can be supplied only by light, the question arises, in how far variations in light intensity influence carbohydrates synthesis. There is evidence that the carbohydrate content in plants is reduced by reducing the energy supplied.

MELVIN and SUTHERLAND (1961) found the average reduction of total carbohydrate content of shaded short rotation rye grass (shaded to about $^1/_4$ of that in the open for 64 hrs. before cutting) to be about 30%, made up of decreases in sucrose (12%), oligosaccharides (5%) and fructozans (13%). ALBERDA (1965), working with *Lolium perenne*, showed that differences in light intensity influence only the total soluble sugar content, while the other organic constituents of the different plant organs remain unchanged when calculated on a sugar-free dry weight basis. The carbohydrate concentration was higher at higher light intensities, the differences being greatest in the leaves compared with the other plant organs. According to KUDRYAVTSEN (1964), ten days shading of tomatoes which decreased the relative illumination by 4–6 times, appreciably affected the starch and sugar content in tissues of various plant organs. The amount of these substances especially decreased in the lower leaves, root system and stem, and to a smaller degree in tissues of growing buds. As illustrated by VERHOEKS (1965), the daily fluctuations in carbohydrate content in the lamina of the potato plant, strongly depend on light intensity. He observed further that the carbohydrate content of the younger (not yet full grown) leaves is much lower than that of the older (mature) leaves. With Italian rye grass grown at 100, 68, and 44% of daylight, NOWAKOWSKI (1966) reported a decline in the percentage of total soluble carbohydrates with decreasing light intensity. On the other hand MATCHES et al. (1963) have shown that the reduction of full daylight down to about 69%, applied when plants were six weeks old, had no apparent effect on the concentration of total available carbohydrates in both roots and aireal parts of three alfalfa varieties, but shading reduced the total amounts of carbohydrates in the roots, measured as grams of total soluble carbohydrate per pot.

It seems that the changes in carbohydrate composition in relation to the age of plants differ according to the plant species. MILLER (1938) has quoted that DAVIS, DAISH and SAWYER (1916) noticed that all the soluble sugars in the leaves of mangold increase in quantity from the first to the final stages of growth. Similarly, MCCARTY (1935) observed in some grass species, that the sucrose and starch trend during the season was from a low concentration early in the growth cycle to a high concentration at the close of the growing season. In Biloxi soybean, according to BORTHWICK and PARKER (1939), the total carbohydrate content increased with the age of the plants during the experimental period (6 weeks), while the maximum was not reached during that time. On the contrary, in Agate soybean, the total carbohydrate content reached a maximum when the plants were 3 weeks old, after which there was a progressive decrease. In both lettuce and radish, ARTHUR et al. (1930) demonstrated that total carbohydrate, in general, decreases with age. Working with *Lolium perenne*, ALBERDA (1965) found no change in carbohydrate content of the different plant organs with time, owing to the fact that growth in this plant takes place by increasing the number of tillers.

2. *Daylength effects*

a. Growth and development

From their extensive work, GARNER and ALLARD (1920) have shown that flowering in many plant species is controlled mainly by the relative length of day and night. Since then a voluminous work has been amassed on the effects of daylength on the growth and development of plants.

The formation of bulbs has several interesting analogies to the flower and fruiting activities of plants. In addition to the powerful mobilization actions which are shared with numerous fruits, bulbs may be formed in response to an induction phenomenon which occurs in the leaves and is transmitted to the part which will do the swelling. There, a morphological differentiation and the growth of the storage organs follows, and to continue the anology, bulbs, like some fruits then undergo a ripening phenomenon (LEOPOLD 1964).

The development of the bulb of the onion plant has two main morphological features; swelling of the leaf bases (sheaths) and the formation of scales from leaf initials produced at the stem apex (HEATH and HOLDSWORTH, 1948). Concerning the daylength effects on bulbing, GARNER and ALLARD (1920) were the first to indicate that the length of the photoperiod relative to the dark period exercises a remarkable regulatory action in inducing or inhibiting bulb formation. Working with a silver skin onion cultivar, the authors reported that the plants did not show any indication of bulbing when grown under short day conditions (10 hours) at full light intensity (105000ft.c.), but bulb development did occur under long-day conditions (14.9 hours) even when light intensity was reduced to as low as $^1/_3$ that of the natural day (35000ft.c.). In 1923, extending these studies, they grew sets of common silver skin onions under different daylengths, namely 10 hours, 13 hours, natural daylength (14.9 hours) and 14.9 hours + 5 hours of electric illumination of 3–5ft.c. The plants grown under natural daylength (14.9 hours) and those grown under natural daylength plus 5 hrs. of artificial light developed bulbs in the same way; in those grown at 13 hrs. of light daily, the tops remained green throughout the summer, and the original bulbs in most instances in the course of the season gave rise to several new individuals, each of which eventually formed a bulb of considerable size. Under 10 hours day there was a permanent failure to form bulbs, although the plants splitted into two or more individuals. The authors came to the conclusion that the onion bulb development and the resultant rest period are induced by the stimulus of long days, while short days favour vegetative growth of indefinite duration. Thus, the duration of the daily light period is an important, and often controlling factor in determining whether the plant may use the photosynthetic products as rapidly as formed in promoting growth or, instead, stores the material, perhaps for its own subsequent use or for the nutrition of its vegetatively produced progeny. In his study on some factors that affect bulb development of 'Yellow Strasburg' and 'Ebenezer' cultivars grown in the water cultures, WILSON (1932) observed that bulbing was related first of all to daylength, then to the amount of root injury, and finally to the general vigour of the plant. Moreover, bulbing was accelerated by reducing the pH of the culture solution to a certain limit (5.0).

The response of a number of European and American onion cultivars to daylength was studied by MAGRUDER and ALLARD (1937). They found that cultivars varied markedly in the minimum photoperiod required for bulb formation, as well as in the rate and uniformity of bulb formation at daylengths that were above the minimum. The photoperiod necessary to produce 100% normal bulbs was longer than that required to produce the earliest-maturing bulbs, indicating that most cultivars are not homozygous in their response to daylength.

That some environmental and physiological factors have a modifying effect on the response of plants to the stimulus of daylength is well established. Such factors are light intensity, light quality, temperature, and plant age. The influence of these items, and in particular the first three, will be considered in some detail.

b. Light intensity effects on the photoperiodic reactions

According to some investigators, the light intensity during the photo-induction is of no importance. For example, GARNER and ALLARD (1923) showed that the reduction of the light intensity to one third of natural full light (35000ft.c.) neither influenced the bulb formation in the silver skin onion cultivar (LDP) nor the flowering response of Biloxi soybean (SDP) as long as the light/dark ratio was appropriate. They, therefore, suggested that using a term such as 'quantity of solar radiation' in relation to specific responses should be abandoned, while involving both intensity and duration of the daily exposure.

In contrast to the above-mentioned, several lines of evidence indicate the importance of the light intensity in the cyclic alternation of light and dark periods in order to bring about the photoperiodic stimulus. In this connection, BORTHWICK and PARKER (1938b) found that a light intensity of at least 100ft.c. during 8 hours of photoperiod is required for the induction of Biloxi soybean plants. Furthermore, they found that initiation of flowers occurs when the main photoperiod of eight hours natural daylight is supplemented with 8 hours of artificial light, provided the light intensity of the supplementary light is below 0.5ft.c. Subsequently, PARKER and BORTHWICK (1939) indicated that when the total light exposure was 8 hours, the flower response of the Biloxi soybean plants increases with increasing total light energy, the effect was not due to increased general growth as the constancy of node number shows. Working with *Xanthium pennsylvanicum* (SDP) LONG (1939) reported that the critical dark period increases slightly in length if plants are shaded to as low as one-tenth of full daylight for ten days. MANN (1940) was able to show that vegetative *Xanthium pennsylvanicum* can be induced to flowering by a single photoinductive cycle. The effect of the length of the photoperiod given during this cycle is related to its light intensity; by increasing the light intensity, the effectiveness of the photoperiod increased, while light of less than 100ft.c. was ineffective.

Additional evidence of the importance of the light intensity in altering the physiological state sufficiently to bring about flowering, may be found in some experiments with long day plants. NAYLOR (1941) with dill grown under continuous light at different intensities, found that the photoperiodic response was almost proportional, up to 300ft.c., to the amount of light received, while with beets *(Beta vulgaris)* flowering did not occur if the intensity did not rise above 700ft.c. during the initiation period.

From these and other results it was deduced that photosynthesis may be involved in the photoperiodic reactions. In fact, PARKER and BORTHWICK (1939), and HARDER and VON WITSCH (1941), showed that CO_2 supply during the light phase is essential. Increase of CO_2 supply up to 5% in the soybean gave rise to greater induction than the use of normal air. The authors concluded that initiation of flower primordia in the Biloxi soybean plants may be limited by photosynthesis; either owing to CO_2 limitation or owing to the reduction of the total amount of light energy supplied. In certain varieties of the Castor bean (LDP), SCULLY and DOMINGO (1947) observed also that both duration of photoperiod and light intensity are factors which may influence the formation of flower primordia. With different varieties of onion, PARIBOK (1962) found that for total production and bulb formation in continuous light it was more effective to lower the illuminating power, while high power was more effective with 12 hours light day.

It is well established that artificial light of low intensity, when used to prolong the main photoperiod beyond the critical, is mostly effective in preventing flowering in short-day plants and in causing flowering in long-day plants. In this respect, the work of WITHROW and BENEDICT (1936), however, demonstrates that the threshold values vary considerably with different species. With two wheat varieties ('Hard federation' and 'Turkey'), HURD-KARRER and DICKSON (1934) have shown that there was no effect of supplementary light of intensities from 15–100 ft. c. on the external appearance or rate of development of the plants; KHALIL (1956) in two other varieties, demonstrated that the progress of plants towards reproduction was favoured by increasing the intensity of supplementary light from zero to 11000 ergs/cm^2/sec. Another point of interest is that, at least in some cases, the effectiveness of supplementary light increases when given immediately after the dark period, rather than preceding it (HAMNER, 1940).

c. Wavelength dependence of photoperiodic reactions

In many photoperiodically sensitive plants, the so-called 'critical daylength' phenomenon has been studied by various investigators. In the past, it has been held by several workers in this field, that the critical daylength is rather fixed, and at most can be slightly modified by other environmental factors. The results of many research workers, however, have distinctly shown that the spectral composition may strongly alter the photoperiodic response, so that a (LDP) may not be induced even at exposure to continuous light of certain wavelengths. The spectral dependence of photoperiodic reactions has been a subject of interest for many investigators. RAZUMOV (1933) reported that radiation from the red and yellow parts of the spectrum, when used to extend short natural photoperiods, was as effective as natural daylight, whereas green, blue or violet were ineffective. Later, WITHROW and BENEDICT. (1936) supported these findings and found that blue light was ineffective, except in *Callistephus chinensis* var. 'Hart of France' which responded equally to all wavelength regions employed. According to KATUNSKIJ (1937) and KLESHNIN (1943), the photoperiodic reactions could be influenced by any part of the visible spectrum, though the intensities required varied from one region to another. KATUNSKIJ noted a close similarity between photoperiodism and photosynthesis in their dependency on the spectral regions. BORTHWICK and PARKER and co-workers (1948–1950) working on the action spectra for both short and long day plants, showed a pronounced maximum effectiveness in the red and a second, much smaller maximum, in the blue. In general, these results support the early findings mentioned above.

FUNKE (1936–1943) distinguished four classes of plants, namely 1. those in which red is as effective as white light, blue acting like darkness; 2. red and blue are equally effective as white; 3. white alone is effective, neither red nor blue alone causing inductions; 4. blue is as effective as white, red acting as darkness, all plants in the latter group belonging to the *Cruciferae*. In attempts to extend this work, WASSINK et al. (1950) and STOLWIJK (1951, 1952), using more reliable equipment, in a variety of *Brassica napa oleifera*, (LDP), found a photoperiodic action spectrum different from that of BORTHWICK and co-workers, and similar to that of FUNKE's fourth type, namely, principal effectiveness in blue and violet. It came as a surprise then, that they found, in addition, light of wavelength regions in the near infra-red had the same effect as blue. Since WASSINK et al. found that the flowering response of *Brassica* in the violet, blue and infra-red regions was independent of daylength to a much greater extent than in white light, they suggested the possibility of an antagonistic effect of the red, yellow and green parts of the spectrum on the activity of the violet, blue and near infra-red. Such antagonism had already been reported for effects on seed germination by FLINT and MCALISTER (1935), MEISCHKE (1936) in *Cucurbita.* Later on LEOPOLD and GUERNSEY (1954) in lettuce and BORTHWICK et al. (1952) with *Xanthium*, a red sensitive plant, reported that the effect of red light could be reversed by subsequent near infra-red irradiation. PIRINGER et al. (1954) working with the long day plant *Hyoscyamus niger* supported these findings, provided the infra-red radiation was not given over too long a time.

In attempt to interprete the action spectra for the various red light responses and the reversibility effects of red and far red light in photoperiodic reactions, BORTHWICK and coworkers (1952), supported by STOLWIJK (1954), deduced the existence of two interconvertible forms of a photoreceptive pigment, a 'red absorbing' and an 'infra-red absorbing' one in many species. Since then, efforts have been made to isolate this pigment from the plant tissues. In 1959, BUTLER et al. using a very sensitive spectrophotometer, could detect the presence of a pigment in two interconvertible forms which in fact showed a spectral shift in the absorption by etiolated plant parts following red or far red radiation. This has been given the name of 'phytochrome'. These authors assume that there are two forms of phytochrome: one with an absorption maximum at 660 mμ (P_R) and another with maximum absorption at 730 mμ (P_{IR}). From the results of these experiments, deductions can be made about the behaviour of the pigment in relation to light, but its nature and the way in which it regulates developmental activities remain to be understood.

Although red light may be the most effective for a brief night break (BORTHWICK and coworkers, 1948 and 1952), it is often relatively ineffective in extending the main photoperiods, and far red may be more effective (WASSINK et al, 1950, STOLWIJK and ZEEVAART 1955; DE LINT 1958). Furthermore, it has been reported that even a small contamination of far red radiation with red light increased the extension effectiveness (VINCE et al. 1964). It follows that, as incandescent light contains approximately equal amounts of red and far red energy, one would expect increased effectiveness in prolonging photoperiods or when admixed to fluorescent light which lacks near infra-red radiation in adequate proportion. In fact, the promoting effect of incandescent light has been recognized by some investigators (BORTHWICK and PARKER 1952; DOWNS et al. 1958, and FRIEND et al. 1961). Also WHEELER (1961) indicated that incandescent light increased internode extension and dry weight formation in several plants, while leaf area was only slightly affected. In *Phaseolus vulgaris*, plants with longer internodes contained more gibberellic acid and IAA-like substances. With the onion plant, PARIBOK (1962) found that the plants quickly formed bulbs when grown under incandescent illumination, while under daylight fluorescent lamps bulb development was strongly retarded, or bulbs did not form at all. The results of PALEG and ASPINALL (1964) show that supplementing a fluorescent light source with incandescent light accelerated apical growth and floral differentiation of barley (cv. 'Prior') in a long photoperiod only. The rate of apical development was linearly related to log incandescent light over a wide range, but varying the intensity of the fluorescent light had only a minor effect on apical growth. The effect of incandescent light on floral initiation was already evident before any internode elongation had occurred. When radish plants were grown at 12 hrs. periods of natural light supplemented with 12 hrs. of incandescent light or red or blue light for a 40-day period following emergence, SHUL'GIN (1964) reported that red light kept development in radish plants at stage 2 or 3, while blue accelerated development and the plants were ready to proceed to flowering (stages 6–7). The development was also accelerated with infra-red light and retarded by orange-red light. According to the author, the incandescent light causes quick development of the plants not because of the orange-red rays in the visible range, but because of the infra-red radiation which constitutes 88–90% of all radiation. With *Lolium temulentum*, EVANS et al. (1965) stated that light, containing approximately equal proportions of red and far-red energy was the most effective for photoperiod extension, the flowering response diminishing as the portion of either red or far red energy increased further.

d. Temperature dependence of photoperiodic reactions

That temperature has a modifying effect on photoperiodism has long been known. Not all short day plants respond with equal rapidity to short photoperiods, nor do they exhibit identical responses at different temperatures (ROBERTS, 1938). The same is true for long day plants. Some varieties may be photoperiodically sensitive at one range of temperatures and day neutral at another (HAMNER and NAYLOR, 1939). As early as 1930, GARNER and ALLARD accounted for the variations of the flowering dates of soybean under field conditions at Washington from year to year by the variations in temperatures as the daylength is constant from one year to another. STEINBERG and GARNER (1936) found that the critical photoperiod for flowering of *Rudbeckia bicolor* and beet (LDPs) may be altered to a limited degree by temperature, and conversely, the favourable temperature range may be shifted by the action of the photoperiod. With *Xanthium*, HAMNER and BONNER (1938) concluded that formation of floral initiation substances may take place during the dark period, and the reactions involved are adversely affected by low temperature. PARKER and BORTHWICK (1939) reported that temperature alone was not effective in causing floral initiation in 'Biloxi' soybean, since plants held at 16 hours photoperiods remained vegetative regardless of the temperature combinations applied during the light and dark phases, and there was a great increase in floral initiation by change in temperature during the dark period from 55–65°F at a photoperiod of 8 hours. As the carbohydrate content decreased with rise of temperature, they concluded that the carbohydrate and nitrogen composition could not be a factor in the observed increase of floral initiation. The results obtained by MURNEEK (1940) with *Rudbeckia bicolor* (LDP) would seem to indicate that, as regards sexual reproduction, this species is attuned not only to relatively long days but also to relatively high temperatures, so that the latter may be substituted for the photoperiod. He also presumed that comparatively warm nights instead of warm days may be more effective in this respect. With dill (LDP) NAYLOR (1941) showed the importance of high temperature on the photoperiodic induction. He found that plants receiving cycles of 20 hrs. light and 4 hrs. darkness at a constant temperature of 4.5 °C were only slightly responsive. The data obtained by VAN DOBBEN (1964), working with red clover, shows an interaction between photoperiodism and temperature, involving that at low temperatures the long day requirement is lowered.

e. Photoperiodic reactions and age of plants

It has been demonstrated frequently with various plant species that the photoperiodic stimulus is received by the leaves, and transmitted to the apex, causing the response (KNOTT, 1934; CAJLACHJAN, 1936; BORTHWICK and PARKER, 1938b). The question arises whether the physiological status of the meristem is important in this respect. There are some indications that it may be so. CAJLACHJAN (1933) found that a short day treatment applied to millet was most effective when the plants were five weeks old. Similarly, PURVIS and GREGORY (1937) reported that none of their manipulations of the environment will produce flowers in the first axillary buds of rye. With soybean plants, BORTHWICK and PARKER (1938a) observed that the effectiveness of photoperiodic treatment increases with age of the plants up to six weeks old (the maximum age applied), while no plants respond at one week of age. According to the authors, the differences in the response may be due to the differences in leaf area. LONG (1939), with *Xanthium*, reported that the plants become more sensitive to photoperiodic treatment as they grow older. From their work with some soybean varieties, BORTHWICK and PARKER (1939b) were able to show that the varieties may differ markedly in the relative ages at which they respond in a similar way to photoperiod, and that the most effective leaf on the plant is the one that has most recently attained its full size, after which the leaves gradually decline in effectiveness. In contrast, BHARGAVA (1964) found very young as well as older plants of *Salvia occidentalis* (SDP) to be equally sensitive to short day treatment, so that a non-sensitive or less sensitive period was not evident. Furthermore, defoliation during short day did not affect the flowering response.

However, we may conclude that the physiological status of the meristem seems important, and that at least several plant species must undergo a certain amount of growth before they can respond to photoperiodic induction.

B. TEMPERATURE

In the following review, the effect of temperature on growth and development of plants in general and in the onion in particular will be considered in some detail. Since the growth and development is a net result of a complex of processes, the rate of which may be differently influenced by temperature, a brief presentation of the temperature dependence of metabolic and translocation processes seems to be in place. This, no doubt, will help in understanding the growth and development phenomena as a function of temperature.

Moreover, in a number of cases, growth and development have been experimentally approached as an entity in its relation to temperature, which cases are discussed separately.

Temperature has importance for nearly every function of the plant. Chemical and physical processes are governed by temperature and accelerated by its increase up to an optimum. The responses to the stimulus of temperature are not localized in a particular organ but occur everywhere in the protoplasm throughout the living tissues (WEAVER and CLEMENTS, 1938).

The rate of reactions as a function of temperature is determined by its temperature coefficient or Q_{10}. This is the ratio of a reaction rate at a given temperature to the rate at 10°C lower; in general it is 1.0–1.4 for physical and photochemical reactions and around 2.0 for biochemical ones (see, e.g., LEOPOLD, 1964).

1. *Temperature dependence of photosynthesis and respiration*

As the photosynthetic process is not a simple one, but physical, photochemical and biochemical reactions are involved which have different temperature coefficients, one may expect that the changes of the rate of photosynthesis with temperature are complex. Consequently, the Q_{10} of photosynthesis will vary according to which steps are rate-limiting. In this connection, GAASTRA (1959), studying the rate of photosynthesis as a function of light intensity, CO_2 concentration and temperature in some field crops found that, at 0.03% CO_2, photosynthesis is almost independent of leaf temperature, while at higher concentrations, the rate shifts to higher values with rising temperature, so that light saturation was not reached at the highest temperatures (31–35°C), indicating that with excess CO_2, a biochemical process limits the rate. The Q_{10} values, then observed, were somewhat lower than those normally occurring in such processes, due to the fact that light saturation was not yet complete, so that the temperature-independent photochemical process still was in part determining the rate. At light saturation and CO_2 concentration round 0.03%, photosynthesis was almost independent of temperature, but it was affected by CO_2-concentration. Shortly, one can say that under conditions where neither CO_2-concentration nor light intensity is a limiting factor, the photosynthetic rate increases with increasing temperature, the steepness of the rise being greatest at temperatures just above freezing and then decreases at higher temperature (STÅLFELT, 1937). In clonal leaves of lowbush blueberry, FORSYTH and HALL

(1965) have shown an increase in the rate of O_2 evolution as the temperature was raised from 13.0 to 29.5 °C. Furthermore, it has been stated by SHAIDUROV (1962) that the photosynthetic rate is determined by the temperature gradient between the leaf and the surrounding air; the higher the temperature of the leaf relative to that of the air, the lower the intensity of photosynthesis, and vice versa.

Studies on the temperature effects on respiration, e.g., WASSINK (1934), MACALISTER (1937), and WAGENAAR (1954), showed a marked increase in respiration rate with increasing temperature. They also observed a decreasing Q_{10} as the temperature increased, between 5–25 °C.

Photosynthesis and respiration proceed simultaneously, in opposite directions, and their rates may well be affected to different degrees by temperature. The work of WENT (1953) indicated that at lower temperature the ratio of photosynthesis to respiration is over 10, while at higher temperatures, respiration is increased relatively more, and low ratios of photosynthesis over respiration are observed. This has been confirmed by TAKEDA and WAICHI (1964) who, studying high temperature effects on photosynthesis and respiration in 'Ladino' clover, found an increase in respiration and a reduction of the photosynthesis/respiration ratio.

Examining the dependence of photosynthesis and respiration in artificial communities of cotton plants on their leaf area index under various temperature regimes, LUDWIG et al. (1965) have shown a decline in the rate of net photosynthesis at high leaf area index values with increasing temperature, owing to the higher ratio of the rate of respiration to that of photosynthesis.

2. *Temperature dependence of translocation*

It has been held in the past, at least by some investigators, that translocation is favoured by low temperatures, having a Q_{10} less than unity. There is some evidence to support this view. For example, WENT (1948) interpreted the high carbohydrate content and the increasing root/top ratio at lower night temperatures to the increased translocation of sugars at lower temperatures compared with higher ones. In subsequent work, WENT and HULL (1949) confirmed these findings by reporting a decrease in the rate of translocation as the temperature increased from 2 °C upwards. RICHARDSON (1956) found an enhanced root growth rate of *Acer saccharinum* with decreased night temperature even when the low night temperature was applied to the above-ground parts, apart from the root system. Increased root growth rate at lower night temperatures is due to increased rate of translocation of photosynthates to the roots; a process having a Q_{10} less than unity. According to RICHARDSON, however, this observed Q_{10} is not due to a direct effect of temperature on translocation. At high temperatures, respiration increases and nocturnal synthetic processes in the shoot may compete successfully with the roots for photosynthates, and the utilizable carbohydrate may be converted into a form unavailable for translocation. These ultimately will reduce the amount of photosynthates available for export to the root. Furthermore, WASSINK (1953) and quoted by RICHARDSON (1956) has shown that an apparent Q_{10} of less than unity may be the net result of a series of interacting processes, each with different temperature coefficients, but all of them greater than unity. Thus, any of the aforementioned processes (each with a Q_{10} greater than unity) may reduce the amount of photosynthates available for export to the roots; and this reduction will increase with increasing shoot temperature. Even though Q_{10} for translocation proper may be greater than unity, if transport is limited by the amount of photosynthates available, an apparent Q_{10} of less than unity results. In accordance to this interpretation, several investigations provided conclusive evidence that translocation rates increased with temperature up to between 20 and 30 °C. In this regard the work of HEWITT and CURTIS (1948) and of SWANSON and BÖHNING (1951), deserves attention. Increased rate of translocation with rising temperature has been substantiated by using the isotope labelling techniques (SWANSON and WHITNEY, 1953).

3. *Temperature dependence of carbohydrate content*

With respect to the carbohydrate content, temperature seems to play a dominant role. It influences the carbohydrate composition of the plants through its effect on various processes, namely photosynthesis, respiration, translocation, hydrolysis, and utilization in growth. This has been proven by many workers. WENT (1944), with the tomato plant, for instance, found that the sucrose content fluctuated most, while the reducing sugars and starch were nearly constant when the plants were grown under different experimental conditions. At higher day temperature, the sucrose is consistently, though insignificantly higher. On the other hand, high night temperatures caused a consistently and significantly higher sucrose content in the leaves. CURTIS and CLARK (1950) found the sugar percentage in carrots to be negatively correlated with temperature. The results of ALBERDA (1965) with *Lolium perenne* indicated that differences in temperature influence the carbohydrate content and the nitrate content, while the other organic plant constituents remain unchanged when calculated on a sugar-free dry weight basis. He demonstrated also that the sugar content decreased as temperature increased up to 25 °C in roots and stubble, and up to 30 °C in the leaves, the differences being largest in the leaves. Because growth in *Lolium perenne* takes place by the production of tillers, there is no change in chemical composition with time.

As to the temperature effects on starch hydrolysis, WASSINK (1953), working with *Helianthus tuberosus* and *H. annuus*, observed maximum hydrolysis at about 0–3 °C, a minimum around 10 °C, and a renewed increase at temperatures above 15 °C. With pea seeds, ROBERTSON et al. (1962) reported that, at low temperatures, the conversion of sugar to starch was much delayed, and sugars continued to increase in concentration during growth while, at higher temperatures, the sugars entering the seeds were rapidly converted into starch; thus, the carbohydrate composition of seeds grown at different temperatures was markedly different. The work of RICHARDSON (1956) on temperature effects on different aspects of growth, also important for our present discussion, has already been commented on in section 2.

4. *Temperature dependence of phenomena related to growth and development*

Temperature influences on growth and development have been studied in several plant species. In this section, the effects of temperature on growth and development of different plant species will be dealt with first, followed by effects on bulbous plants, including more specifically onions.

KHALIL (1956), with wheat, stated that the most favourable night temperature for stem elongation was between 10–20°C; the higher the night temperature, the greater the number of leaves and the smaller the numbers of tillers. He also found a decline in the root/top ratio as temperature increased. A morphogenetic effect of temperature on leaf growth of lettuce plants has been demonstrated by BENSINK (1958), who observed increased length/width ratio at high night temperature.

ABD EL RAHMAN et al. (1959), working with tomatoes, found the height of the plants to be sensitive to changes in air temperature. Thus, lowering the temperature from 26 to 10°C caused a large reduction of the plant dry weight as a result of the reduction of the height, of the number of leaves/plant, and of the mean area of mature leaves. When the young tomato plants were grown at a constant day temperature of 25.3°C and different night temperatures, ranging between 25 and 9°C, the authors observed a decline of stem growth rate, and of dry weight of leaves and shoots, as the night temperature decreased. Investigating the rate of dry weight accumulation in 'Marquis' wheat in relation to temperature, FRIEND et al. (1962) found the optimum temperature for the mean absolute growth rate over the whole growth period to be 20–25°C, whereas the optimum for the mean relative growth rate was 15–20°C. KUIPER (1962), with sugar beet, observed a linear relationship between total leaf area at light saturation and temperature. Surprisingly, he found higher water content at higher temperatures. He concluded that the percentage of water in the leaves is determined by the environmental conditions rather than by the actual rates of water uptake and transpiration. According to DALE (1965), the most important influences of temperature on the expansion of the leaf surface of *Phaseolus vulgaris* appear to be by controlling the rate at which leaves unfold from the stem apex, and by controlling the partition of dry matter between the leaves and the rest of the plants.

Some evidence shows that optimal temperatures shift to lower values as the plants advance in age. In this connection, LEWIS and WENT (1945), working with some California annuals, found that during the seedling stage, the largest leaves were produced at 26.5°C night temperature; on the contrary, as the plants advanced towards maturity, the largest leaves were produced under lower night temperatures. DORLAND and WENT (1947) noticed that the optimum night temperature for stem elongation of Chili peppers decreased gradually from 30 to 2°C as the plants aged. With the 'Vinco' pea, WENT (1957) observed the maximum rate of elongation at 79, 73, 68, 63, and 57°F for plants 9, 13, 18, 27, and 40 days after germination respectively. TAYAMA and MILLER (1965) have shown that in the Snap dragon, the optimum temperature for NAR shifts to lower value as the plants proceed in age owing to the decrease in leaf dry weight relative to plant dry weight, and probably to increase in the intensity of mutual shading when plants advance towards maturity.

The interaction between optimum temperature for growth and light intensity has been observed by many investigators. In general, there is a shift in the optimum temperature towards higher values with increasing light intensity till saturation. HOFFMAN (1938) with the tomato, for instance, advises that the night temperature should be kept around 15–16 °C, and the temperature during cloudy days be raised to 18 °C and during sunny days to 21–24 °C. Similarly, WENT (1944), MITCHEL (1953), and ALBERDA (1965) have all reported shifts of the optimal temperature to higher values as the light intensity increased. According to ALBERDA (1965), this can be explained on the basis that light intensity influences only the rate of photosynthesis and respiration remains unchanged, while temperature affects both in different ways.

The importance of temperature fluctuations for growth and development has been reported by many investigators. WENT (1944) emphasized the benificial effect of lowering the night temperature for optimal growth of tomatoes as compared with the maintenance of constant temperature during day and night. According to WENT, the so called thermoperiodicity in tomato is due to the interaction of two processes, one occurring in the dark, the other in the light, of which the dark process should have a much lower temperature optimum than that taking place in the light. In another set of investigations, the necessity of changing temperature during different developmental phases could be clearly shown, viz., in the work of BLAAUW, LUYTEN and HARTSEMA (1936, 1939); HARTSEMA, LUYTEN and BLAAUW (1930); LUYTEN, VERSLUIJS and BLAAUW (1932); VERSLUIJS (1927); BLAAUW, HARTSEMA and VAN BEEKOM (1941); HARTSEMA (1947). In their work with bulbous plants, such as tulips, hyacinths, onions and daffodils, they emphasized that a succession of processes occurs, for instance, leaf initiation, flower induction, flower initiation, preparation for stem elongation, actual stem growth and flowering, all of which require very different temperatures for completion. These temperatures lie so far apart that many of these bulbs can not develop in anyone temperature, if kept constant, or even with daily fluctuations.

Considering growth and development of the onion plant, although daylength seems to play a major role, as discussed before, temperature also is important. As the photoperiodic stimulus is received by the leaves, some foliage must be present in order that the plant may respond to daylength, but in any stage of its life, even as a dormant bulb, the onion may respond to temperature. WALKER (1921) working with 'Red globe' and 'Yellow Bermuda' onion varieties found that the optimum temperature for germination was 25 °C. Rapid growth of tops as compared with roots occurred at 20 °C or higher, while root growth was best at lower temperatures (12–20 °C). THOMPSON and SMITH (1938), with 'Ebenezer' onion plants, grown under long days and at three different temperatures, found that the plants under different temperatures did not react in the same way. Plants at 50–60 °F did not bulb; those at 60–70 °F, developed mature bulbs with still green tops; those at 70–80 °F had mature bulbs and the tops were dead. High temperature under short days, however, was not effective in causing bulbing, indicating that bulbing is determined by the interaction of long day and high temperature. For seed production from large bulbs, extremely high or low storage temperatures delay or inhibit flower formation, while temperatures ranging from 4.5 to 14°C, with an optimum at about 11 to 12°C, are best for storage of the mother bulbs (JONES and EMSWELLER, 1939; HARTSEMA, 1953; ATKIN and DAVIS, 1954). Concerning the temperature effects on sprouting, ABDALLA (1962) stored mature bulbs of the 'Excell' cultivar at three different temperatures, namely 0, 15, and 30°C. By periodic dissections of bulbs he established that at 15°C a leaf was initiated about once every two weeks, while at 0 and 30°C leaf initiation took place at about half the rate observed at 15°C. The root systems, developed on bulbs that had previously been stored at 15°C were much heavier than those on bulbs stored at lower or higher temperatures.

As for the production of bulbs from onion sets (the onion set is simply a very small blub, the bulk of which is formed from scales (bladeless leaves), the results of many workers (BLAAUW et al., *1941*; HEATH, *1943* and HARTSEMA, 1947) have clearly shown that when onion sets are stored at high temperatures, viz., 28°C or above, or very low ones, e.g., zero °C or less, the percentage of bolters in the field may be prevented or greatly reduced; on the other hand relatively low temperature (round 12°C) stimulates bolting, thus spoiling the crop from the economical point of view. Furthermore, the onion plants in the field, whether produced from seeds or from sets, will fail to develop bulbs if the temperature does not exceed a certain minimum (THOMPSON and SMITH 1938).

CHAPTER III

MATERIALS AND METHODS

A local cultivar of the ordinary large onion *Allium cepa L.* (Common onion Group) Rijnsburger type cv. Wijbo was chosen for this study. Experiments were made outdoors in the experimental garden and indoors in the phytotron of the Plant Physiological Research Laboratory of the Agricultural University.

A. ABBREVIATIONS AND SYMBOLS

For simplicity, these abbreviations are used throughout the paper.

CL	continuous light
Incand.	incandescent light
TL	fluorescent light
TL × Incand.	a mixture of fluorescent and incandescent light
SD	short day treatment
LD Incand.	long day treatment with incandescent as a supplementary light
LD TL	long day treatment with fluorescent as a supplementary light
R	red light
FR	far-red light
L/W	leaf length/width ratio
LAR	leaf area ratio
LWR	leaf weight ratio
LAI	leaf area index
LAD	leaf area duration
NAR	net assimilation rate
SLA	specific leaf area

B. FIELD EXPERIMENTS

1. *Shading experiments*

In order to investigate the shading effect on the growth and development of the onion, four treatments were applied during the growing seasons of 1964 and 1965, viz., 100 percent (full daylight), 75, 37, and 12 percent of natural day light. To reduce daylight intensity to the desired values, cages of metal gauze screens of different density as designed in this laboratory and described earlier (cf. KAMEL) were placed on the appropriate plot. Each unit covered about 2 × 2m. Two rows were planted outside the screens or fields (the latter in case of 100% light). The cages were put on after an initial period, sufficient to secure full emergence and uniformity between the plants.

2. *Daylength experiments*

The growth cabinets described by WASSINK et al. (1953) were used for this purpose. In the growing season of 1964, the following treatments were applied:

a. A short-day treatment (SD), in which the plants received eight hours of natural daylight only.

b. A long-day treatment (TL), in which the plants received eight hours of natural daylight + 8 hours from daylight type fluorescent tubes (Philips, 55) giving a low intensity of about 700 ergs/cm²/sec (LD TL).

In the growing season of 1965, a third treatment was carried out in addition to the mentioned treatments of 1964, viz.,

c. A long-day treatment in which the plants received eight hours of natural daylight + 8 hours of incandescent light of about 750 ergs/cm²/sec intensity in the visible region of the spectrum (LD Incand.). Furthermore, as there were no signs of bulb development after a growth period of 140 days from the date of sowing, both long day treatments (items b and c) were divided into two parts by a vertical black screen in the middle of each plot. One part of each was maintained at the same light intensity, while in the other part the light intensities of the supplementary light were raised to about 3000 egrs/cm²/sec for the fluorescent light treatment and to about 8000 ergs/cm²/sec for the incandescent light one.

3. *General preparations*

Sandy soil only was available for the experiments. The field was prepared for planting and plots of 2 × 2m laid out. In the shading and daylength experiments, the distances between plants were 12 × 12cm, giving an area of 144 cm²/plant as in usual planting, though the arrangement of the plants differs, being equidistant in this case. Sowing took place in the first two weeks of April. To secure good emergence, uniformity and regularity, about five seeds per locus were planted by hand. After an initial period of about 5 weeks from sowing, the onion plants were thinned, and one plant per locus left. The plots were fertilized with 100 grams of compound artificial fertilizer 12: 10: 18 (NPK) once every month during the growing season. The plants were watered when necessary. Periodic harvests were taken during the entire life cycle of the plants; five to ten plants were chosen randomly at each harvest. On sampling days a representative plant of each treatment was photographed.

C. PHYTOTRON EXPERIMENTS

1. *Light intensity series*

Philips TL MF 120 W/33 Rs tubes have been used as a source of light in the phytotron. The spectral composition of this light is illustrated in fig. 1.

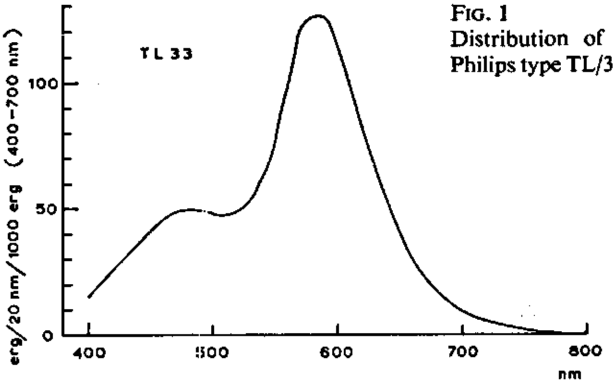


Fig. 1
Distribution of energy of fluorescent tube. Philips type TL/33.

In order to study the light intensity effect, four treatments, namely 93000, 68500, 31200 and 9700 ergs/cm²/sec were applied. In order to ensure sufficient vegetative growth, plants were grown under short day conditions (12 hrs. photoperiod) from July 5th, 1965, the date of transplanting, until the first of October when incandescent light was admixed to the fluorescent light and the daylength extended to 16 hrs. From that time up to the end of the experiment, the light intensities were as follow:

a. 85000 ergs/cm²/sec fluorescent light + 8700 ergs/cm²/sec incandescent light, in the visible region amounting to 93700 ergs/cm²/sec.
b. 68500 ergs/cm²/sec fluorescent light + 4750 ergs/cm²/sec of incandescent light, amounting to 73250 ergs/cm²/sec.
c. 31200 ergs/cm²/sec fluorescent light + 1500 ergs/cm²/sec of incandescent light amounting to 32700 ergs/cm²/sec.
d. 9700 ergs/cm²/sec fluorescent light + 300 ergs/cm²/sec of incandescent light, amounting to 10000 ergs/cm²/sec.

Temperature was maintained at 20 °C and relative humidity at 70%.

2. *Light quality*

Plants of 12 weeks old, grown in pots under short day condition (12 hrs.) and constant light intensity and temperature were divided into groups and exposed to the following treatments:

a. A 24 hrs. light period (continuous) supplied by TL 120 W/33 (56000 ergs/cm²/sec), at 15 °C.
b. A 24 hrs. light period consisting of a mixture of fluorescent light (55000 ergs/cm²/sec) and 1000 ergs/cm²/sec of incandescent light, at 15 °C.
c. Treatments no. 1 and 2 carried out at 25 °C.
d. A 12 hrs. daily period of fluorescent light only (70000 ergs/cm²/sec) + 12 hrs. of supplementary red light (5000 ergs/cm²/sec), at 20 °C.
e. A 12 hrs. daily period of fluorescent light only (70000 ergs/cm²/sec) + 12 hrs. of supplementary far-red light (5000 ergs/cm²/sec), at 20 °C.

Owing to the limited number of plants available in these experiments, no periodic harvests were taken but the plants were periodically photographed.

3. *Temperature experiments*

Plants were grown under five different temperatures, viz., 10, 15, 20, 25, and 30°C. From July 27th until the first of October, fluorescent light (TL 120W/33) was the only source of light for a duration of 12 hrs. (short day). Then (1st of October) incandescent light of about 8700 ergs/cm^2/sec was admixed to the fluorescent light and the photoperiod extended to 15.5 hrs. for all treatments till the end of the experiment.

4. *Daylength experiments*

The light regimes applied are represented in the following diagram:

Main photoperiod (12 hrs. fluorescent light, 62000 ergs/cm^2/sec)
- + 4 hrs. incand. light at intensities of
  - 720 ergs/cm^2/sec.
  - 3200 ergs/cm^2/sec.
  - 4750 ergs/cm^2/sec.
  - 8700 ergs/cm^2/sec.
    - 8700 ergs/cm^2/sec.
    - 11250 ergs/cm^2/sec.
- + 8 hrs. incand. light at intensities of
  - 720 ergs/cm^2/sec.
  - 3200 ergs/cm^2/sec
  - 4750 ergs/cm^2/sec.
  - 8700 ergs/cm^2/sec.

All treatments received 12 hrs. as a main photoperiod of high intensity (62000 ergs/cm^2/sec) from TL 120W/33 Rs. The main photoperiod was extended by four or eight hrs. of supplementary incandescent light of different intensities ranging from 720 to 8700 ergs/cm^2/sec. Two months after the start of the experiments, the high intensity treatment of supplementary light (4 hrs.) was divided into two parts, one of which continued at the same light intensity (8700 ergs/cm^2/sec) while the other was exposed to a still higher intensity (11250 ergs/cm^2/sec). As there was no indication of bulb development in all treatments receiving 4 hrs. extension, regardless of the intensities applied, even after a 175 days growth period, each of these treatments was divided into two parts, one of which was maintained at 4 hrs. extension, whereas the second part received 6 hrs. of supplementary light. Temperature in all cases was 25°C.

5. *Photoperiodism in relation to plant age and size*

Plants were grown under short day (SD) conditions (12 hrs.) at mixture of 62000 and 5700 ergs/cm^2/sec of fluorescent and incandescent light respectively. When 45 days old, a group of plants was shifted to LD (16 hrs.) condition of the same light mixture. Four weeks later another group of plants (74 days old) was treated in the same way. This has been continued so as to obtain a series of different plant ages ranging from 45 days up to 189 days growing under SD condition and exposed thereafter to long days as shown in the following diagram. Furthermore, a group of plants was kept under SD conditions continuously, to serve as a control, while another set of plants was grown from the date of sowing until maturity under LD conditions. In this way we had a range of plant ages from 0–189 days, to be exposed to the stimulus of long days.

The following treatments were applied:

Treatments	Age of plants in days as grown under SD (12 hrs.) at a mixture of fluorescent and incandescent light.	Growth period at LD (16 hrs.) at a mixture of 62000 + 8700 ergs/cm^2/sec fluorescent and incandescent light respectively until the end of the life cycle
1	45	from the 45th day onward.
2	74	„ „ 74th „ „
3	101	„ „ 101st „ „
4	130	„ „ 130th „ „
5	158	„ „ 158th „ „
6	189	„ „ 189th „ „
7	the entire growth period	– – – – –
8	–	the entire growth period

6. *General preparations*

In all the phytotron experiments (except those on light quality) plants were grown in a fertile soil in wooden boxes of 60 × 40 × 20 cm. Each treatment consisted of two boxes close together on a movable truck. The inter- and intra-row spacing was 10 cm, resulting in 100 cm^2 per plant. In this way, 48 plants were available in each treatment. The plants were fertilized monthly by 5 grams of artificial fertilizer 12:10:18 (NPK) for each box. Water was supplied daily in adequate amounts.

Periodic harvests were taken during the whole life cycle of the plants. Five to eight plants from a closed area were chosen randomly at each harvest.

D. GENERAL OBSERVATIONS AND MEASUREMENTS

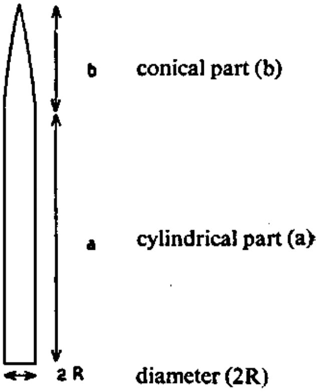
At the time of harvest, the plants under investigation were carefully dug up, and washed to remove the soil particles. The following observations and determinations have been made:

1. Number of (tubular) blades per plant.
2. Leaf dimensions, length of the cylindrical and conical parts, diameter recorded for every well developed blade.

Then the blade area (A) was computed from the formula:

$$A = \pi R\,(2a + b)$$

in which R = half diameter, a = length of the cyclindrical part, b = length of the conical part.



When the area, calculated in this way, was compared with that obtained by the planimeter (the leaf slit open at one side and pressed flat), no more than 5% difference was observed.

It could be questioned whether our calculation procedure really is the most correct one, since, especially in later stages, the tubular leaves are appearing somewhat more flat, but, in general, it seems most indicated in a case like this to consider the total outer surface on the leaf, as has been done here.

Moreover, it does not seem necessary to advocate especially any possible procedure as it is clearly defined what has been done.

3. Thickness of blades, determined by the dial micrometer.
4. Neck (pseudostem) length and diameter.
5. Bulb length and diameter, and bulbing ratio (the relation between the maximum diameter at the base and the minimum diameter of the neck).
6. Fresh and dry weight, recorded separately for roots, blade, neck and bulb.

Drying was carried out for 48 hours at 70°C, followed by 15 minutes at 105°C, in an electric oven with ventilation. Then the dried material was finely ground and preserved in tightly corked tubes for carbohydrate determinations.

1. *Calculations of various growth correlations and indices*

The dry weight percentage of roots, blades, necks, and bulbs. Top/root ratio on dry weight basis (dry weight of blades + neck + bulb/dry weight of roots), leaf length/width ratio (leaf length/leaf diameter), leaf area ratio (total green blades area per plant/entire plant dry weight), leaf weight ratio (blade dry weight/entire plant dry weight), top/bulb ratio, and daily growth rate.

2. *Chlorophyll determination*

Two grams of freshly gathered blades cut into small pieces were extracted with 70% ethanol (10 ml) in thick walled pyrex tubes immersed in a water bath maintained at 70°C. The extracts were transferred into volumetric flasks chilled in ice and covered with a black cloth. To ensure complete recovery of chlorophyll, repeated extracts were made. Thereafter, ethanol was added to make up to a fixed volume. Chlorophyll was estimated comparatively in the various treatments by measuring the extinction values of extracts in the colorimeter at 665 mμ.

3. *Carbohydrate determinations*

A constant weight (250 mg) of the dried material was used for sugar extraction in 25 ml 80% ethanol. To ensure complete recovery of sugars, two successive extracts were made; the extracts were centrifuged, filtered, combined and then made up to 50 ml by ethanol 80%. The extracts were divided into two parts, one of which was treated with 300 mg active charcoal (trade mark 'Norit') for clarification and removal of glycosides. The charcoal has proven to be effective in this respect without any adsorption of the sugars present in the extracts. Total sugar concentration was determined by the anthrone reagent procedure. The green colour produced when carbohydrates are heated with anthrone in acid solution was first used as a qualitative test by DREYWOOD (1946). The quantitative estimation of carbohydrates has originally been developed by TREVELYON and HARRISON (1952), and modified by YEMM and WILLS (1954). VERHOEKS (1965) detected that ethanol has some influence on the colour development during the reaction. Therefore, this author pointed out that, when dilution of the original sugar extracts is desired, this should be achieved with 80% ethanol, and calibration curves should be made with sugar solutions in 80% ethanol. In the course of our determinations, this has been taken into consideration. Application of paper chromatography indicated the presence of fructose, glucose and sucrose; no other sugars could be detected.

CHAPTER IV

LIGHT INTENSITY EFFECTS (FIELD CONDITIONS), RESULTS AND DISCUSSION

A. GROWTH IN WEIGHT

1. *Fresh weight per plant*

Under the conditions of the experiment, as shown graphically in fig. 2a, the fresh weight of the entire onion plant increased with increasing light intensity. The differences between treatments became pronounced as the plants advanced in age and were maximal at the end of the growing season.

At all light intensities applied, plants increased only slowly in weight between the first and second harvest, after which a marked increase was observed till the plants were 105 days old. At more advanced age, the fresh weight increased sharply, and the more so under higher light intensities. This big rise in fresh

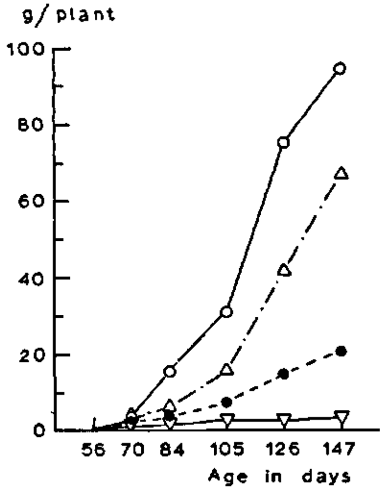


FIG. 2a
The effect of light intensity on the fresh weight of the whole plant.
Field experiment 1964.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

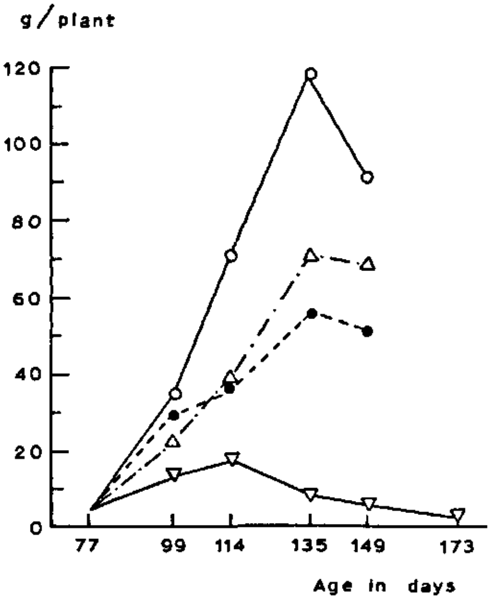


FIG. 2b
The effect of light intensity on the fresh weight of the whole plant.
Field experiment 1965.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

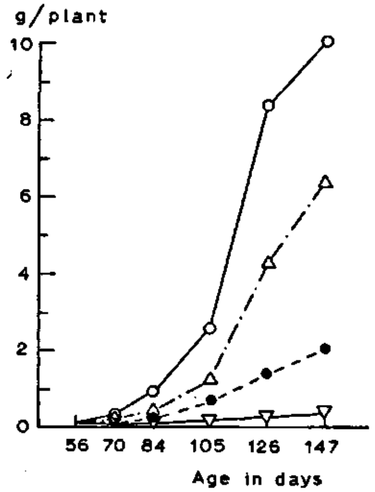


FIG. 3a
The effect of light intensity on the dry weight of the whole plant.
Field experiment 1964.
○———○ : Full light.
△—·—△ : 75 per cent.
●----● : 37 per cent.
▽———▽ : 12 per cent.

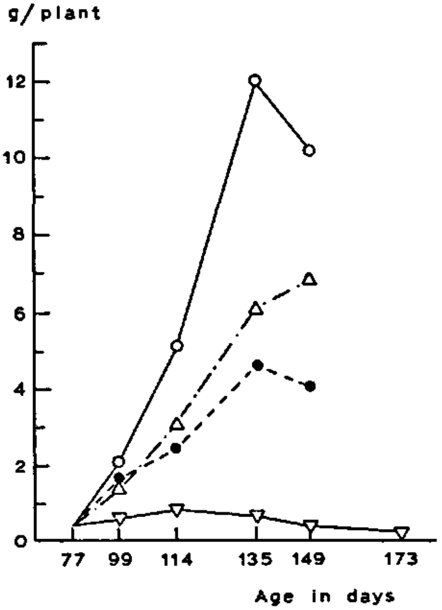


FIG. 3b
The effect of light intensity on the dry weight of the whole plant.
Field experiment 1965.
○———○ : Full light.
△—·—△ : 75 per cent.
●----● : 37 per cent.
▽———▽ : 12 per cent.

weight is connected with rapid bulb bulking which serves as an intense sink for photosynthates accumulation.

Light intensity influences photosynthesis. The latter increases with each increase in the former till an optimum (light saturation) is reached. Under field conditions this light saturation is unlikely to occur in the onion fields so long as water and CO_2 are in liberal supply; moreover, the upper blades cast shadow on the lower ones. Thus, the higher fresh weight per plant found with increasing irradiance could be expected. At the lowest light intensity, presumably, owing to the higher ratio of respiration to photosynthesis, the gain in fresh weight was less marked so that the curve seemed flattened.

Similar results were obtained in 1965 with only few exceptions (fig. 2b). In all treatments, the fresh weight per plant after reaching its maximum tended to decrease especially at the highest light intensity because of earlier onset of senescence induced by high radiation. The differences between the two years may lie in the fact that shading in 1965 was applied at a more advanced stage of development (after 77 compared with 56 days in 1964) so that plants in 1965 received the total energy of sunlight for a longer period which, in turn, speeded up their maturation.

2. *Dry weight per plant*

Fig. 3a shows that the gain in dry weight as a function of light intensity and developmental stage in 1964 followed closely that of the fresh weight. This also holds true for the 1965 experiment with only one exception (fig. 3b). At 75% daylight dry weight, in contrast to fresh weight, continued to increase until a peak was found at the end of the season. This may arise from the fact that the fresh weight by that time consisted mainly of bulbs which yielded higher dry weight values compared with the preceding harvest containing a larger fraction of leaves.

The slightly larger dry weight of the 37% treatment as compared with the 75% one observed in the second harvest is due to a somewhat more vigorous growth in the former than in the latter prior to screening. This also may account for the less marked difference in maximal dry weight between these two treatments in 1965 in comparison with those in 1964.

Since the onion plant consists of different organs, viz., roots, blades, neck and bulb, it is interesting to follow the changes that may occur in these parts as a result of light intensity and age.

3. *Dry weight of roots*

Data illustrated in fig. 4 indicate that root dry weight was greatly depressed with decreasing light energy. Roots themselves do not produce sugars, but depend for this material on the tops, and since in the latter the cabohydrate production was reduced as a consequence of shading, therefore, it is not surprising that root dry weight diminished with the reduction of light intensity. It may also be assumed that the sugar transport through tubes is the limiting process in the dry matter production of roots. In plants grown in strong light more sieve tubes may develop and the sugar transport capacity of each sieve tube may be larger (this should of course be checked by anatomical studies); this accompanied with increased photosynthetic activity at higher

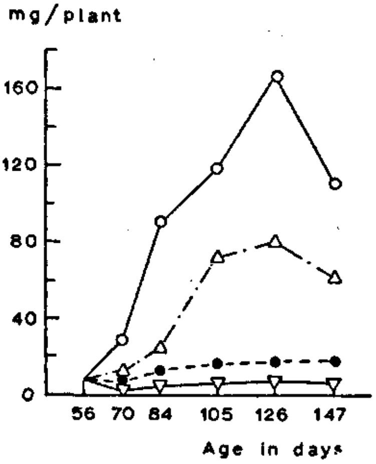


FIG. 4
The effect of light intensity on root dry weight. Field experiment 1964.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

light intensity, so that more sugar becomes available for transport to the roots may account for the rise in dry weight gain of roots observed with increasing light intensity.

4. *Dry weight of blades*

The influence of light intensity on the dry weight of blades is given in fig. 5a. It can be seen that the higher the light intensity, the higher the dry weight of the blades was. This increase is due to the greater leaf number as well as to greater specific leaf weight for plants grown at higher light intensities. In the early stages of growth, the injurious effect of shading was not yet harmful so that differences in dry weight were less pronounced. At more advanced age differences became more marked till a maximum was attained 126 days after sowing. In all treatments, blade dry weight increased with age and the more so under higher light intensity, due to increased leaf number and size as plants proceeded towards maturity. After 126 days, because of the reduced rate of leaf emergence caused by bulb development, leaf dry weight tended to decrease at 100% light intensity owing to early maturity, and also at 37% and 12% possibly because of increased rate of blade senescence induced by heavy shading, whereas at 75% treatment, dry weight remained more or less at the same level, in relation to the extension of the growth period, owing to shading to this limit.

Similar results were obtained in 1965 with only few exceptions. The dry weight

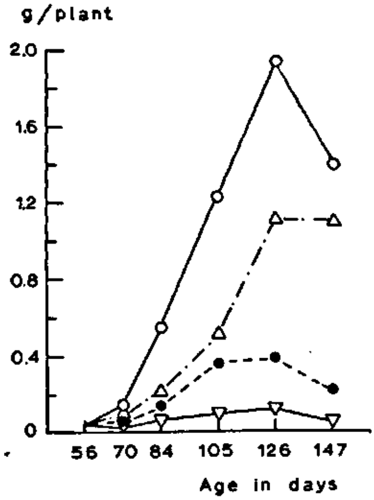


FIG. 5a
The effect of light intensity on dry weight of green leaf blades.
Field experiment 1964.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

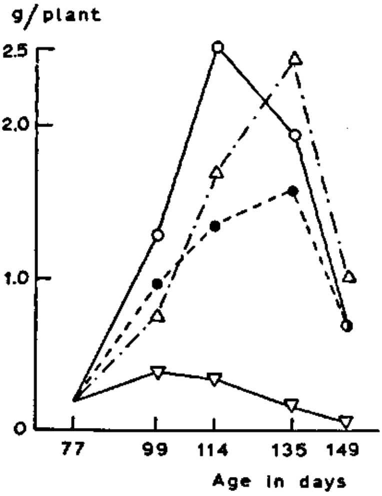


FIG. 5b
The effect of light intensity on dry weight of green leaf blades.
Field experiment 1965.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

of blades in 37% light intensity, found at the second harvest, surpassed that in the 75% treatment, owing to the fact that plants in the latter plot showed a relatively less vigorous growth prior to screening than those in the former (fig. 5b). Furthermore, the maximum dry weight was reached at a moment which differed according to treatment, being three weeks later in the 75% and 37% plots than that at full daylight. This may be attributed to the extension of vegetative growth period induced by medium light intensities. In the 12% treatment, maximum dry weight was attained at the second harvest (99 days from sowing) after which there was a progressive decrease, presumably because of increased death rate of emerged blades and owing to limitted leaf production as a result of severe shading.

5. *Dry weight of neck (pseudostem)*

It is apparent from fig. 6a that also the dry weight of the neck increased with increasing light intensity. This increase is mainly a result of the greater number of leaf sheaths and possibly of their greater thickness produced in strong light.

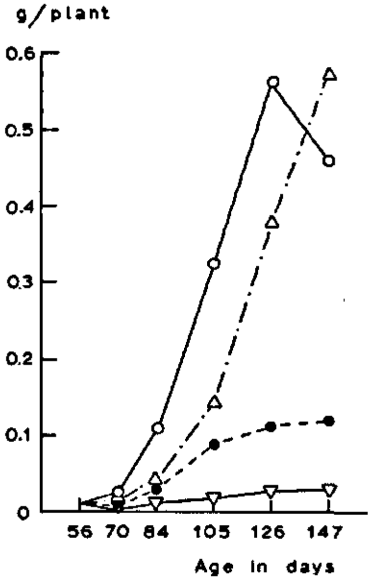


FIG. 6a
The effect of light intensity on dry weight of the neck.
Field experiment 1964.
○———○: Full light.
△—·—△: 75 per cent.
●----● : 37 per cent.
▽———▽ : 12 per cent.

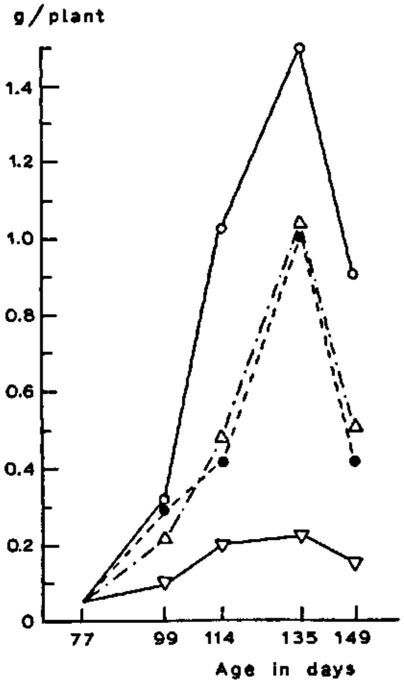


FIG. 6b
The effect of light intensity on dry weight of the neck.
Field experiment 1965.
○———○: Full light.
△—·—△: 75 per cent.
●----● : 37 per cent.
▽———▽ : 12 per cent.

At all light intensities, the neck dry weight increased as plants advanced in age and the more so in as much as the light intensity was higher, until a peak was reached at 100% light intensity after 126 days from sowing; thereafter it tended to decrease owing to the depression of new leaf emergence from within the older leaf sheaths, because of early maturity, while in the shaded plots the neck dry weight continued to increase up to the end of the growing season. The rise in dry weight of the neck observed with time may be a consequence of increased number and thickness of leaf sheaths found as plants proceeded in age.

In the 1965 experiment (fig. 6b), owing to the fact that screening started at a more advanced age (77 days compared with 56 days in 1964) so that plants in 1965 received total day light energy for an extended period, dry weight of the neck at all light intensities reached its peak after 135 days and then decreased, indicating earlier maturity in 1965 in comparison with 1964.

6. *Dry weight of bulb*

The dry weight of the bulb at different stages of growth as a function of light intensity is illustrated in fig. 7a. It should be noticed that in the early stages of growth (up to 84 days after sowing), there was no bulb development in its proper meaning, but merely a slight swelling of the neck base which can occur even at exposure to short photoperiods.

The onion bulb is a storage organ, it can make none of its stored material but depends on the other plant organs for this supply. As the other plant parts

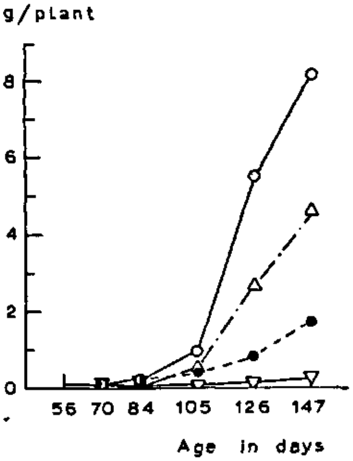


FIG. 7a
The effect of light intensity on the dry weight of the bulb.
Field experiment 1964.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

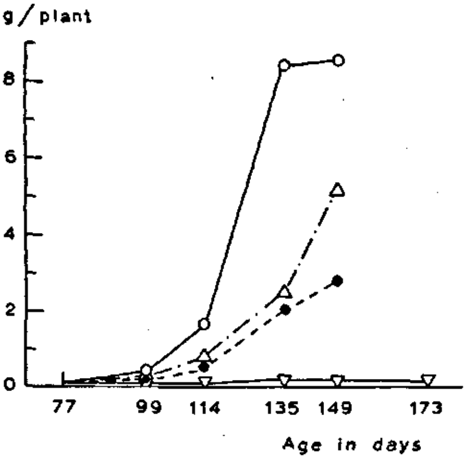


FIG. 7b
The effect of light intensity on the dry weight of the bulb.
Field experiment 1965.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

were influenced by light intensity, one may expect that this will be reflected on dry weight of the bulb. Indeed, it could be observed that increasing light intensity caused a marked increase in the bulb dry weight. Differences became more pronounced with progress towards maturity. The maximum dry weight was found to be 8.18, 4.65, 1.70 and 0.30 g for 100, 75, 37 and 12% respectively.

What was found in 1964 is compatible with that in 1965 (fig. 7b). The only difference is that in the full daylight plot, maximum dry weight of the bulb reached its peak after 135 days from sowing, and thereafter only a slight increase was observed at the end of the growing season, indicating that plants reached maturity earlier than in 1964.

7. *Daily growth rate*

The gain in dry matter in mg/plant per day in relation to light intensity at different developmental stages is presented in fig. 8a. In general, increasing irradiance resulted in an increase in daily growth rate. This increase may be attributed to the higher photosynthetic capacity and/or to its efficiency under

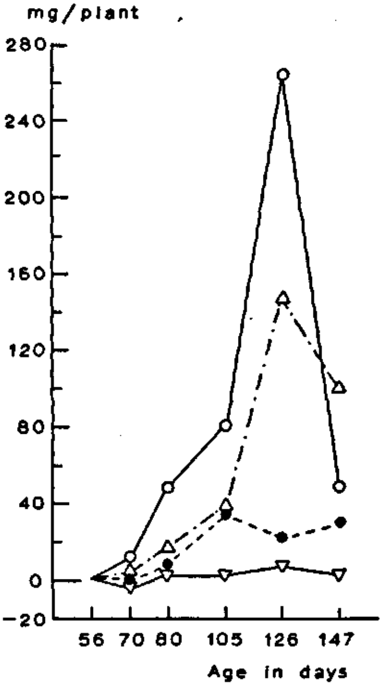


FIG. 8a
The effect of light intensity on daily growth rate (dry matter increase in mg/plant/day).
Field experiment 1964.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

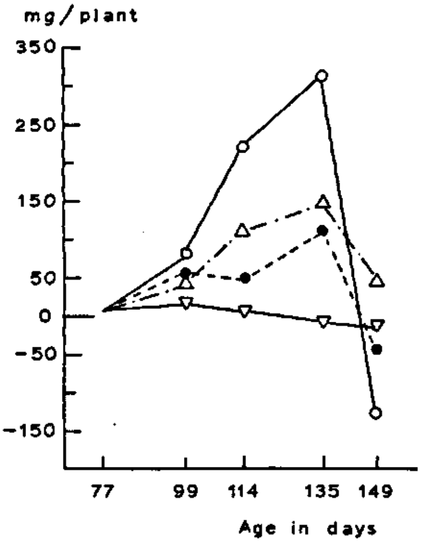


FIG. 8b
The effect of light intensity on daily growth rate (dry matter increase in mg/plant/day).
Field experiment 1965.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

conditions of increased intensity of radiation. In full daylight, and in the 75% and 37% treatments, the daily growth rate increased steadily with age up to the fourth harvest (105 days after sowing), then a sharp increase was observed at the two higher light intensities, while at 37% it came to a standstill.

This rapid rate of dry matter gain per plant per day in the interval between 105 and 126 days was associated with rapid bulb bulking (increased intensity of sinks) which may in turn have speeded up the photosynthetic rate of the leaves. There is evidence that the rate of photosynthesis is appreciably influenced by the capacity of sinks in the plant (MOSS, 1961). For example, it has been found that removal of potato tubers which serve as sinks for photosynthates slowed down the photosynthesis of leaves (NÖSBERGER and HUMPHRIES, 1965). In 37% and 12% it seems that the marked rise in photosynthesis as a result of sinks was masked by the effect of reduced light intensity on the photosynthetic activity. During the period from 126 to 147 days, the daily growth rate was found to decline more steeply in full daylight owing to earlier maturity and less so in the 75% treatment. At the lowest light intensity changes in gain in dry weight per day in relation to time were flattened. The maximum daily growth rate varied from 262 to 7 mg/plant/day observed at the highest and lowest light intensity respectively.

More or less the same trend was observed in 1965 (fig. 8b).

8. *Average daily growth rate over the entire season as a function of light intensity*

Plotting the average daily growth rate per plant over the entire season versus relative light intensity, a fairly exponential and linear curves were obtained

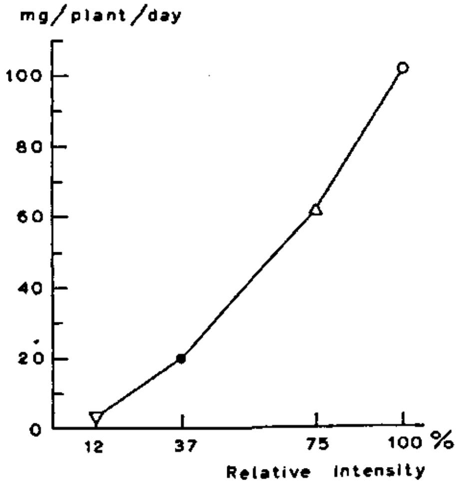


FIG. 9a
The mean daily growth rate over the entire season in relation to light intensity.
Field experiment 1964.

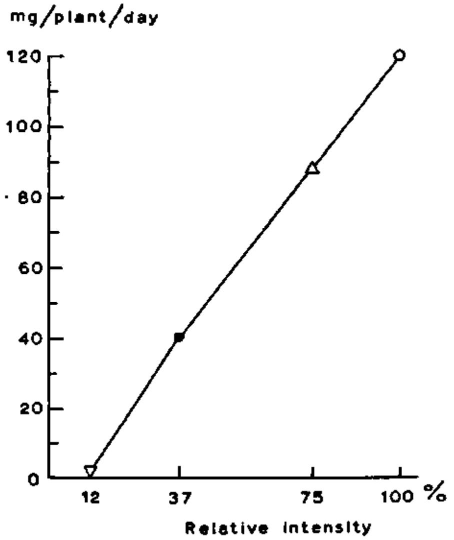


FIG. 9b
The mean daily growth rate over the entire season in relation to light intensity.
Field experiment 1965.

for 1964 and 1965 respectively (fig. 9a, b). This indicates that the amount of photosynthesis for an entire onion plant increases progressively with increasing light intensity up to full sunlight.

9. *Net assimilation rate in relation to light intensity*

Still of interest is the question whether the increase in the daily growth rate with increasing light intensity is only due to increase in the photosynthetic capacity (total green leaf area) or whether the photosynthetic efficiency (rate of dry matter increase per unit leaf area per unit time) is also involved. In other words, is the increase in light intensity up to full daylight still profitable per unit leaf area present. Fig. 10a shows the average NAR over 126 days growth period in g/m² week as a function of relative light intensity. It can be perceived that the NAR increased linearly with increasing light intensity up to full daylight. This is undoubtedly connected with the fact that many of the lower leaves were shaded by the upper ones. Even in full sunlight, therefore, many of the leaves do not photosynthesize at their maximum capacity. The linear curve of NAR versus light intensity seems to demonstrate that with increasing the intensity of light up to 100% of full daylight (over long periods) practically no increase in actual light saturation takes place so that NAR is practically proportional to incident light intensity, to which, the effective incident light intensity within the whole plant, again is proportional.

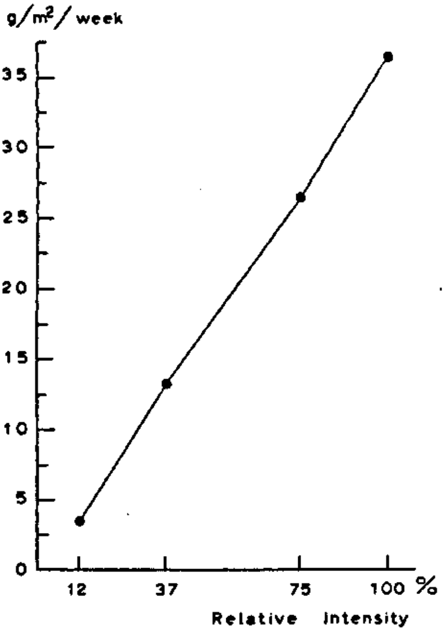


FIG. 10a
The effect of light intensity on mean NAR over the period 56–126 days from sowing. Field experiment 1964.

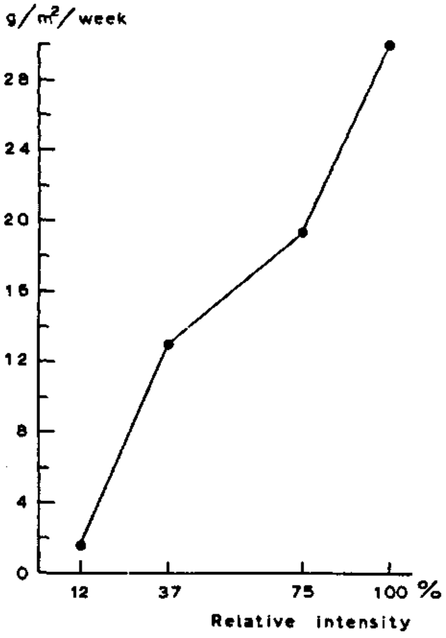


FIG. 10b
The mean NAR over the period 77–135 days from sowing in relation to light intensity. Field experiment 1965.

More or less the same trend was obtained in 1965 (fig. 10b). It suggests something very nice and simple, but probably, in detail, it may be difficult to understand. We have looked into some details connected with the NAR, which is elaborated in chapter VI.

10. *Leaf area ratio (LAR)*

This growth function expresses the relationship between leaf area and dry weight of the entire plant at each harvest. As shown in fig. 11a, the LAR increased with decreasing light intensity. As calculations show, this increase is due to increased leaf weight ratio (dry weight of leaves/entire plant dry weight) as well as to the greater specific leaf area (total leaf area/total leaf weight) under conditions of low irradiance. This seems 'reasonable' for a sun plant like the onion if it will successfully adapt itself to the imposed low light intensity in order to compensate – at least to a certain degree – for the decline in its photosynthetic efficiency (rate of dry matter increase per unit of surface area of leaves) as a result of shading.

At all light intensities, with the exceptional rise observed at the second harvest

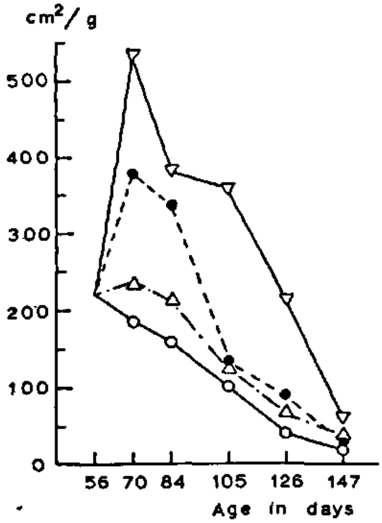


FIG. 11a
The effect of light intensity on leaf area ratio (total green leaf area/ entire plant dry weight).
Field experiment 1964.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

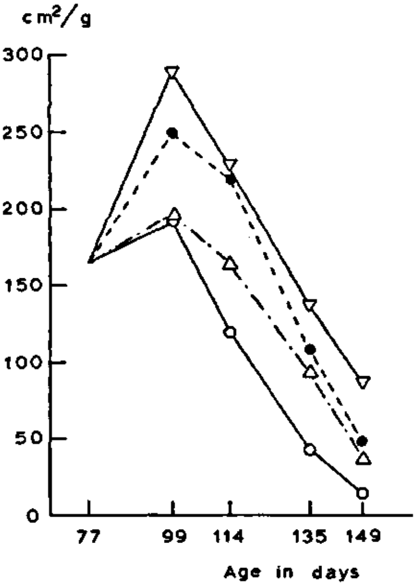


FIG. 11b
The effect of light intensity on leaf area ratio.
Field experiment 1965.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

in the 75, 37 and 12% treatments, the leaf area ratio decreased with age. This may be explained by the fact that as plant proceeded in growth, leaf area as well as entire plant dry weight increased, simultaneously a larger proportion of photosynthates was used in building up useful organs other than the leaves, as a result of which a decline in leaf area in proportion to total gain in dry weight was observed. Only after 126 days from sowing the absolute leaf area decreased.

A point of special interest is that the increase in LAR in the second harvest may be due to the fact that plants having received full daylight prior to placing the screens, have adapted themselves to the shading.

Similar results were obtained in 1965 (fig. 11b).

B. SOME MORPHOGENETIC FEATURES

1. *Root production*

It is apparent from fig. 12 that the number of roots per plant was positively correlated with light intensity. Roots supply the above ground parts with water and nutrient solutions, while they are dependent on the photosynthetic system for their sugar supply. It could be assumed that under conditions where photosynthesis is restricted, e.g., low light intensity, carbohydrates are preferentially used in aerial organs whereas the growth of sub-soil parts (roots), furthest from the source, is slowed down most, This explanation, however, seems very simple and it is more likely that dry matter distribution over the plant organs is governed by a formative mechanism which, however, may well be affected by the energy balance.

In full daylight, 75%, and 37%, root number increased with time till a maximum was reached 84 days after sowing after which it tended to decline, especially in the latest stages of growth. At a given time the number of roots found on an onion plant is a net yield of their rate of formation from the new tissue of the true stem and the rate of decay of old roots. In the early stages of growth, the plant is actively growing and enlarging its top, therefore, a greater

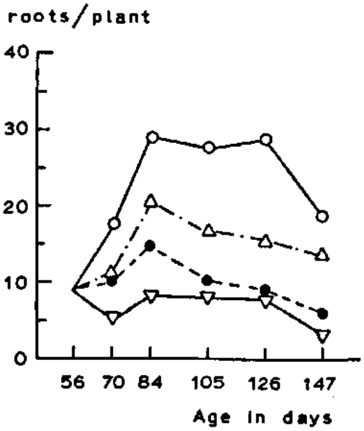


FIG. 12
The effect of light intensity on root number/plant. Field experiment 1964.
○——○: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽——▽ : 12 per cent.

number of roots should emerge if the enlarged top is to be adequately supplied with water and nutrients. At more advanced age, after bulb formation has begun, the emergence of new roots is depressed (inhibitory effect of bulbing, HEATH and HOLDSWORTH, 1948). This, along with a higher rate of old root destruction, may account for the decline in the number of roots observed at the end of the growing season. At the lowest light intensity no appreciable increase in root number was observed with time, possibly because under conditions of heavy shading root development is greatly reduced.

2. *Leaf production*

a. Leaf number per plant

The number of green blades found on the onion plant in relation to light intensity at different stages of growth is illustrated in fig. 13. It can be observed that, the higher the light intensity, the greater the number of blades was. The increase in green blade number as a result of increasing radiation presumably is due to the higher rate of leaf initiation and emergence under such conditions. FRIEND et al. (1962) found that increase in light intensity from 200 to 2500 ft.c. resulted in an increasing rate of leaf initiation and emergence in 'Marquis' wheat.

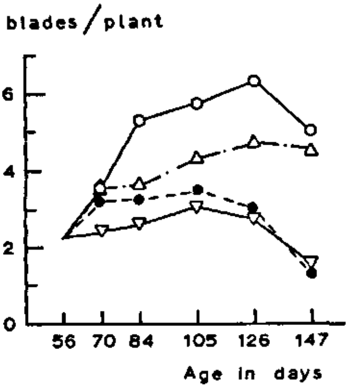


FIG. 13
The effect of light intensity on the mean number of blades per plant.
Field experiment 1964.
○———○ : Full light.
△— —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

The time trend of leaf number per plant shows an increase as plants advanced in age till a maximum was reached, after which it declined, except in the 75% plot, where no appreciable decrease was observed, probably because of the prolongation of the growing period, caused by shading to a certain limit.

b. Specific leaf weight (dry weight of leaves in mg/total surface area of leaves in cm^2)

Variations in specific leaf weight as influenced by light intensity at successive intervals is shown graphically in fig. 14a. It can be seen that reduction of light intensity caused a decrease in specific leaf weight. This may be ascribed to a decline in non-protein compounds and to the higher water content under conditions of low light intensity. Also, increased leaf expantion relative to leaf weight (specific leaf area) induced by low light intensity is a contributing factor in this respect. Similar results were obtained by WASSINK et al. (1956). They found a linear relationship between the specific leaf weight of *Acer pseudoplatanus* and the light intensity of exposure.

With the exception of the decrease observed between the first and second harvest, the specific leaf weight increased as plants advanced in age till a maximum was reached at the end of the season. This increase in dry weight per cm^2 of leaves may be mainly due to increased accumulation of carbohydrate and possibly to decreased water content of leaves as they proceeded towards maturity. The tendency of specific leaf weight to decrease in the first stages of growth may be attributed to the fact that plants, having received full daylight prior to placing the screens, were adapting themselves to the shading.

The same trend was found in 1965 (fig. 14b).

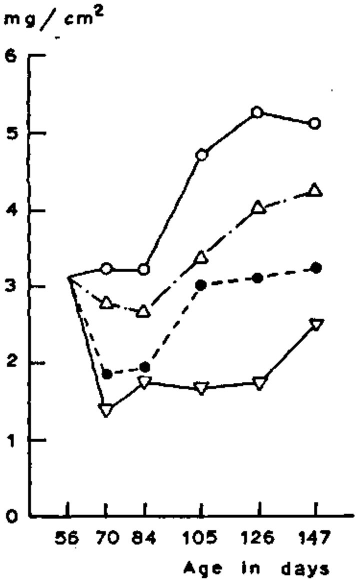


FIG. 14a
The effect of light intensity on specific leaf weight.
Field experiment 1964.
○———○: Full light.
△— · △: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

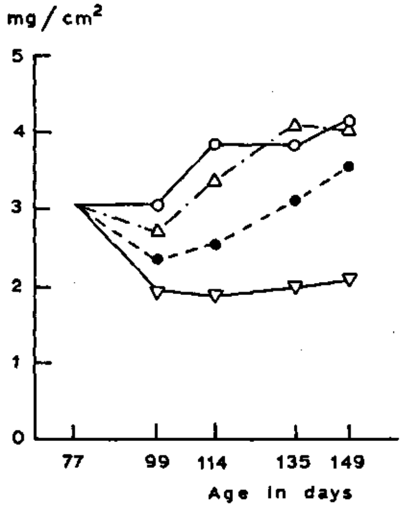


FIG. 14b
The effect of light intensity on specific leaf weight.
Field experiment 1965.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

c. Leaf growth

α Leaf length (average longest leaf). It is apparent from fig. 15a that, in general, leaf length at full daylight intensity tended to exceed that at other treatments. Between the first and the fourth harvest, the elongation effect induced by the reduction of light intensity down to 37% of natural light became more pronounced so that leaf length at this treatment surpassed that at 75%, but was not sufficient to reach that at 100%, while leaf length in the lowest light intensity was always lagging behind, presumably because light energy becoming more limiting under such conditions. At more advanced age, the position changed in favour of 75%, owing to the extension of the growth period caused by shading to this limit.

At all light intensities, leaf length increased progressively with time until a maximum was attained at the fifth harvest after which it tended to diminish. The fact that each successive leaf is longer than the preceding one while the plant is actively growing, may account for the increase in leaf length observed with time (till 126 days after sowing). At more advanced age this no more holds true, besidesdying off of leaf tip caused leaf length to decrease after its maximum.

In the 1965 experiment (fig. 15b), the reduction of light intensity to 37% of full daylight resulted in a marked increase in leaf length so that it surpassed that at all light intensities in all harvests. The reasons for that were not definitely clear, but perhaps may be a consequence of the relatively low light intensity prevailing in 1965 as compared with that of 1964. Also the developmental stage at which shading was applied may be involved. (Shading in 1965 started after 77 days, and after 56 days in 1964).

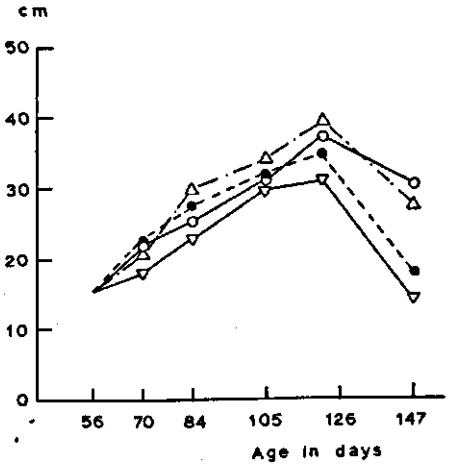


FIG. 15a
The effect of light intensity on leaf blade length.
Field experiment 1964.
O———O: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

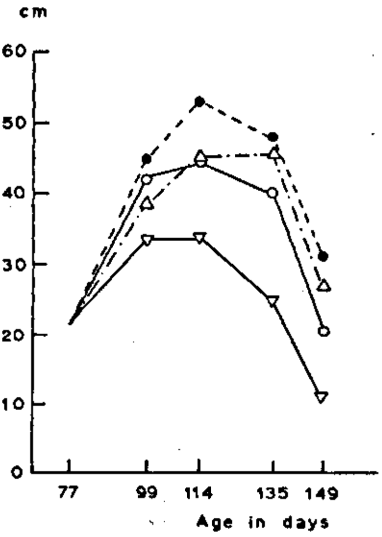


FIG. 15b
The effect of light intensity on leaf blade length.
Field experiment 1965.
O———O: Full light.
△—·—△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

β. **Leaf diameter.** Data presented in fig. 16a show that, in general, the higher the light intensity, the greater the leaf diameter was. With the only exception found at the second harvest in the lowest light intensity, the leaf diameter increased as the plants proceeded in growth till the highest values were reached after 126 days from sowing, thereafter it decreased in 100, 37, and 12%, while at 75% leaf diameter continued to increase up to the end of the season. This is another indication of the extension of the growth period induced by shading to a certain limit (75%).

With only few exceptions the same results were obtained in 1965 (fig. 16b).

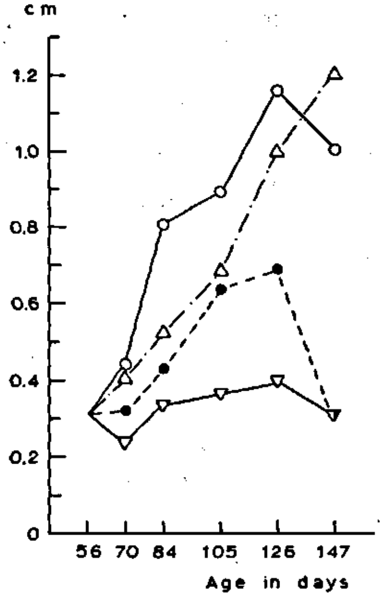


FIG. 16a
The effect of light intensity on leaf blade diameter (measured half way along the blade). The data are those of the largest leaf present on each plant at each sample.
Field experiment 1964.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

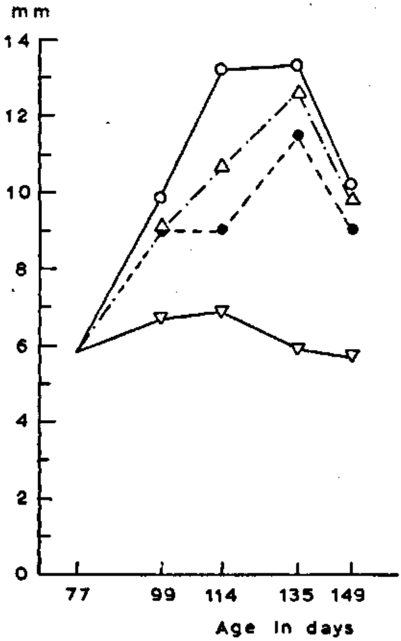


FIG. 16b
The effect of light intensity on leaf blade diameter (measured half way along the blade). The data are those for the largest leaf present on each plant at each sample.
Field experiment 1965.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

γ. **Leaf length/diameter ratio** (L/D). The morphogenetic changes in leaf shape as a function of light intensity is easily noticed when the leaf length: diameter relation is considered. It can be seen from fig. 17a that relatively long and narrow leaves were formed at lower light intensities, whereas the reverse was true at higher ones. With the exceptional rise observed at the second har-

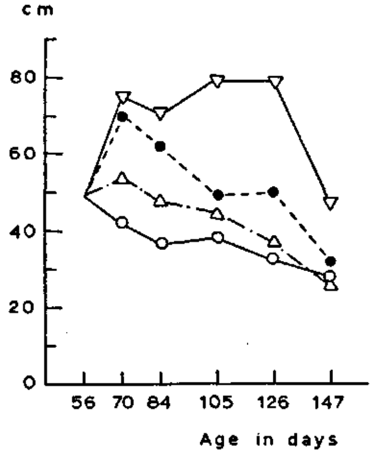


FIG. 17a
The effect of light intensity on leaf length/diameter ratio.
Field experiment 1964.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

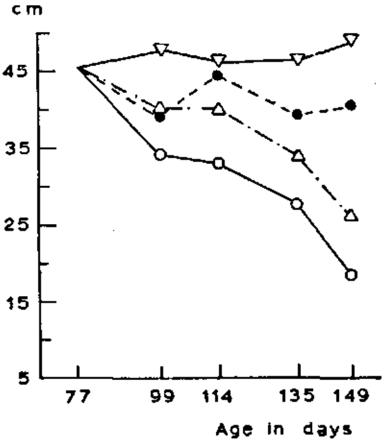


FIG. 17b
The effect of light intensity on leaf length/diameter ratio.
Field experiment 1965.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

vest, the length/diameter ratio decreased with age at 100, 75 and 37%, while with further reduction of light intensity it continued to increase until 126 days, and then decreased. The tendency of leaf length/diameter ratio to increase at first in the shaded plots may be a result of adaptation, after having grown in full daylight. In the lowest light intensity, it seems that light energy prevented any appreciable increase in leaf diameter along with the elongation effect induced by shading to this degree.

In 1965, more or less the same trend was obtained (fig. 17b). Why plants at 75% and 37% plots do not respond to shading by a marked increase in their relative length at the second harvest (after 99 days from sowing) like their analogues in the 1964 experiment, appears somewhat obscure. But it may be linked with the plant age at which shading was applied. In 1965, plants were shaded at relatively more advanced age, and it seems possible that the largest leaf (of which length and diameter values were recorded) still had matured in full daylight. WASSINK et al. (1956) demonstrated that the adaptability to light intensity can only occur during the growth period of the leaf; once the leaf is structurally mature, further adaptation will not occur.

δ. Total green leaf area. Fig. 18a indicates that the green leaf area per plant increased with increasing irradiance. This increase is mainly due to the greater leaf number and size (length × diameter) produced at higher light energy. In all treatments, there was a progressive increase, and the more so under higher light intensities, as plants proceeded in growth till maximum values were at-

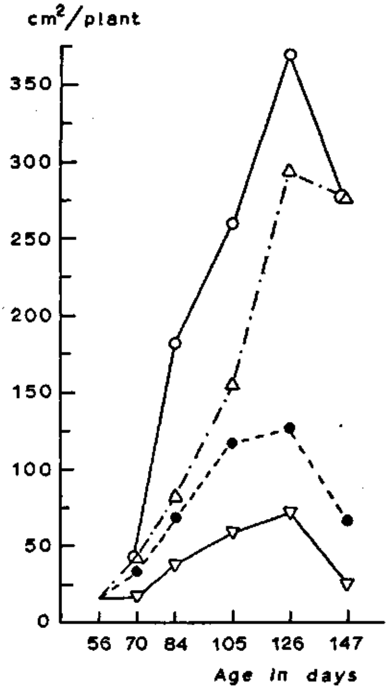


FIG. 18a
The effect of light intensity on green leaf blade area/plant.
Field experiment 1964.
○———○: Full light.
△— · —△: 75 per cent.
●- - - - -● : 37 per cent.
▽———▽ : 12 per cent.

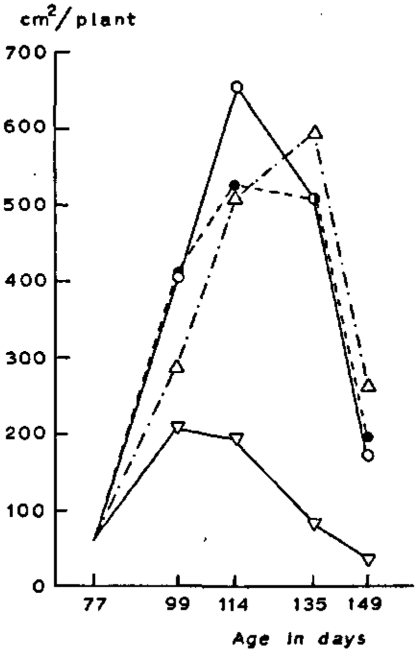


FIG. 18b
The effect of light intensity on green leaf blade area/plant.
Field experiment 1965.
○———○: Full light.
△— · —△: 75 per cent.
●- - - - -● : 37 cent per.
▽———▽ : 12 per cent.

tained 126 days after sowing. Owing to earlier senescence caused by high as well as low light intensities, leaf area at full daylight, 37% and 12% decreased more markedly in comparison with the 75% treatment. Increase in leaf area with time is a result of greater leaf number and size as the plant progresses in age.

In 1965 (fig. 18b), because the elongation effect was much more pronounced with the reduction of light intensity to 37% of full light, the leaf area under this condition was found to exceed that at 75% treatment between the first and second harvest. At more advanced age, the situation changed in favour of 75% as a result of the prolongation of the growth period induced by shading to this extent.

3. *Neck (pseudostem) growth*

a. Neck length

The reduction of light intensity to as low as 37% of natural light appeared to have no appreciable effect on the neck length so that in full daylight, and in the

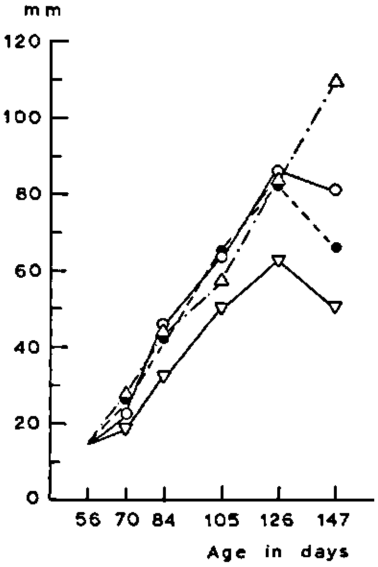


FIG. 19a
The effect of light intensity on neck length.
Field experiment 1964.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

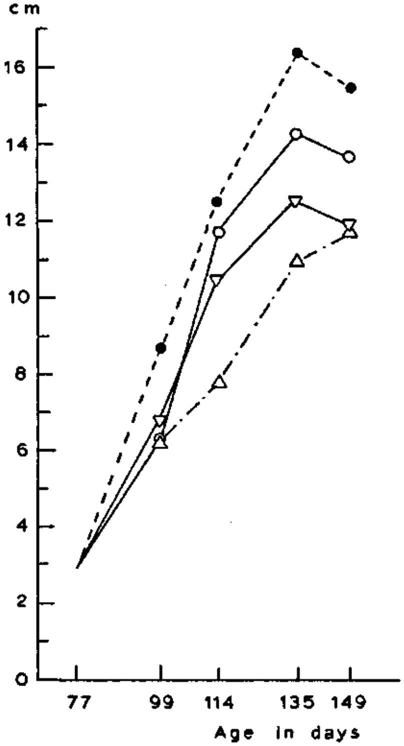


FIG. 19b
The effect of light intensity on neck length.
Field experiment 1965.
○———○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

75% and 37% plots, neck lengths were more or less close together (fig. 19a). With further reduction a marked decline was observed. In all cases, neck length increased progressively with age till a maximum was attained 126 days after sowing in the 100, 37 and 12% treatments after which it tended to decrease, owing to earlier onset of senescence resulting from high light intensity as well as from heavy shading, whereas in the 75% plot it continued to increase until the end of the growing season. The tendency of neck length to increase as the plants proceeded in growth, however, may lie in the fact that in an actively growing plant each successive leaf sheath is longer than its predecessor.

Neck length in 1965 showed a rather irregular response to shading (fig. 19b). The highest values were obtained in the 37% plot. Furthermore, neck length at 12% light intensity exceeded that at 75% one, but failed to do so with respect to the full daylight plot, possibly because the elongation effect was limited by the low energy supply. Differences in neck response to shading in 1964 and 1965 experiments may be due to variations in the environmental conditions, i.e., light intensity, temperature and rainfall prevailing in each growing season. In the 1965 season, a comparatively lower light intensity, lower temperature and greater amount of rainfall were recorded. Hence, neck length was a net result of the combined effects of these factors altogether. Evidence can be provided from the fact that neck length in 1965 was greater than that in the 1964 experiment, even in full light (max. length was 143 against 85 mm.) Moreover, our results of temperature effects in the phytotron showed that neck length was favoured by relatively low temperature. Moreover, in 1965 shading was applied at a somewhat later stage of growth.

b. Neck diameter

Neck diameter, unlike length, was greatly influenced by light intensity. It is clear from fig. 20a that increasing light intensity resulted in a marked increase in neck diameter. The greater number of leaf sheaths as well as increase in their

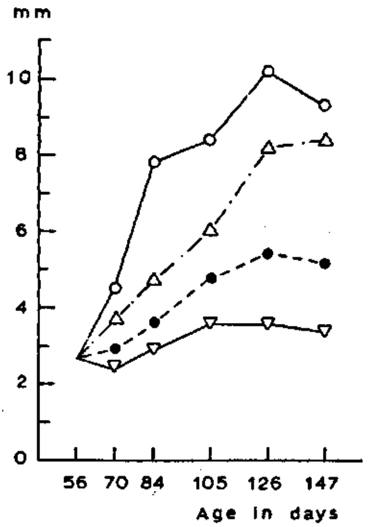


FIG. 20a
The effect of light intensity on neck diameter.
Field experiment 1964.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

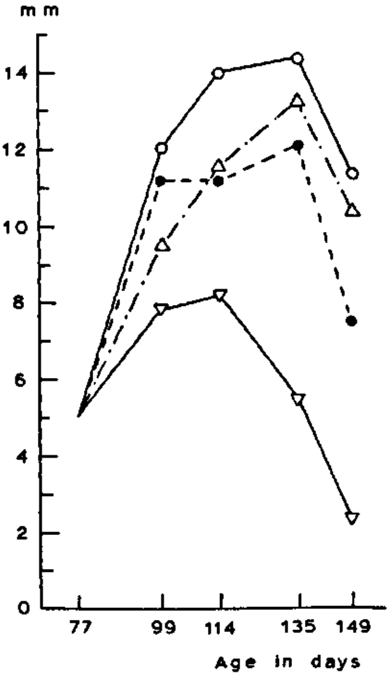


FIG. 20b
The effect of light intensity on neck diameter.
○———○ : Full light.
△— · —△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

thickness produced at high light energy may account for this observation. At all light intensities studied, neck diameter increased with age until maximum values were observed in 100, 37 and 12% after 126 days from sowing, thereafter, it tended to decrease as a consequence of maturity, while at 75% the highest value was attained at the end of the season. Increased neck diameter as plants progressed in growth is due to increased number as well as to thickness of the separate leaf sheaths which constitute the neck.

Similar results were obtained in 1965 (fig. 20b).

4. *Bulb growth*

a. Bulb diameter

Differences in the bulb diameter in relation to light intensity at successive intervals are shown in fig. 21a. It can be seen that the higher the light intensity, the greater the bulb diameter was. The larger diameter of the onion bulb produced under conditions of higher radiation is attributed to the greater number and thickness of swollen leaf sheaths and scales in such cases. Between the first and third harvest, bulb diameter increased slowly, while at more advanced age it increased rapidly, and the more so at higher light intensities. Maximum bulb diameter values were obtained at the end of the growing season. It should be borne in mind that actual bulb development started only after 84 days from

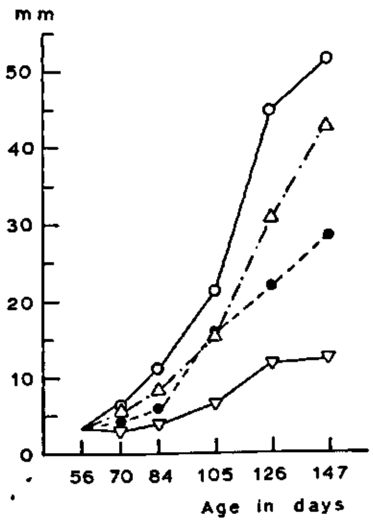


FIG. 21a
The effect of light intensity on bulb diameter.
Field experiment 1964.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -●: 37 per cent.
▽———▽: 12 per cent.

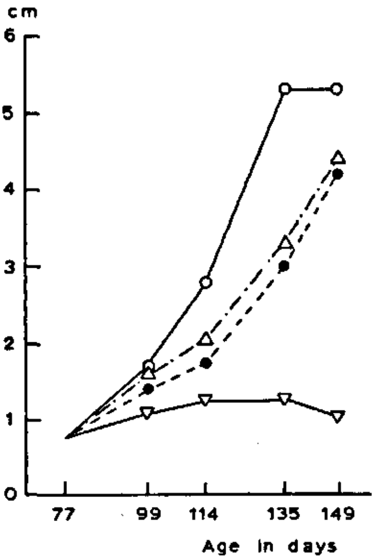


FIG. 21b
The effect of light intensity on bulb diameter.
Field experiment 1965.
○———○: Full light.
△—·—△: 75 per cent.
●- - - -●: 37 per cent.
▽———▽: 12 per cent.

sowing; the increased bulb diameter recorded before that time is merely a slight swelling in sheath bases which may occur even under short day conditions.

The same trend was observed in 1965 (fig. 21b).

b. Bulb length

As illustrated in fig. 22, bulb length as related to light intensity and developmental stage followed the same trend as bulb diameter. This may be explained by assuming that, as plants proceed in age, a relatively larger proportion of photosynthates is available for translocation to the sheath bases, especially at conditions of higher light intensities, causing a longer part of the pseudostem to swell.

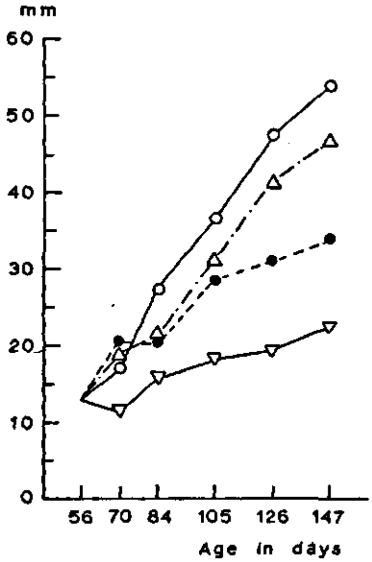


FIG. 22
The effect of light intensity on bulb length.
Field experiment 1964.
○———○ : Full light.
△—·—△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

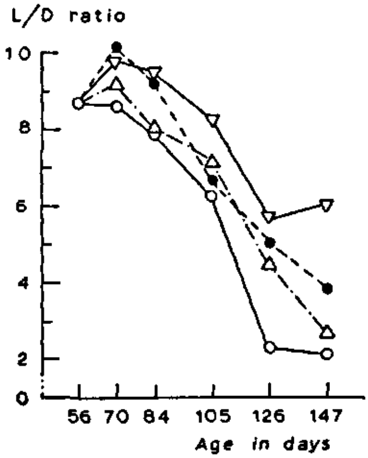


FIG. 23
The effect of light intensity on bulb length/diameter ratio.
Field experiment 1964.
○———○ : Full light.
△—·—△ : 75 per cent.
●- - - -● : 37 per cent.
▽———▽ : 12 per cent.

c. Bulb length/diameter ratio

The morphogenetic effect of light intensity on leaf shape (blade length/diameter ratio) appeared to be reflected on bulb shape, so that also relatively long and slender bulbs were formed at lower light intensities (fig. 23). This increase in bulb length/diameter ratio does not necessarily mean that absolute bulb length was greater at lower light intensities than that at higher ones. On the contrary, both bulb length and diameter were found to diminish as light intensity was decreased (see bulb length and diameter), but bulb diameter decreased relatively more, resulting in higher ratio at lower light intensities. At higher light intensities, the number and thickness of swollen foliage leaf bases and bladeless leaves as well as the number of lateral buds may increase, resulting in a greater absolute bulb diameter and consequently in a decline in bulb length/diameter ratio. HEATH and HOLDSWORTH (1948) have noted that little food storage takes place in the foliage leaf bases of onion sets and the bulb consists mostly of only few thickened sheaths of bladeless leaves. Also, lateral buds are usually not formed in sets so that during their seond season of growth, plants from sets produce bulbs with a single top or, if they flower, with a single seedstalk. Considering that onion sets are produced under very dense stand so that competition especially for light may be at maximum, one would assume that growth of the onion bulb under heavy shade is more likely to be similar to that for onion set production. Thus, the onion bulb produced under heavy shading may be regarded as onion set. Indeed, we found additional evidence in this direction. When onion bulbs, previously grown under 12% of full daylight were replanted in the second season under different light intensities, ranging from full daylight to 12% of the latter, a single top or only one inflorescence, if any, was produced from each bulb even at full light intensity (to be published in detail elsewhere).

The time trend shows that bulb length/diameter ratio in all shaded plots increased between the first and second harvest, thereafter, the ratio in all cases decreased. The increase indicates that plants after having received full daylight prior to screening were adapting themselves to the newly applied light intensities. In all treatments, the ratio decreased slowly up to 84 days from sowing after which a rapid decline was observed. This shows that in the early stages of growth (up to 84 days), increase in bulb length is predominant while at later stages, growth in bulb diameter prevailed. However, it should be emphasized that the ratio recorded up to 84 days merely expresses the relationship between the length of the slightly swollen neck bases and their diameter, as actual bulb development (with bulbing ratios of 2.0 or more) was still absent. When bulbing begins, the enlargement of the bulb is first brought about by swelling of the leaf sheath bases which had already elongated. As bulbing progresses, young leaves near the centre of the bulb abort their blades and become storage sheaths (JONES and MANN 1964).

5. *Correlation of formative effects induced by light intensity on leaf and bulb shape.*

It is interesting to compare the formative effect of light intensity on leaf shape with that on bulb shape. Comparison of figs. 17a and 23 shows that, in both cases, relatively longer organs (blades and bulbs) were produced as light intensity decreased. This similarity does not seem surprising as the onion bulb is mostly built up by thickened leaf bases (sheaths), so that it is quite likely to experience much the same influences from environmental conditions, at least in so far as morphogenetic effects are concerned.

It is worthy to note that BENSINK (1961) pointed out also that the morphogenetic effects of light and other environmental factors are correlated with an influence on the top/root ratio. The correlated formative effects on different plant organs suggest that within the plant an adaptive regulation exists which may well be influenced by the energy balance, but not merely through an 'over flow' mechanism since, as demonstrated by BENSINK (1961) no formative effect of sugar, applied to plants at low light intensity, could be detected. Thus, some unknown morphogenetic agent signals the direction of the flow as well as shape and size of tissues.

It may be added here that – as will see later – onions proceed to bulbing at very different energy levels and carbohydrate contents provided the required daylength conditions in the proper spectral regions are fulfilled.

C. TOTAL SOLUBLE SUGAR CONTENT

1. *Blade sugar content*

Since the energy stored by green plants in carbohydrates during photosynthesis can be only supplied by light, one would expect a rise in sugar content with increasing light intensity. The percentage of soluble sugars as a function of light intensity at different developmental stages is illustrated in fig. 24a. It can

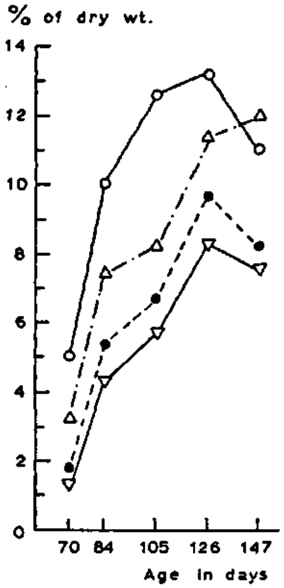


FIG. 24a
The effect of light intensity on leaf blade sugar content.
Field experiment 1964.
○——○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽——▽ : 12 per cent.

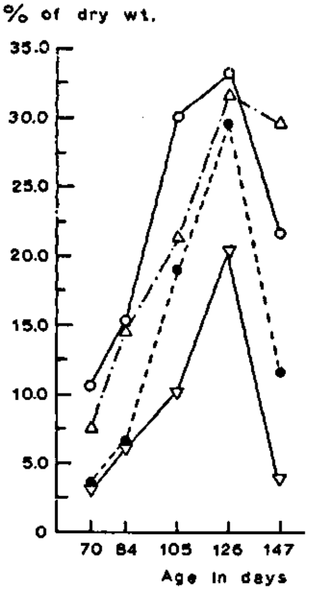


FIG. 24b
The effect of light intensity on on neck sugar content.
Field experiment 1964.
○——○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽——▽ : 12 per cent.

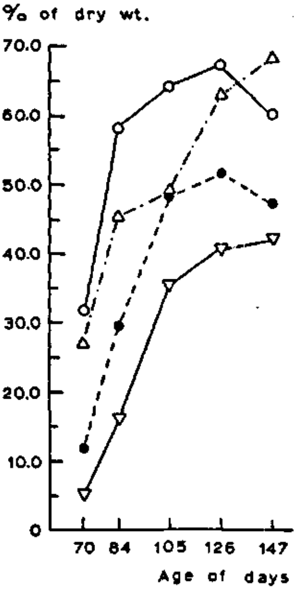


FIG. 24c
The effect of light intensity on bulb sugar content.
Field experiment 1964.
○——○: Full light.
△— · —△: 75 per cent.
●- - - -● : 37 per cent.
▽——▽ : 12 per cent.

be seen that the higher the light intensity, the higher the carbohydrate content in the blades. In all treatments, the sugar content increased as plants advanced in age till a maximum was reached after 126 days from sowing, thereafter, it declined in 100%, 37% and 12%, while it continued to increase at 75% of natural light, probably owing to the extension of growth period during which photosynthesis continue induced by the reduction of light intensity to this limit. The observed increase in sugar content with age may be due to the greater number of mature blades found on the plant as it proceeded in time as a result of which the total amount of sugars formed surpassed that consumed in respiration, utilized in growth, and translocated to the other plant organs.

2. *Neck (pseudostem) sugar content*

The onion neck is not a major photosynthesising organ. Hence, it can make none of its carbohydrate requirements, but it is dependent on blades for this material. Since, in blades, carbohydrate content was found to be positively correlated with light intensity, a higher sugar content could be postulated in the neck with increased irradiance. Fig. 24b shows that the reduction of light intensity greatly depressed total soluble carbohydrate in the neck. The time trend indicates an increase of sugar content in the neck until a peak was found in all cases 126 days after sowing. Probably owing to reduced photosynthetic capacity of the blades, and possibly because a larger fraction of carbohydrate of the neck passed into the bulb, the sugar content of the neck strongly decreased after the maximum.

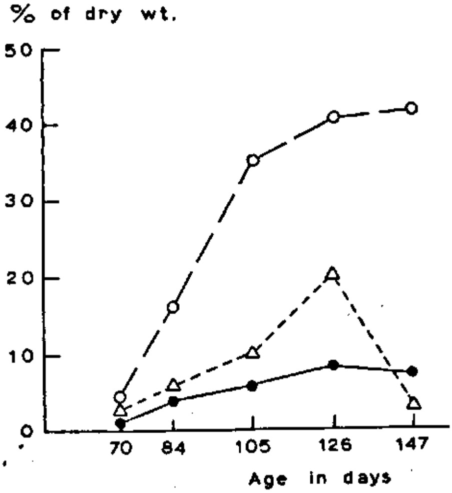


Fig. 25a
Sugar content of various plant organs at 12% light intensity.
Field experiment 1964.
●——● : blades
△- - - -△: neck
○— —○: bulb

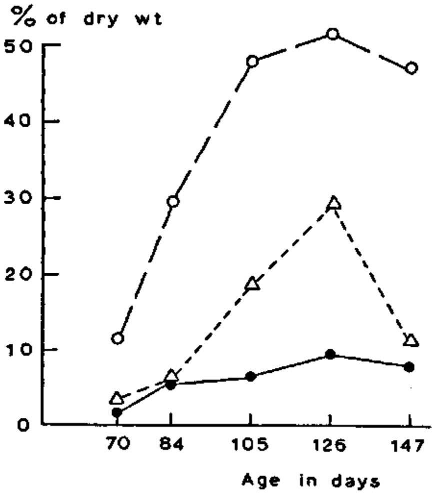


Fig. 25b
Sugar content of various plant organs at 37% light intensity.
Field experiment 1964.
●——● : blades
△- - - -△: neck
○— —○: bulb

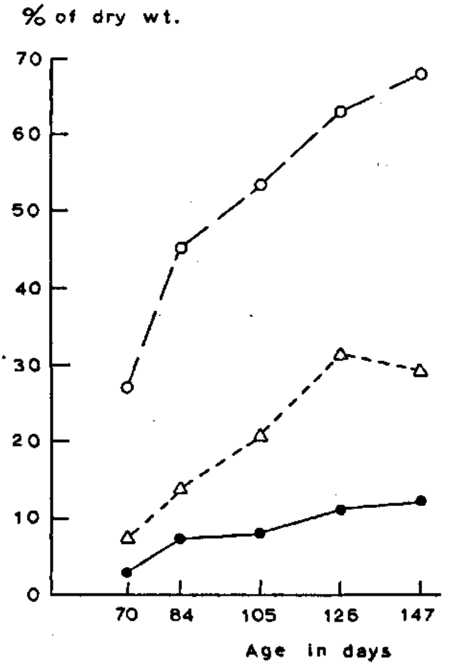


FIG. 25c
Sugar content of various plant organs at 75% light intensity.
Field experiment 1964.
●———● : blades
△- - - -△: neck
○— —○ : bulb

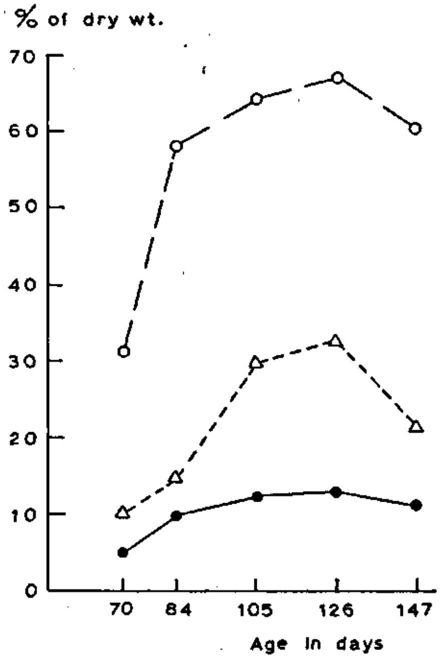


FIG. 25d
Sugar content of various plant organs at 100% light intensity.
Field experiment 1964.
●———● : blades
△- - - -△: neck
○— —○ : bulb

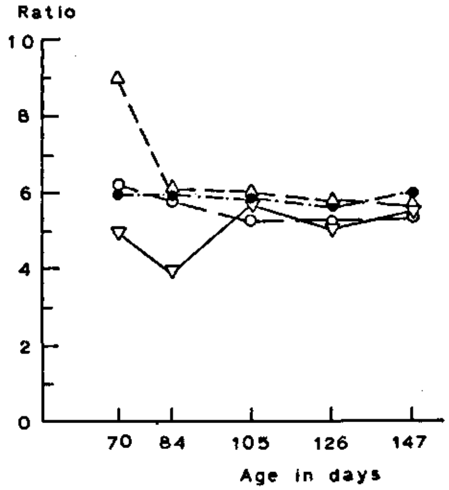


FIG. 25e
The effect of light intensity on the ratio of bulb/blade sugar content.
Field experiment 1964.
○— —○: Full light.
△- - - -△: 75 per cent.
●— · —● : 37 per cent.
▽———▽ : 12 per cent.

3. *Bulb sugar content*

The onion bulb as a storage organ serves as an intense sink for carbohydrate. Data presented in fig. 24c demonstrate that the rise of sugar content in blades and neck observed with increasing light energy and with age, was reflected in a rise in the sugar content of the bulb. At each harvest the new increment of carbohydrate in the blades was reflected then on an enlarged scale in addition to that in the mobilizing sink.

What is of great interest, is that the total sugar content in the bulb was much higher than that in the neck; while in the latter it was greater than that in the blades. This implies that movement of assimilates is against an apparent concentration gradient. This in turn indicates some sort of pulling forces acting on the translocation systems since in a storage organ as the onion bulb, large accumulation of carbohydrates can not be regarded as a consequence of the activities of enzymes which convert the soluble translocated carbohydrate into insoluble forms, thus creating a gradient for further accumulation (onion is a non-starch forming plant).

In order to substantiate the concept of accumulation of sugar in the course of time in the bulbs, via the necks from the blades, we have presented the time course of sugar content of the various organs in % of their dry weight in figs. 25a–25e. These show that the difference in sugar concentration between, e.g., bulbs and blades increases continually during development, indicating that a true accumulation mechanism, operating against an ever increasing concentration gradient. It implies the presence of a, probably topographically separate, part of the bulb tissue (e.g., vacuoles) in which sugar should be actively accumulated.

It seems of special interest in this connection that, in the period from 105 days onward practically the same proportion between sugar content of bulbs and blades exists at all light intensities, irrespective of the absolute sugar contents involved.

CHAPTER V

LIGHT INTENSITY EFFECTS (CONTROLLED CONDITIONS), RESULTS AND DISCUSSION

In order to study the influence of light intensity on growth and development of the onion plant under more controlled environmental conditions, it was decided to run some experiments in the phytotron where all factors affecting growth, except that under investigation, can be maintained constant. It should be noticed, however, that the growth regime under which the plants were grown in the phytotron differed from that under natural conditions. In the Netherlands, daylength progressively increases from April (the proper date of onion sowing) till daylength and temperature requirements for bulbing of the cultivar 'Wijbo' are met which is in June, when bulb development actually begins. In our phytotron experiment, daylength was restricted to 12 hrs. in the daily cycle up to 100 days from sowing, thereafter, extension of daylength to 16 hrs. was applied until the end of the growing season.

Temperature was kept at 20°C and the relative humidity at 70% throughout the entire season. In this way, vigorous vegetative growth was assured before bulbing was induced by long day condition. This has to be taken into consideration, since it was found from a series of experiments which will be reported later, that what is called the juvenile phase prior to ripeness to bulbing in the onion plant is very short.

A. GROWTH IN WEIGHT

1. *Fresh weight per plant*

As shown in fig. 26a, the reduction of the light intensity from 93700 to as low as 10000 ergs/cm^2/sec in the phytotron resulted in a decrease in the entire onion plant fresh weight. The decrease was relatively greater with decreasing light intensity from 32700 to 10000 ergs/cm^2/sec than with decrease from 93700 to 32700 ergs/cm^2/sec. This may be due to the detrimental effect of heavy shading on growth of open habitat plants.

At all light intensities, the plants increased only slowly in weight during the first stages of growth, and the more so under heavy shading. From the second harvest onwards they increased rapidly till a maximum was reached after 172 days from sowing at the highest light intensity owing to earlier maturity, whereas in the other treatments they continued to increase up to the end of the growing season.

2. *Dry weight per plant*

Data presented in fig. 26b show also that the dry weight as a function of light intensity and age followed more or less the same trend as the fresh weight with

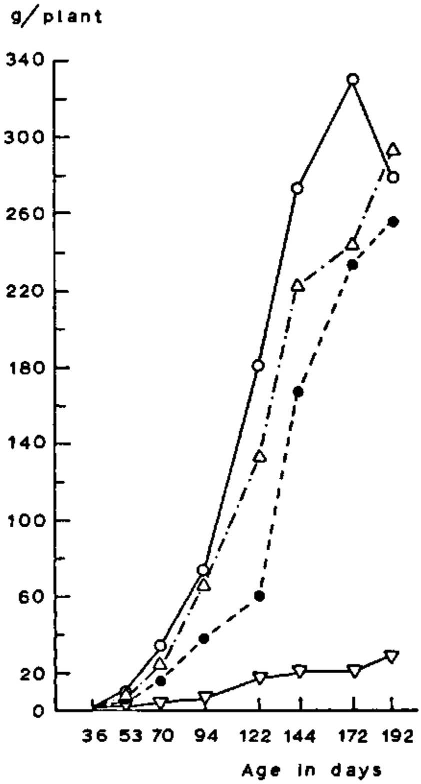


FIG. 26a
The effect of light intensity on fresh weight of the whole plant.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△— · —△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -● : 35 per cent
(32700 ergs/cm²/sec).
▽———▽ : 11 per cent
(10000 ergs/cm²/sec).

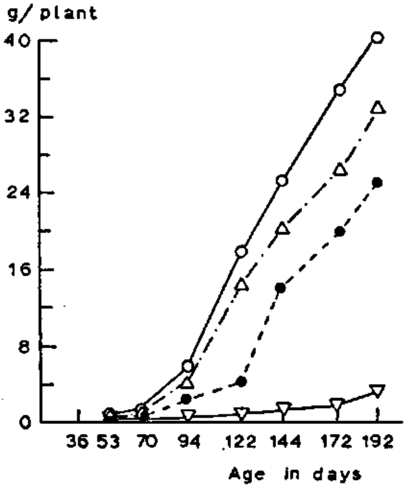


FIG. 26b
The effect of light intensity on dry weight of the whole plant.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△— · —△: 78 per cent.
(73250 ergs/cm²/sec).
●- - - -● : 35 per cent.
(32700 ergs/cm²/sec).
▽———▽ : 11 per cent
(10000 egs/cm²/sec).

only few exceptions. The dry weight at the highest light intensity, in contrast to the fresh weight, attained its peak value at the end of the growing season, like in the other treatments. This may be explained by the fact that the fresh weight at the last harvest in the highest light intensity consists mainly of the bulb which contains less water than the other plant organs, so that upon drying it yielded a higher total dry weight than in the preceding harvest.

In the early stages of growth, because the plants were still small and the photosynthetic system was not yet well developed to trap a larger fraction of the incident light energy, differences in dry weight between treatments did not yet amount to large absolute values. At more advanced age, plants at higher light intensities possessing a larger size and a more elaborate photosynthetic apparatus, produce more and hence grow more rapidly. At each harvest there is a repeated new increment of dry matter, reflected then in the capital and hence plants become larger, increase more rapidly, can thus grow still more. Due to this compound interest action, differences in dry weight among treatments become more pronounced as plants proceeded in age, and the more so, the higher the light intensity is.

At the lowest light intensity, it seems that this intensity was not far beyond the compensation point at which photosynthesis balances respiration. Thus, the plants produce less surplus to be added to capital, hence they grow increasedly more slowly and increase in weight also correspondingly slowly.

Since the onion plant is composed of different organs, viz., roots, blades, neck and bulb, we have, as before, followed the changes that will occur in the fresh and dry weight increase of these parts separately, resulting from variation in light intensity, at different stages of growth and development.

3. *Fresh weight of roots*

It is evident from fig. 27a that the fresh weight of roots was greatly influenced by the light intensity. In general, the higher the light intensity, the higher the fresh weight was. Root was the organ most affected by reducing irradiance in comparison with the other plant parts. This was especially marked with decreasing light intensity further down than 73250 ergs/cm^2/sec. It appears that under conditions of limited photosynthesis, a relatively greater fraction of assimilates is preferentially used in growth of the tops, while a smaller fraction is translocated to the roots. This, besides the fact that in the plants grown at lower light intensity, the number of sieve tubes as well as their capacity for sugar transference probably are restricted, may account for the decrease in the fresh weight of roots observed with the reduction of light energy.

The time curve of root fresh weight shows an increase up to a maximum followed by a decrease thereafter. The highest values of root fresh weight were attained in 100% and 78% light intensities after 144 days from sowing; at 35% 4 weeks later. At the lowest one, no appreciable increase was detected so that the curve seemed flattened. The weight increment of roots observed in the early stages of growth is due to the increased number of roots, emerging from the new true stem tissue, and perhaps to their greater thickness and branching especially at the higher light intensities. Owing to the depression of new root production caused by bulb development, and also because of the increased rate of root senescence, particularly at the highest light intensity, the fresh weight tended to decrease after its maximum.

4. *Dry weight of roots*

The dry weight of roots followed closely the same trend as the fresh weight (fig. 27b).

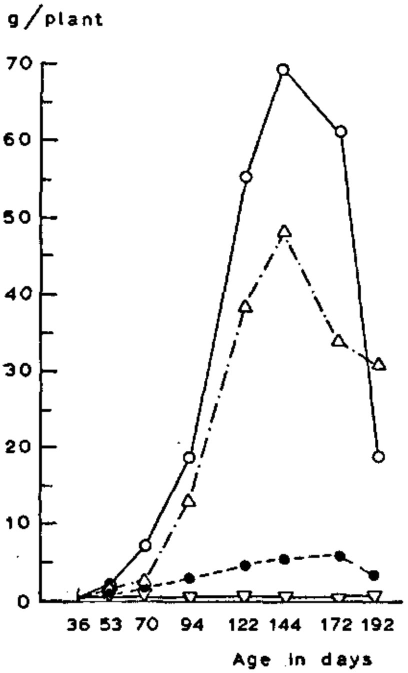


Fig. 27a
The effect of light intensity on root fresh weight.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△— · —△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -● : 35 per cent
(32700 ergs/cm²/sec).
▽———▽ : 11 per cent
(10000 ergs/cm²/sec).

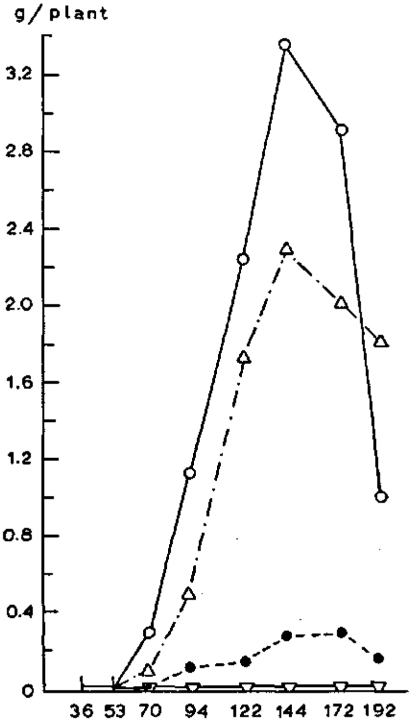


Fig. 27b
The effect of light intensity on root dry weight.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△— · —△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -● : 35 per cent
(32700 ergs/cm²/sec).
▽———▽ : 11 per cent
(10000 ergs/cm²/sec).

5. *Fresh weight of blades*

The influence of light intensity on the fresh weight of blades is brought out in fig. 28a. It is clear that the fresh weight of blades was not so mucht affected as root fresh weight. Due to greater number of leaves produced as well as their increased thickness and size, the fresh weight of blades at the highest light intensity in all cases but the last harvest tended to exceed that in other treatments. In the period between 36 and 122 days after sowing, the fresh weight of blades in 78% light intensity, because of the greater number and size of blades produced under this condition, was found to be higher than the fresh weight of blades at 35% light intensity. At more advanced age (between 144 days and 172 days after sowing), owing to the fact that the elongation effect induced by lowering the

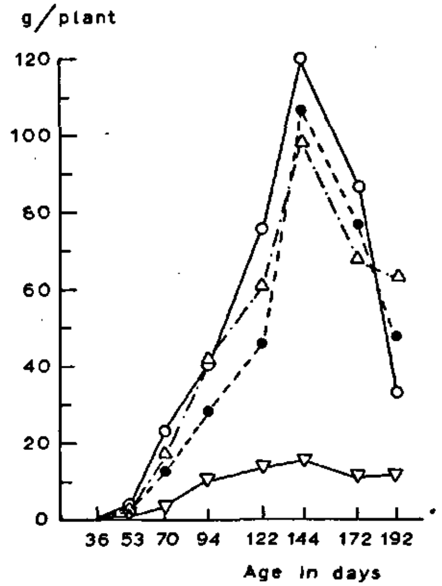


FIG. 28a
The effect of light intensity on fresh weight of leaf blades.
Phytotron experiment 1965.

○———○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -●: 35 per cent
(32700 ergs/cm^2/sec).
▽———▽: 11 per cent
(10000 ergs/cm^2/sec).

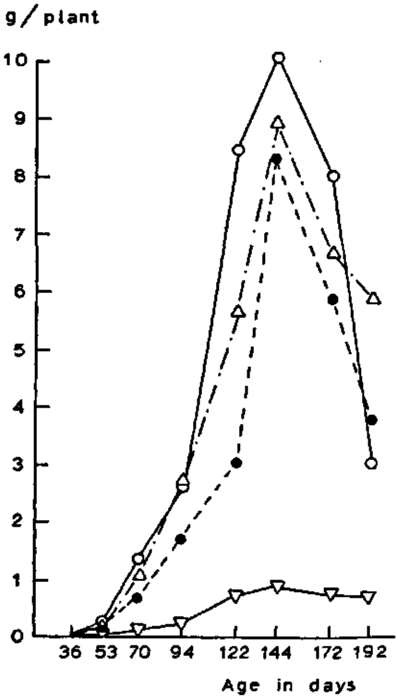


FIG. 28b
The effect of light intensity on dry weight of leaf blades.
Phytotron experiment 1965.

○———○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -●: 35 per cent
(32700 ergs/cm^2/sec).
▽———▽: 11 per cent
(10000 ergs/cm^2/sec).

light intensity to 35% by that time compensated the reduced number of leaves and their reduced thickness, the fresh weight of blades at 78% light intensity was surpassed by that in the 35% treatment. As a result of growth cycle prolongation, induced by lowering the intensity of light to a certain limit, the position was converted again in favour of the 78% treatment at the end of the season. At the lowest light intensity, however, the fresh weight of blades lagged behind throughout the entire season. This may be attributed to the detrimental effect of heavy shading on a sun plant.

At all light intensities studied, fresh weight of blades increased with time till maximum values were found 144 days after sowing after which it declined more rapidly at the highest light intensity, owing to earlier onset of senescence. The increase in fresh weight of blades with time is a result of increased leaf production and also of the greater leaf size and thickness as the plants advanced in growth. Between the sixth harvest and the last one, new leaf emergence is highly depressed (an inhibitory effect of bulbing) and in addition to increased rate of older leaf death caused the fresh weight of blades to decrease after attaining its maximum.

6. *Dry weight of blades*

Fig. 28b represents the dry weight of blades in relation to light intensity and age. With only few differences, the same trend as in fresh weight was observed. At 73250 ergs/cm^2/sec, the dry weight in all harvests, in contrast to the fresh weight, was superior to that at 32700 ergs/cm^2/sec. This is in accordance with the observation of a higher water content of blades with decreasing intensity of light.

7. *Fresh weight of neck (pseudostem)*

As shown in fig. 29a, the reduction in light intensity resulted in a decrease of the neck fresh weight. This decrease was remarkable at 10000 ergs/cm^2/sec. With lowering of the irradiance, the number of leaf sheaths and their thickness are much reduced and also the size of newly emerging leaves from within the sheath bases responsible for the rigidity of the neck is small. This results in a thinner neck and, consequently, lower fresh weight.

The fresh weight of the neck, however, increases with time in all treatments until a maximum was reached 144 days after sowing and thereafter decreased as the plants proceeded towards maturity. The rise in fresh weight of the neck with time (in the period between 36 and 144 days from sowing) is the result of the greater number of leaf sheaths as well as of their increasing thickness and length, as the plant progressed in growth. Due to the reduction of new leaf emergence as a result of bulb development, and also because a larger fraction of assimilates has passed into the bulb, the fresh weight of the neck declined after its maximum.

8. *Dry weight of neck*

The influence of light intensity on the neck dry weight at successive intervals is presented in fig. 29b; more or less the same curve as in fresh weight is found. Owing to the higher water content in 73250 ergs/cm^2/sec as compared with 93700 ergs/cm^2/sec, differences in dry weight between these two treatments in the period between the third and fifth harvest, were more pronounced than those in fresh weight.

9. *Fresh weight of bulb*

Data illustrated in fig. 30a demonstrate that the higher the light intensity, the greater the fresh weight of the bulb was. It should be noticed here that the plants were growing under short day conditions from the date of sowing up to 100 days old as a result of which actual bulb development was absent until then. Consequently, data recorded in the first four harvests represent only

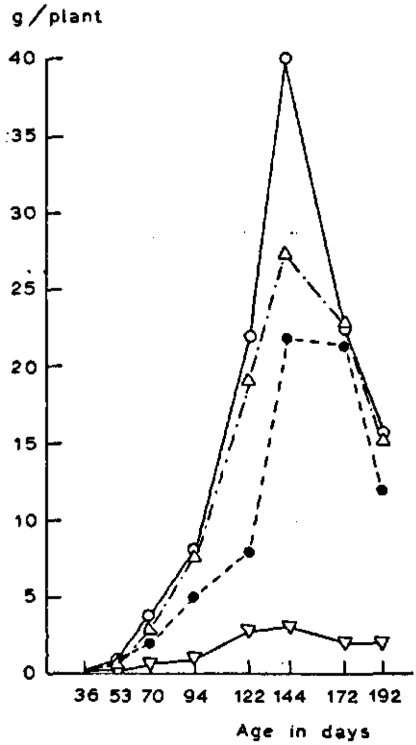


FIG. 29a
The effect of light intensity on neck fresh weight.
Phytotron experiment 1965.
○———○: Full light (93 700 ergs/cm²/sec).
△—·—△: 78 per cent (73 250 ergs/cm²/sec).
●- - - -●: 35 per cent (32 700 ergs/cm²/sec).
▽———▽: 11 per cent (10 000 ergs/cm²/sec).

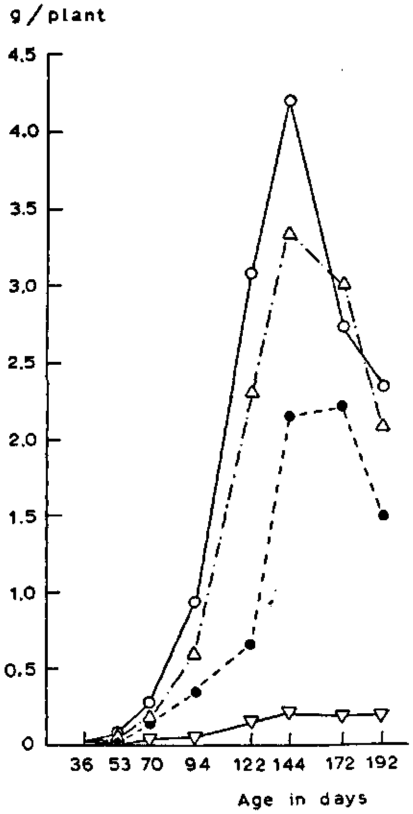


FIG. 29b
The effect of light intensity on neck dry weight.
Phytotron experiment 1965.
○———○: Full light (93 700 ergs/cm²/sec).
△—·—△: 78 per cent (73 250 ergs/cm²/sec).
●- - - -●: 35 per cent (32 700 ergs/cm²/sec).
▽———▽: 11 per cent (10 000 ergs/cm²/sec).

the fresh weight of the slightly swollen base of the neck which we considered as a bulb merely as a base of comparison. After 100 days, daylength was extended to 16 hrs. till the end of the growing season. Actual bulb development then started under the influence of long days.

Whatever may be of this consideration, we would like to point out that the greater bulb fresh weight found under conditions of high light intensity is due to increase in products of photosynthesis as well as to the shift in distribution of assimilates over the various plant organs in favour of the bulb under long day conditions (top/bulb ratio will follow).

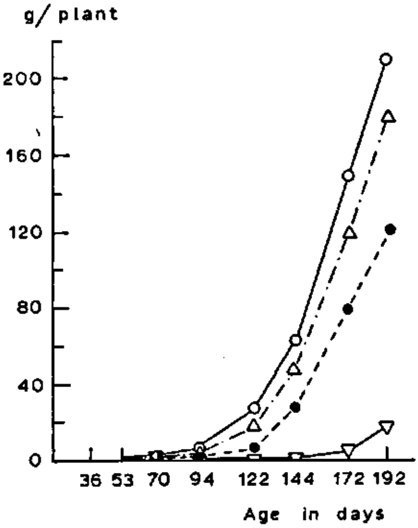


FIG. 30a
The effect of light intensity on bulb fresh weight.
Phytotron experiment 1965.
○———○: Full light (93700 ergs/cm^2/sec).
△—·—△: 78 per cent (73250 ergs/cm^2/sec).
●----● : 35 per cent (32700 ergs/cm^2/sec).
▽———▽ : 11 per cent (10000 ergs/cm^2/sec).

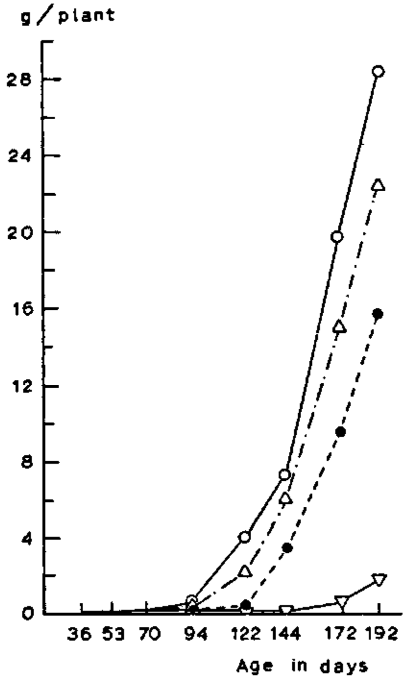


FIG. 30b
The effect of light intensity on bulb dry weight.
Phytotron experiment 1965.
○———○: Full light (93700 ergs/cm^2/sec).
△—·—△: 78 per cent (73250 ergs/cm^2/sec).
●----● : 35 per cent (32700 ergs/cm^2/sec).
▽———▽ : 11 per cent (10000 ergs/cm^2/sec).

At the early stages of growth (up to 100 days after sowing), there were no apparent differences in the fresh weight of the bulb (plants were grown under 12 hrs. photoperiod). Extension of day length thereafter to 16 hrs. resulted in an immediate increase in bulb fresh weight at the two higher light intensities, in the following harvest (3 weeks after day length extension) while at 32700 ergs/cm^2/sec a marked increase was observed 3 weeks later (6 weeks after extension); in the lowest one 10 weeks later (172 days after sowing). Maximum bulb fresh weight was obtained in all treatments at the end of the growing season.

10. *Dry weight of bulb*

As apparent from fig. 30b, the dry weight of the bulb followed more or less the same trend as bulb fresh weight. A point of interest is that bulb dry weight obtained in the phytotron experiment by far exceeded that in the field series; being about 28.2, 22.5, 15.6 and 1.8 grams in the phytotron as compared with 8.18, 4.65, 1.70 and 0.30 grams in the field from the highest to the lowest light intensity respectively. It seems that the conditions in the phytotron were more favourable for growth of the onion plant so that a higher daily growth rate was obtained (see below), and also the growth period during which photosynthesis proceeded was extended (192 days as compared with 147 days in the field). Furthermore, the control of daylength under 12 hrs. (short days) for a period of 100 days from sowing secured vigorous growth before bulbing was induced by the stimulus of long days. In this respect a positive correlation between the plant size at the moment at which bulbing is stimulated and the final size of the bulb at lifting was reported.

11. *Daily growth rate (dry weight increase/plant/day) in relation to relative light intensity*

The average dry weight increase per plant per day over the entire season as a function of relative light intensity (phytotron conditions) is presented in fig. 31a. First of all it should be kept in mind that the dry matter production depends on the photosynthetic capacity expressed as total leaf area per plant and the photosynthetic efficiency measured in terms of net assimilation rate. The rate of increase in dry weight per unit leaf area per unit time, in turn, will vary through changes in the relationship between leaf area and the soil area available for the

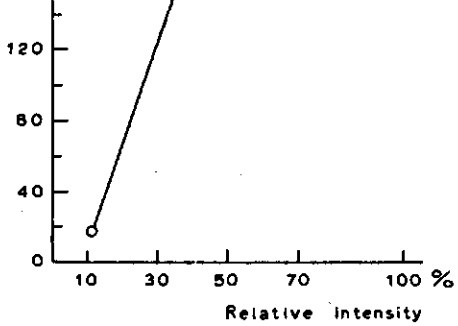


FIG. 31a
The effect of light intensity on mean daily growth rate over the entire season.
Phytotron experiment 1965.

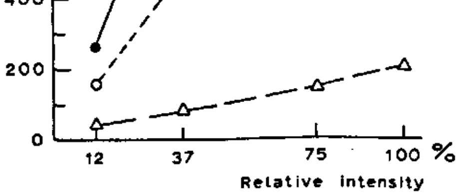
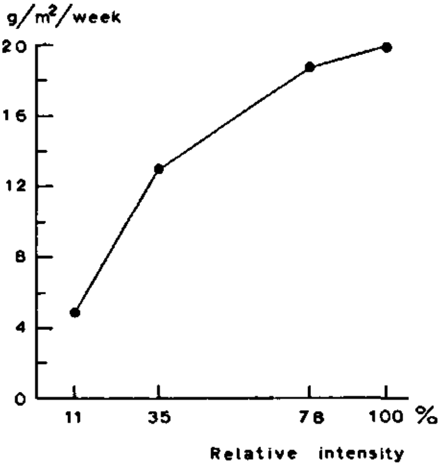


FIG. 31b
Mean leaf area/plant over 144, 126 and 135 days for the phytotron, 1964 and 1965 field experiments respectively.
●——● : Phytotron 1965.
○- - - -○: Field 1965.
△— —△ : Field 1964.

FIG. 31c
The effect of light intensity on mean NAR over the period 36-144 days from sowing. Phytotron experiment 1965.



plant or leaf area index (LAI). Therefore, at decreased light intensity the growth rate expressed in dry matter gain per plant per day will not be correlated with effects on the rate of assimilation but also with those on total leaf area. The low value at 11 % is not only brought about by reduction in the photosynthetic rate but also by reduction in the photosynthetic capacity as leaf growth was also greatly checked by this very low light intensity.

One is inclined to also consider a less favourable balance between photosynthesis and respiration, but it seems difficult to evaluate this on a relative scale as also the plants remain much smaller at low light intensity. As light intensity increased to 35 %, leaf growth was considerably promoted so that the average amount of leaf area over the entire season at 35 % was about 3.4 times that at 11 % (fig. 31b); also NAR increased to about 3 fold that at 11 %. Thus the sharp increase in dry weight gain per plant per day is the yield of increase in the photosynthetic capacity as well as of an increase in photosynthetic efficiency. However, the increase in the photosynthetic capacity (leaf area) appears slightly more effective (3 : 3.4). It is interesting to note that with increasing light intensity further than 35 %, leaf area appeared to be saturated so that no appreciable increase was observed. On the other hand NAR continued to increase; this increase progressively diminished or in other words the relationship between light intensity and NAR was curvilinear (fig. 31c.) Hence, the increase in daily growth rate with increasing light intensity beyond 35 % is mainly due to increase in photosynthetic efficiency owing to the fact that light of appreciable intensities penetrates deeper into the canopy at higher light intensities. The lower leaves or their proportion deprived from sufficient light for active photosynthesis, accordingly, decreases and the compensation point shifts to a deeper layer of leaves. This implies that in this case (high light intensities) the upper leaves become more efficient in photosynthesis and also several of the lower leaves may contribute positively, perhaps partly only to a small extent, in the dry matter production (the curvilinear relationship between NAR and light intensity above

35% indicates that then part of the leaves for some reason do not use the light with maximum efficiency).

The relationship between daily growth rate (dry weight increment per plant per day) over the entire season and relative light intensity under field (1964, 1965) and phytotron conditions followed different trends; being exponential in 1964 (fig. 9a), linear in 1965 (fig. 9b) and curvilinear in the phytotron (fig. 31a). The exponential curve in 1964 is the resultant of a linear relationship between light intensity and both NAR and leaf area. In the 1965 field experiment and in the phytotron one, the leaf area followed a similar trend in relation to relative light intensity in that leaf area increased with increasing light intensity up to about 37% and then levelled off (fig. 31b). On the other hand the NAR as related to light intensity was linear in the 1965 field experiment and curvilinear under phytotron conditions. This results from the facts that LAI in the phytotron was about two times that in the 1965 field experiment and that the incident light intensity in the latter (field 1965) was greater than under phytotron conditions.

A point of special interest is that NAR for the entire plant under phytotron conditons was far lower than under field conditions. Notwithstanding this, the dry matter production per plant per day under the phytotron conditions (at 100% light) was twofold that in the field (225:120). Two explanations are possible for this, i.e., in the phytotron the growth regime favoured the portion of dry matter increase into leaves and accordingly the photosynthetic apparatus was much larger; secondly, the growth period during which photosynthesis continued was extended (192:147 days in the phytotron and the field respectively). This suggests that the growth of the onion plant under the natural conditions prevailing in the Netherlands may be checked by factors other than the prevailing light intensity, viz., the fact that the available daylength sequences induce the plant to somewhat premature bulbing, reflected in the development of a much smaller total leaf area; this decline in leaf area appears more effective than the reduction in NAR for total gain in dry weight.

12. *Correlations*

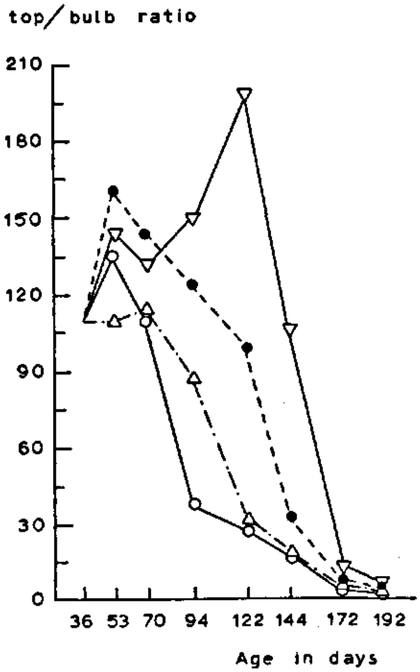
a. Top/bulb ratio (dry weight of blades + neck/dry weight of bulb)

Of great importance is the question in how far the top: bulb relationship is influenced by light intensity. It can be seen from fig. 32a that, in general, the top: bulb ratio shifts in favour of the tops with decreasing light intensity. This is due to the fact that under conditions of limited photosynthesis, assimilates appear to be preferentially utilized in promoting top growth and only a small part of the material is available for translocation. Thus, growth of tops competes with bulb growth, causing the ratio to be higher at lower light intensity.

The time trend of the top/bulb ratio demonstrates that between the first and the second harvest a rise in this ratio was observed; thereafter it tended to decrease in the higher three light intensities, while at the lowest it continued to increase up to 144 days after sowing, and then declined. It appears that in the early stages of growth, the plant mainly produces leaves, it converts most of

FIG. 32a
The effect of light intensity on top/bulb ratio. Phytotron experiment 1965.

○———○: Full light (93700 ergs/cm^2/sec).
△— · —△: 78 per cent (73250 ergs/cm^2/sec).
●- - - -●: 35 per cent (32700 ergs/cm^2/sec).
▽———▽: 11 per cent (10000 ergs/cm^2/sec).



its acquired dry matter into tops. Moreover, lowering the light intensity to 10000 ergs/cm^2/sec seemed to prolong this effect. Between the period from 53 to 144 days after sowing, the top dry weight still greatly increases together with a still more pronounced increase in dry weight of the bulb at 93700, 73250 and 32700 ergs/cm^2/sec treatments, whereas no appreciable increase in bulb dry weight at 10000 ergs/cm^2/sec was noticed causing, the top/bulb ratio at the lowest light intensity, in contrast to the others, to increase. At more advanced age (from 144 days up to the end of the growing season) the weight of tops in all cases actually decreases, while dry weight of the bulb increasingly prevails.

b. Top/root ratio (on dry weight basis)

It has been known that the top/root ratio is influenced by reciprocal correlative influences between the aerial parts of a plant and its roots. The kind and magnitude of these correlative effects depend largely upon the environmental conditions to which the plant is exposed. Fig. 32b shows the effect of light intensity on the top/root ratio at successive intervals; the bulb weight was included neither in top nor in roots.

In general, this ratio increased with decreasing light intenstiy, and the more so in as much as the latter was lower. This effect may be interpreted in terms of the influence of light intensity upon the internal food relations of the plant. At low light intensity the rate of photosynthesis decreases, consequently a diminution in the quantity of carbohydrate produced in the photosynthesizing tis-

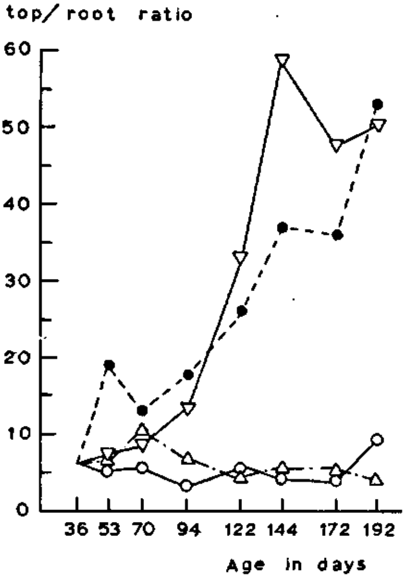


FIG. 32b
The effect of light intensity on top/root ratio. The values for 11% light intensity have been halved. Phytotron experiment 1965.
○———○: Full light (93700 ergs/cm²/sec).
△—·—△: 78 per cent (73250 ergs/cm²/sec).
●- - - -●: 35 per cent (32700 ergs/cm²/sec).
▽———▽: 11 per cent (10000 ergs/cm²/sec).

sues occurs. Accordingly, most of it is utilized in the synthesis of new cells of the top, while a small part is available for export to the roots. Thus, the weight of the top increases, accompanied with a smaller increase of root weight under such environmental conditions, causing the ratio to shift in favour of the top. What seems interesting is that in the 93700 and 73250 ergs/cm²/sec light intensities, the time trend of top/root ratio tended to be flattened, indicating an equilibrium between top and root production, while at lower light intensities the top/root ratio increased as the plants advanced in age up to 144 days after sowing; thereafter a decrease was observed followed by another increase till the end of the growing season. The decline in the top/root ratio between the 6th and 7th harvest is associated with rapid bulb bulking. It seems possible, therefore, that most of the assimilates were attracted to the bulb, resulting in depression of new root emergence. In the latest stage of growth it is likely that senescence sets in more rapidly in the roots than in the tops.

c. Leaf area ratio (total green blade area per plant/total dry weight per plant)

The relationship between total plant area and total plant dry weight as a function of light intensity at different developmental stages is brought out in fig. 33a. It is apparent that the lower the light intensity, the higher the LAR was. This indicates that a larger gain in leaf surface relative to total plant dry weight results as light intensity decreases. The question arises whether this change in LAR is merely due to differences in leaf expansion relative to leaf weight (specific leaf area) or whether also a change in the relation of leaf weight over entire plant dry weight (leaf weight ratio) is involved. As shown in fig. 33b, calculation of average LWR over different growth periods, i.e., from 36 to

94; 36 to 144; 94 to 192 and from 36 to 192 days after sowing, revealed that this ratio (LWR) increased with decreasing light intensity in all cases except in the period from 36 to 94 days which showed an increase with decreasing the light intensity from 100% to 78% and then levelled off with further reduction. This shows that differences in the LWR component besides differences in specific leaf area in all periods except in the adaptation period (from 36 to 94 days) contribute to increase values of LAR.

With only one exception, LAR at all treatments decreased with age till a minimum was noticed at the end of the season. The reaction between 36 and 53 days may well be considered as adaptation period, which differed somewhat in character from that under field conditions. It appears that under phytotron conditions the decrease with age was relatively stronger than the increase at the lower light intensities owing to adaptation so that no new increase in LAR at the lower light intensities came into appearance. Reasons for this might be that plants in the phytotron experiment were raised at lower light intensity compared with those in the field experiment prior to applying treatments. Furthermore, the age at which plants were exposed to varying light intensity might be a contributory factor in this respect (plants in the phytotron experi-

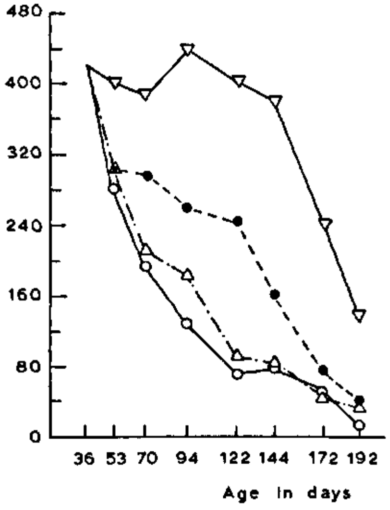


FIG. 33a
The effect of light intensity on leaf area ratio.
Phytotron experiment 1965.
○———○ : Full light
(93700 ergs/cm²/sec).
△—·—△ : 78 per cent
(73250 ergs/cm²/sec).
●----● : 35 per cent
(32700 ergs/cm²/sec).
▽———▽ : 11 per cent
(10000 ergs/cm²/sec).

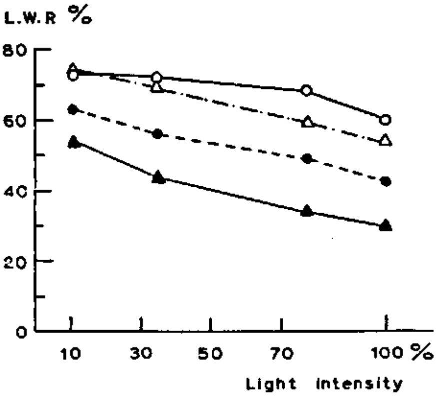


FIG. 33b
Leaf weight ratio expressed as a percentage over different growth periods in relation to light intensity.
Phytotron experiment 1965.
○———○ : over the period 36 to 94 days
△—·—△ : over the period 36 to 144 days
●----● : over the period 36 to 192 days
▲———▲ : over the period 94 to 192 days

ment were younger when the treatments started). In the next period which differed in length according to light intensity, the LAR decreased only slowly since most of the acquired dry weight was used in building up the photosynthetic apparatus. Owing to differences in length of this period (94 to 144 days) the LAR's for the various light intensities reached very different values. At the end of this period a rather deep decrease in LAR values was manifest at all light intensities, which may be ascribed to the fact that most of the gain in dry weight was then used in promoting growth of the bulb while the total leaf area gradually decreased.

Altogether it seems that, comparing the phytotron experiment with the field one, the overall behaviour of the LAR curves is quite similar, but that in the phytotron experiment dry weight increase relatively dominates over leaf expansion which could be related to the fact that suitable conditions for photosynthesis of the existing leaf area as light intensity and temperature probably prevail more constantly over longer periods in the phytotron. Something in this line was, e.g., manifest by the development of very large bulbs in the phytotron experiment.

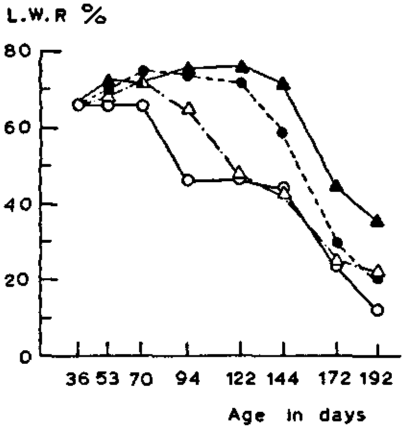


FIG. 34a
The effect of light intensity on leaf weight ratio.
Phytotron experiment 1965.
○——○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -●: 35 per cent
(32700 ergs/cm^2/sec).
▲——▲: 11 per cent
(10000 ergs/cm^2/sec).

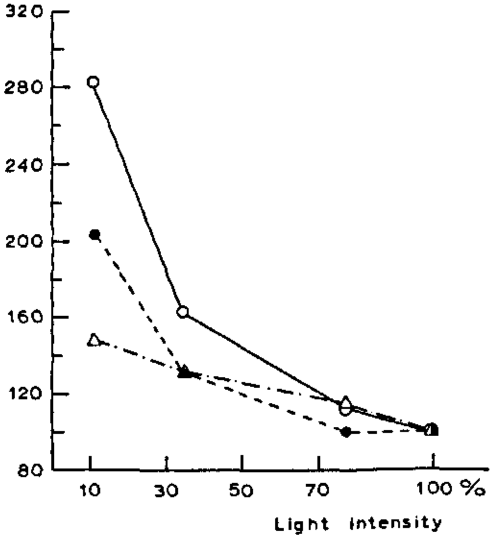
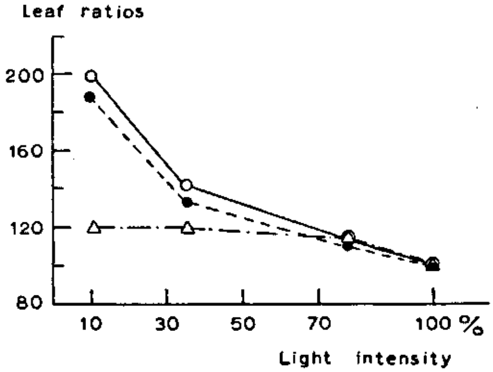


FIG. 34b
The effect of light intensity on LAR, LWR and SLA over the entire growth season (mean of seven harvest values). Full light intensity = 100.
Phytotron experiment 1965.
○——○: LAR
△—·—△: LWR
●- - - -●: SLA

FIG. 34c
The effect of light intensity on LAR, LWR and SLA mean values of 3 harvests over the period 36 to 94 days after sowing. Full light intensity = 100.
Phytotron experiment 1965.
○———○ : LAR
△— · —△ : LWR
●- - - -● : SLA



Additionally, we show the curve of LWR against time for the different light intensities (fig. 34a) and the relation to light intensity for the entire season (fig. 34b) and for the period from 36 to 94 days (fig. 34c), representing more or less the 'adaptation period'. The last figure shows that the adaptation is nearly wholly due to adaptation of the specific leaf area since the LWR remains practically the same for 78, 35 and 11 % light intensities. Fig. 34b shows that, taken over the entire season, both specific leaf area and LWR contribute more or less equally to the differences in LAR between the various light intensities.

B. SOME MORPHOGENETIC FEATURES

1. *Leaf growth*

a. Leaf number

The difference in leaf number per plant in relation to light intensity at different developmental stages is brought out in fig. 35a. In general, the higher the intensity of light, the greater this number was. This may be due to increased rate of leaf initiation and emergence under conditions of high light energy. The time trend of leaf number shows an increase up to a maximum and then a decrease. It seems that in the early stages of growth, the plant mainly uses most of its gain in dry weight in producing new leaves preparing itself for the big rise in dry weight associated with bulb formation.

Owing to the inhibitory effect of bulb development, new leaf emergence is highly depressed; this along with a higher rate of dying off of the older leaves caused the number of green leaves on the plant to decrease after they reached their maximum.

b. Leaf length

Data illustrated in fig. 35b indicate that leaf length was greatly influenced by light intensity. Between the first and second harvest, leaf length tended to be correlated with light energy so that the higher the intensity of light, the longer the leaf was. As the plants advanced in age (between the 2nd and 3rd harvest), owing to limited photosynthesis, leaf length at the lowest light intensity lagged

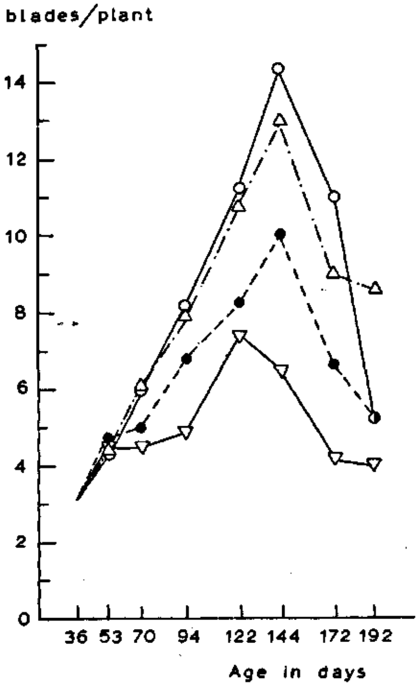


FIG. 35a
The effect of light intensity on leaf number per plant.
Phytotrón experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△—·—△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -●: 35 per cent
(32700 ergs/cm²/sec).
▽———▽: 11 per cent
(10000 ergs/cm²/sec).

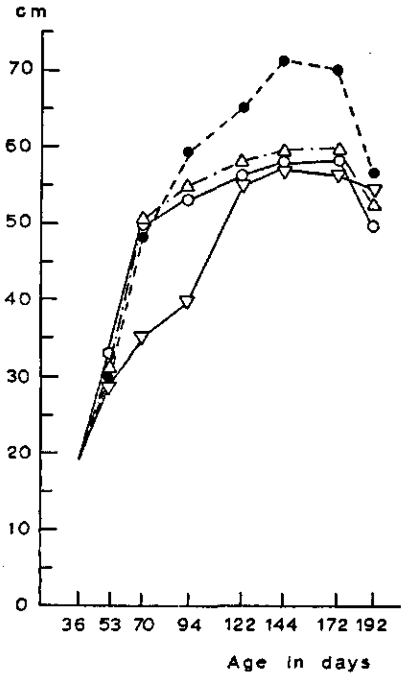


FIG. 35b
The effect of light intensity on length of the longest leaf.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm²/sec).
△—·—△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -●: 35 per cent
(32700 ergs/cm²/sec).
▽———▽: 11 per cent
(10000 ergs/cm²/sec).

behind; at 93700 and 73250 ergs/cm²/sec it tended to surpass that at 32700 ergs/cm²/sec. At more advanced age, possibly because the elongation effect induced by lowering the light intensity to a certain limit became more pronounced, leaf length in 32700 ergs/cm²/sec treatment was greatest, followed in order by 73250 and 93700 ergs/cm²/sec. It seems that at the lowest light intensity, the elongation effect was masked by the very low light energy available as a result of which leaf length in this treatment failed to overtake that at the highest one though it was very close to it in the later stages of growth. In all treatments, leaf length increased with age till a maximum was attained 144 days after sowing, and then tended to level off. In the latest stage of growth leaf length decreased again, because leaf tips dried and tops started to collapse. What seems interesting, however, is that increase of the total daily radiation associated with the day length extension (after 100 days from sowing) resulted in a sharp increase in leaf length three weeks later at the lowest light intensity, while in the 32700 ergs/cm^2/sec treatment this rapid increase continued longer; at the two higher ones, the plants appeared to profit less and the increase was less marked.

c. Leaf diameter

Unlike length, leaf diameter in all cases was positively correlated with light energy (fig 35c). This increase is more likely due to greater cell number as a result of increased rate of cell division, induced by high light intensity, rather than to an increase in cell size. As stated by HUMPHRIES and WHEELER (1963) differences in blade width in *Lolium temulentum* mainly reflect differences in cell number,

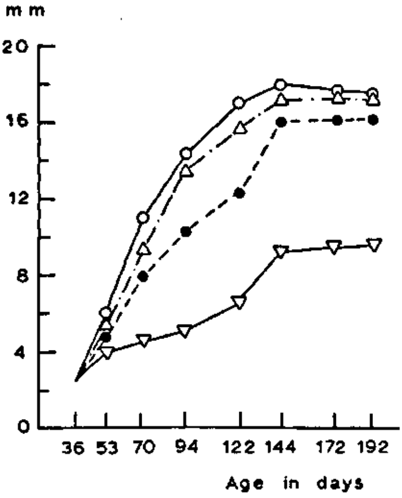


FIG. 35c
The effect of light intensity on the diameter of the largest leaf.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm^2/sec).
△— · —△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -● : 35 per cent
(32700 ergs/cm^2/sec).
▽———▽ : 11 per cent
(10000 ergs/cm^2/sec).

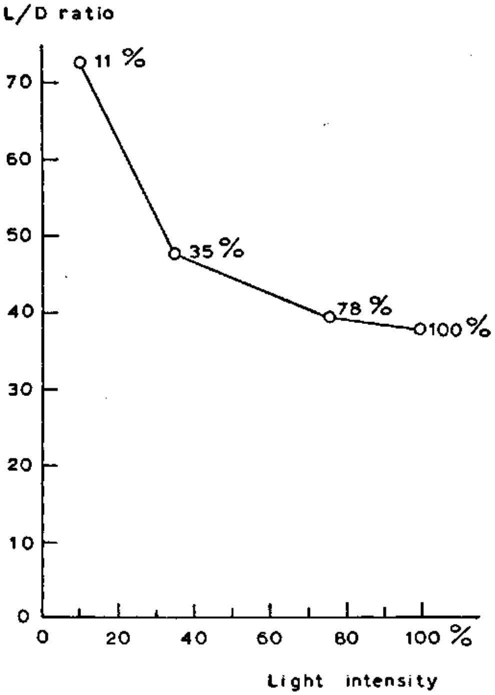


FIG. 35d
The effect of light intensity on the ratio of L/D of the largest leaf. Mean over the period 53 to 192 days from sowing.
Phytotron experiment 1965.

but changes in blade and sheath length result mainly from differences in cell length. Under all light intensities applied, leaf diameter increased progressively with time, till a peak was observed after 144 days from sowing; thereafter it came to a standstill till the end of the growing season. The increase is due to the fact that each successive mature leaf is greater in diameter than its predecessor in an actively growing plant.

d. Leaf length/diameter ratio

The morphogenetic effect on leaf shape induced by light intensity is adequately expressed by the leaf length/diameter ratio. Fig. 35d illustrates this relationship (average from 53 to 192 days). This ratio decreased with increasing light intensity from 73 at the lowest to 37.5 at the highest one. This formative effect of light intensity has also been reported by BENSINK (1958, 1960) on lettuce, and by WASSINK (1960) on *Gladiolus.*

e. Total green leaf area

It is apparent from fig. 36 that up to 122 days after sowing, the green leaf area per plant increased with increasing light intensity. This increase is mainly due to the greater leaf number and size (diameter × length) formed as a result of the increase in light intensity. In the period from 122 to 144 days, owing to the great increase in leaf length caused by reduction of light intensity to a certain limit, which effect became more pronounced by that time and more than compensated for the reduced leaf number, the green leaf area at 32700 ergs/cm^2/sec surpassed that at the higher light intensities. With still further reduction, because of restricted photosynthesis, the elongation effect was less marked, and did not compensate the reduced number of leaves so that the green leaf area at all ages lagged behind. Changes in leaf area with time indicate

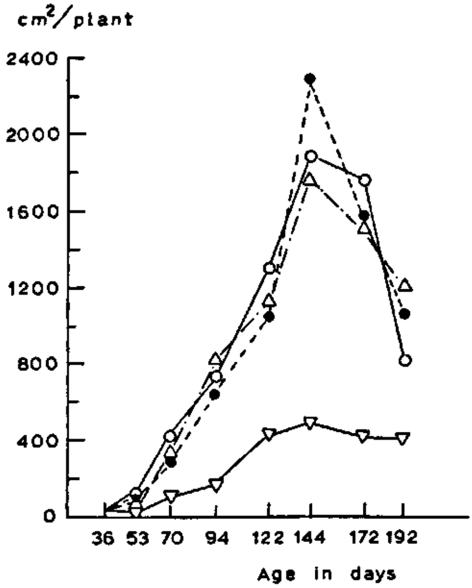


FIG. 36
The effect of light intensity on leaf area per plant.
Phytotron experiment 1965.
○———○: Full light (93 700 ergs/cm^2/sec).
△— · —△: 78 per cent (73 250 ergs/cm^2/sec).
●- - - -● : 35 per cent (32 700 ergs/cm^2/sec).
▽———▽ : 11 per cent (10 000 ergs/cm^2/sec).

that, in all treatments, due to increased number and size of leaves produced, the green leaf area increased as the plants advanced in age till a peak was reached after 144 days from sowing, after which it decreased. This decline is attributed to the depression of new leaf emergence resulting from bulb development, and also to increased rate of leaf senescence as the plants approached maturity.

2. *Neck (pseudostem) growth*

a. Growth in length

Neck length as affected by light intensity is brought out in fig. 37a. Between the first and third harvest (from 36 to 70 days after sowing), differences between treatments were not yet appreciable, though neck length at the lowest light intensity tended to exceed that at other treatments. At more advanced age, possibly because the injurious effect of heavy shading becoming more pronounced

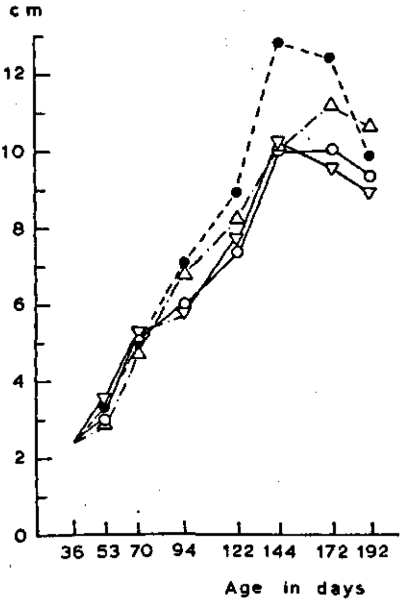


FIG. 37a
The effect of light intensity on neck length.
Phytotron experiment 1965.
○——○: Full light
(93700 ergs/cm²/sec).
△—·—△: 78 per cent
(73250 ergs/cm²/sec).
●- - - -●: 35 per cent
(32700 ergs/cm²/sec).
▽——▽: 11 per cent
(10000 ergs/cm²/sec).

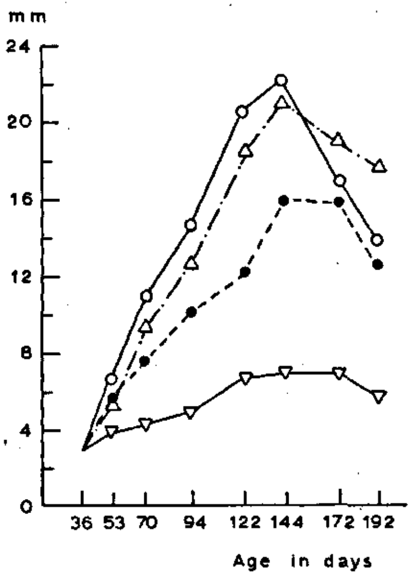


FIG. 37b
The effect of light intensity on neck diameter.
Phytotron experiment 1965.
○——○: Full light
(93700 ergs/cm²/sec).
△—·—△: 78 per cent
73250 ergs/cm²/sec).
●- - - -●: 35 per cent
(32700 ergs/cm²/sec).
▽——▽: 11 per cent
(10000 ergs/cm²/sec).

with time, neck length at the lowest light intensity failed to surpass any but that at the highest one, whereas the elongation effect induced by lowering the light intensity to a certain limit was so marked that neck length in the 32700 ergs/cm²/sec treatment was the highest, followed by 73250 ergs/cm²/sec. In all cases, leaf sheaths increased in length up to a maximum and then tended to decrease. This increase is due to the fact that the leaf sheath of every successive mature leaf is longer than the preceding one in an actively growing plant.

Owing to the extension of the growth period, induced by decreasing the intensity of light to a certain limit, the maximum neck length at 73250 ergs/cm²/sec was attained three weeks later than in the other treatments. The decrease in neck length after a maximum may be connected with the possibility that bulb length increases at the expense of neck length.

b. Growth in diameter

Unlike length, neck diameter increased with increasing irradiance (fig. 37b). This increase is mainly due to increased number as well as increased thickness of leaf sheaths produced at higher light intensities. In all light intensities applied, the neck increased progressively with time till a peak was reached 144 days after sowing; thereafter it decreased, and the more so under the highest light intensity.

In the absence of definite bulb development (prior to 144 days) new leaf blades continue to emerge from within the older leaf sheaths, causing the neck diameter to increase, whereas, as bulbing progresses, leaves near the bulb centre abort their blades (scale formation); thus the solid core of growing leaf blades which gives the neck its rigidity before bulbing is no longer there.

Along with the passage of stored material from the neck to the bulb this may account for the diminution of neck diameter in the later stages of growth.

3. *Bulb growth*

a. Growth in diameter

It is apparent from fig. 38a that, the higher the light intensity, the greater the bulb diameter was. The higher number of swollen foliage leaf bases, scales (bladeless leaves) as well as their increase in thickness account for the greater bulb diameter, observed with increasing irradiance. Increased number of lateral buds which the bulb contains may also be responsible for the increase in bulb diameter. From the date of sowing, up to 100 days old, the plants were growing under short day conditions (12 hrs. photoperiod), and swelling of the leaf sheath bases tended to increase only slowly, and the more so under the lower light intensities. At the first harvest, following the extension of daylength to 16 hrs. (taken after 3 weeks from daylength extension), a marked increase in bulb diameter was detected at the two higher light intensities, and a less pronounced increase at the lower ones. At later stages of development (between 122 and 144 days after sowing) there was a sharp increase in bulb diameter in the 32700 ergs/cm²/sec treatment, while this rapid increase was found to occur 3 weeks later at the lowest light intensity. In all treatments, however, owing to

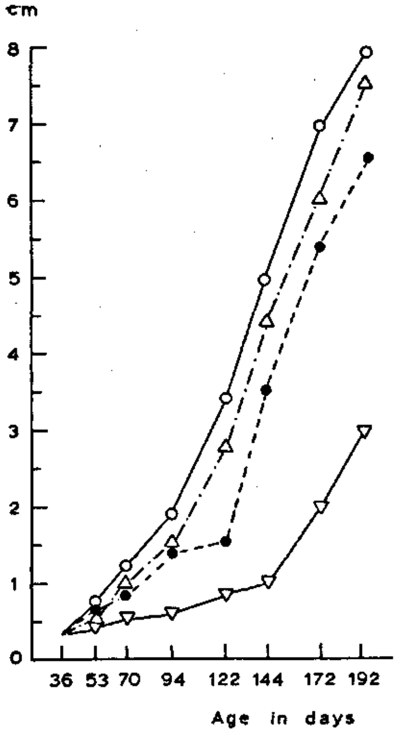


FIG. 38a
The effect of light intensity on bulb diameter.
Phytotron experiment 1965.
○——○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -● : 35 per cent
32700 ergs/cm^2/sec).
▽——▽ : 11 per cent
(10000 ergs/cm^2/sec).

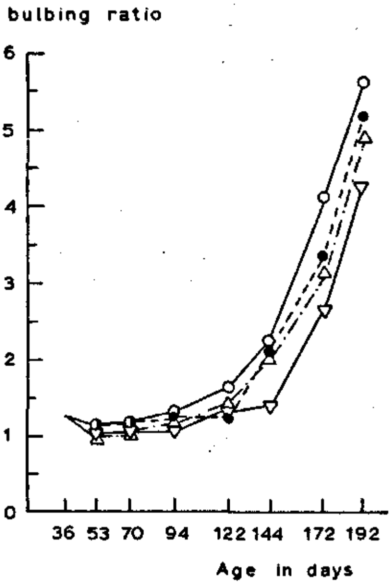


FIG. 38b
The effect of light intensity on bulbing ratio.
Phytotron experiment 1965.
○——○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
73250 ergs/cm^2/sec).
●- - - -● : 35 per cent
(32700 ergs/cm^2/sec).
▽——▽ : 11 per cent
(10000 ergs/cm^2/sec).

increased thickness of leaf sheath bases and also to the greater number of scales formed, bulb diameter increased with time till it reached its highest value at the end of the growing season.

A point we would like to stress here, is that data recorded for bulb diameter in the period from the date of sowing up to 100 days old at which the plants were exposed to short days (12 hrs.) expresses merely the slight increase in thickening of leaf sheath bases which may take place even under short photoperiods (actual bulb development occurred only after the extension of the daylength to 16 hrs.).

b. Bulbing ratio

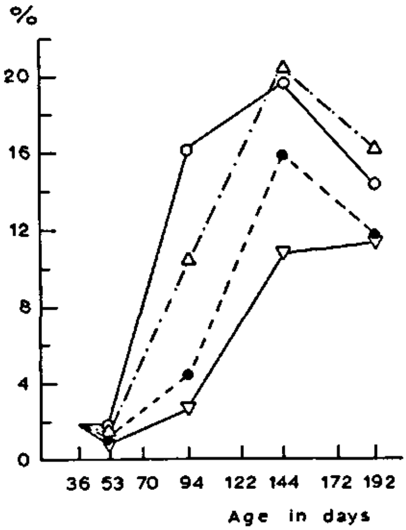
The relation between the greatest diameter near the base and the minimum neck diameter can be regarded as an assessment of bulb development. It has been reported by MANN (1951) with garlic that any ratio above 2 indicates definite bulb formation, and ratios of 5 to 6.7 indicate maturing bulb. It can be seen from fig. 38b that 3 weeks after the extension of daylength, the bulbing ratio in the two higher light intensities (93700 and 73250 ergs/cm^2/sec) showed a marked increase while at 32700 and 10000 ergs/cm^2/sec, the increase was not yet detectable, indicating delay of bulbing with decreasing light intensity beyond certain limits (further than 73250 ergs/cm^2/sec). In the period from 122 to 144 days after sowing, bulbing ratio in 32700 ergs/cm^2/sec reached the other two higher light intensities (93700 and 73250) and seemed even to surpass the ratio in 73250 ergs/cm^2/sec, whereas at the lowest light intensity it continued to lag behind, showing prolongation of the retardation effect by further reduction in light energy. At more advanced age (from 144 days up to the end of the growing season), bulbing ratio in all treatments increased progressively up to the end of the growing season, indicating progress of bulb development and advance towards maturity. It should be noticed, however, that the increased bulbing ratio observed in the latest stage of growth may be a result, at least to some extent, of leaf shrivelling which reduces neck diameter, thus causing the ratio to increase even after swelling of the sheath bases, and also scale formation have ceased. The reasons why the bulbing ratio at 32700 ergs/cm^2/sec in the period from 144 to 192 days after sowing tended to exceed that at 73250 ergs/cm^2/sec seem not quite clear. They may be linked with the increased root injury found as a result of decreasing light intensity to this degree, while with further reduction in irradiance, this effect appeared to be masked at the very low light energy. Data obtained by HEATH and HOLLIES (1963) show the tendency of the mean bulbing ratio of plants fed with different sugar concentrations and grown at half full daylight intensity, to surpass that at full daylight intensity though they stated that the differences were insignificant. Whatever may be from this consideration, we would like to point out that the reduction of light intensity to as low as 10000 ergs/cm^2/sec delayed bulb formation though it did not prevent it.

C. TOTAL SOLUBLE SUGAR CONTENT

a. *Blade sugar content*

The percentages of sugars (on dry weight basis) in blades as a function of light intensity at different developmental stages are presented in fig. 39a. It is conceivable that, in general, the higher the light intensity, the higher the sugar content was. This increase can be attributed to the increase in photosynthetic rate as light energy increased, while the respiration rate was not affected. Between the first and second harvest, the sugar content of the blades in the 73250, 32700 and 10000 ergs/cm^2/sec treatments tended to decrease, presumably because the rate of production of material was not rapid enough to keep pace with its utilization and translocation to other plant organs.

Owing to increased number of mature leaves (the photosynthetic capacity of



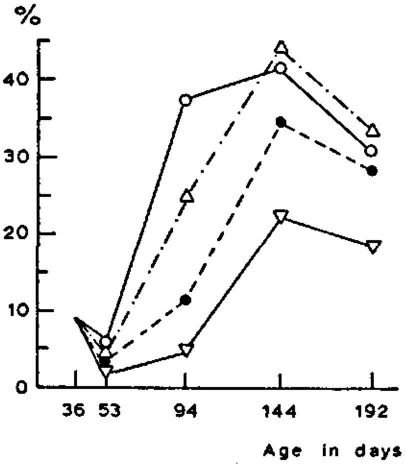


FIG. 39a
The effect of light intensity on leaf blade sugar content.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/sec).
●- - - -●: 35 per cent
(32700 ergs/cm^2/sec).
▽———▽: 11 per cent
(10000 ergs/cm^2/sec).

FIG. 39b
The effect of light intensity on neck sugar content.
Phytotron experiment 1965.
○———○: Full light
(93700 ergs/cm^2/sec).
△—·—△: 78 per cent
(73250 ergs/cm^2/s.ec)
●- - - -●: 35 per cent
(32700 ergs/cm^2/sec).
▽———▽: 11 per cent
(10000 ergs/cm^2/sec).

the plant), and possibly to increase in the efficiency (rate of photosynthesis) of the assimilating tissues, the sugar content in all cases was found to increase with age of the plants up to a maximum, and then decreased in the 93700, 73250 and 32700 ergs/cm^2/sec treatments, while it continued to increase though less markedly, till the end of the growing season at the lowest light intensity. In the period from 144 to 192 days after sowing bulb development was in progress, and a large fraction of sugars obviously moved from the blades simultaneous with increase in C/F ratio, i.e., the ratio of non-photosynthetic tissue to photosynthetic one (green leaf blades) as the plants proceeded towards maturity. This may well explain the tendency of the sugar content in blades to decrease after reaching a maximum. That the sugar content in 73250 ergs/cm^2/sec surpassed that in the highest light intensity could be interpreted as a consequence of the extension of the growth period during which positive photosynthesis continues, caused by lowering the intensity of light to this limit.

b. *Neck sugar content*

The sugar content in the neck closely followed the trend in the blades, fig. 39b. The neck is incapable of carrying on photosynthesis but depends for its sugar

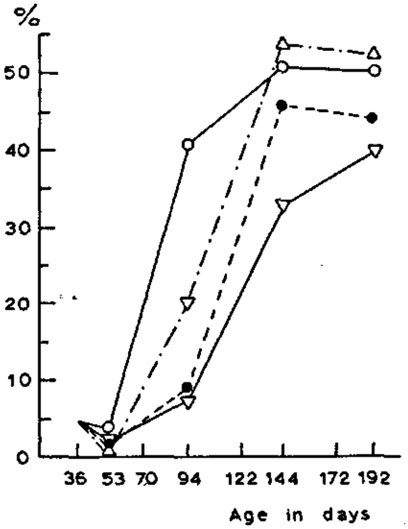


FIG. 39c
The effect of light intensity on bulb sugar content.
Phytotron experiment 1965.
○———○ : Full light
(93700 ergs/cm^2/sec).
△—·—△ : 78 per cent
(73250 ergs/cm^2/sec).
●- - - -● : 35 per cent
(32700 ergs/cm^2/sec).
▽———▽ : 11 per cent
(10000 ergs/cm^2/sec).

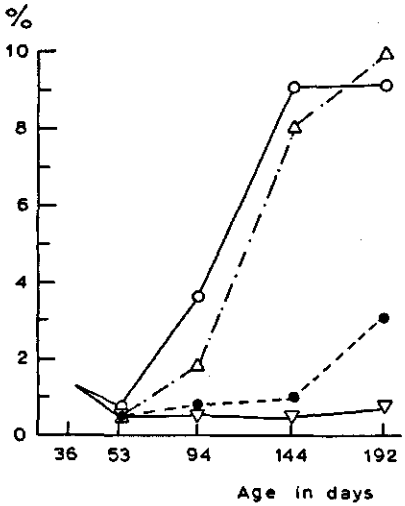


FIG. 39d
The effect of light intensity on root sugar content.
Phytotron experiment 1965.
○———○ : Full light
(93700 ergs/cm^2/sec).
△—·—△ : 78 per cent
(73250 ergs/cm^2/sec).
●- - - -● : 35 per cent
(32700 ergs/cm^2/sec).
▽———▽ : 11 per cent
(10000 ergs/cm^2/sec).

supply on the blades, and since in the latter the carbohydrate content increased with increasing light intensity and with time, it is not surprising that the sugar content in the neck followed more or less the same course as in the blades. Between the first and second harvest, the plants still very young, form small and thin leaves and have produced only three or four blades. Apparently, the photosynthetic capacity of the plant was not high enough to supply adequately the neck with sugars and a decline in the neck's sugar content was observed. As the plants develop, more and thick blades are formed, securing a well developed photosynthetic apparatus as well as mechanical and conductive tissues. Accordingly, the rate of photosynthesis increases so that more sugar is available for transport in addition to increased transport capacity. All these factors may cooperate in causing the rise of sugar content in the neck in the period from 53 to 144 days after sowing. Sugar content in the necks showed a decline in the interval between 144 and 192 days after sowing because by then a large proportion of the sugars has passed into the developing bulb, and photosynthetic capacity of blades has decreased as a result of senescence so that sugar export to the neck is reduced.

c. *Bulb sugar content*

Fig. 39c shows the total soluble sugar content in the bulb as a function of light intensity and age. With few exceptions, the sugar content in blades and neck appears reflected in the sugar content of the bulb. The bulb is a storage organ acting as an extensive sink for carbohydrate accumulation. It depends on the tops for its sugar supply. Since in blades, the sugar content increased with increasing light intensity and with age as a result of increased photosynthetic capacity, one would assume a rise in the sugar content of the bulb with increased light energy and with time. It seems, however, in the period between 36 and 53 days after sowing that sugar consumption in the different physiological processes (respiration, new tissues formation, etc) was in excess of sugar supply to the bulb as a result of which a decline in the sugar content of the bulb was observed. Between the second and sixth harvests, sugar export to the bulb surpassed its utilization so that the excess accumulated resulting in higher sugar content. At more advanced age (144 to 192 days after sowing) owing to reduced photosynthetic capacity of the blades as a result of senescence and possibly because of increased respiration rate of the bulb as it reached maturity, the sugar content of the bulb showed a slight decrease in 93700, 73250 and 32700 ergs/cm^2/sec treatments.

Translocation of organic materials is frequently considered to be a movement of substance from regions of higher to regions of lower concentration. This does not seem true in the formation of the onion bulb, as appears from the sugar concentrations in the different plant parts. Furthermore, owing to the fact that the onion bulb is not an organ forming starch or any other insoluble carbohydrate, there are no reasons for large accumulation of carbohydrate in this storage organ as a consequence of the activities of enzymes which convert the soluble translocated forms to insoluble ones thus creating a gradient for further accumulation. There is evidence, however, implying that movement of substance may be against concentration gradient. For example, as quoted by LEOPOLD (1964) the data of MASON and MASKELL (1928) showed higher total sugar content in the cotton fruit than in the leaves.

d. *Root sugar content*

It is apparent from fig. 39d that increasing the light intensity resulted in an increase in the total soluble sugar content of the roots. Like in root dry weight, reduction of irradiance further than to 73250 ergs/cm^2/sec caused a pronounced decrease in the sugar content of roots so that 32700 and 10000 ergs/cm^2/sec treatments lagged behind, while the higher two tended to be close together.

With the exceptional decline noticed between the first and the second harvest, sugar content of roots at 93700, 73250 and 32700 ergs/cm^2/sec treatments increased with age till a maximum was attained at the end of the growing season. At the lowest light intensity it seems that the rate of supply of sugars to the roots was equivalent to its rate of utilization in different physiological processes so that no appreciable increase could be detected with time.

It seems interesting that the sugar content of roots, in contrast to that of blades and neck, continued to increase in the interval between 144 and 192 days after sowing. This indicates that roots were continuously supplied with sugars while their growth rate was greatly depressed (roots dry weight decreased after 144 days from sowing) causing sugars to accumulate.

ON PERCENTAGE DRY MATTER DISTRIBUTION OVER THE DIFFERENT PLANT ORGANS AND ON PARTIAL NET ASSIMILATION RATES

1. *Dry matter distribution in % of total over the various plant organs in relation to light intensity*

In the previous chapters we have discussed the effects of light intensity on growth of the different plant organs expressed as absolute weights. Of further interest is the question in how far the growth of each of the plant organs, expressed as a percentage of the entire plant weight, is affected by light intensity. Not only is this expression of theoretical interest but may also be of considerable practical importance.

Fig. 40a represents light intensity effects on growth of roots, leaf blades, neck and swollen neck base, expressed as percentage of the total dry weight of the plant, at 94 days after sowing, in the experiment under controlled conditions. It is obvious that roots and blades are the organs most affected by light intensity. They show opposite trends in that relative root growth is positively correlated with increasing light intensity, whereas the relative growth of blades increases with decreasing light intensity. Like roots, the percentage of dry matter

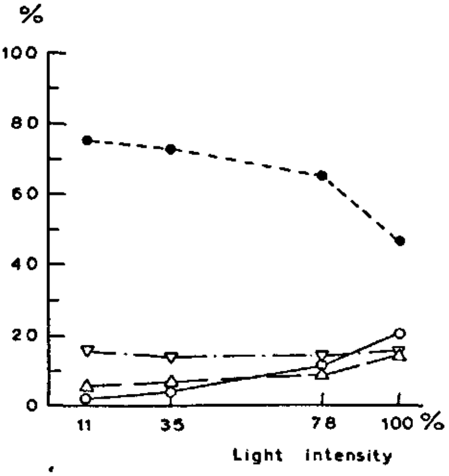


FIG. 40a
Percentage dry matter distribution between the various plant parts in relation to light intensity, 94 days from sowing.
Phytotron experiment 1965.
●– – – –● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots

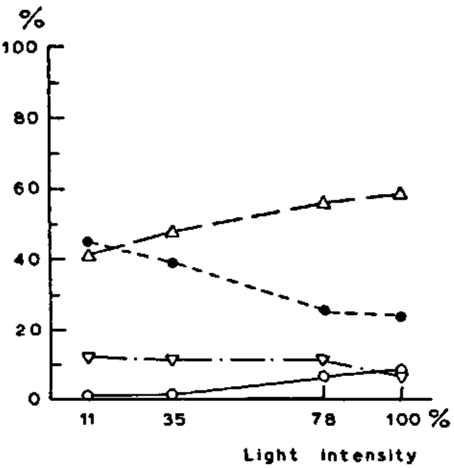


FIG. 40b
Percentage dry matter distribution between the various plant parts in relation to light intensity, 172 dyas from sowing.
Phytotron experiment 1965.
●– – – –● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots

distribution over swollen neck base (bulb) is favoured by increased light intensity. The curve of the neck appears flat, indicating no influence of light intensity on relative growth of this organ. During this growth period, most of the gain in dry weight, at all light intensities, is utilized in building up the photosynthetic apparatus while a smaller fraction of dry weight is distributed over the other plant organs.

Fig. 40b also shows the percentage of dry weight distribution over the various organs, 172 days after sowing, in the phytotron experiment. The same trends as in the preceding period (at 94 days) are observed. At this harvest, the portion of dry weight converted into the bulb becomes prevailing, mostly at the expense of those of leaves and roots. The curve of the neck, while remaining flat, shifts to slightly lower values.

2. *Total NAR in relation to light intensity*

As dry matter increase is attributable to photosynthesis, apart from the small contribution of mineral nutrient uptake from the soil, the rate of increase of dry weight per unit leaf area obviously is a measure of the excess of the rate of photosynthesis over the rate of dry matter loss by respiration. In most studies on photosynthesis, work has been done on the simplest systems, particularly on unicellular plants, in the WARBURG apparatus, where control of the environmental conditions can be reasonably well achieved. Measurement of the rate of photosynthesis in higher plants, however usually has been confined to observations on leaves, either attached or detached.

In direct measurements of photosynthesis of a single leaf, apart from the difficulties accompanied with the control of environmental conditions such as leaf temperature etc., several requirements are easily fulfilled, one of which is the fact that the leaf is horizontally placed in the assimilating chamber so that light may fall on the leaf surface from one direction and, mutual shading is avoided. In most of such studies, with few exceptions, e.g., maize, the rate of photosynthesis increases linearly with light intensity until light saturation occurs, and then the curve of photosynthesis levels off as light intensity increases further. These investigations show that the saturation light intensity is about $^1/_3$ to $^1/_4$ that of full daylight. Obviously, such a leaf is unable to utilize the full daylight completely, i.e., at the prevailing conditions, especially with regard to the CO_2-concentration.

In a plant community, the case is different. The inter- and intra-plant competition for light etc. interfere in a complex manner so that photosynthesis of a canopy not only depends on light intensity and photosynthesis function of the single leaves, but also on factors which affect the distribution over the leaves of the canopy. According to DE WIT (1965) the most important of these latter factors are the number and size of the leaves and their position with respect to the soil and to each other, the transmission and reflection of the leaves and the ratio between diffuse and direct light (for further detail l.c., 1965).

As far as the present author is aware, no direct or indirect NAR measurements of photosynthesis in relation to light intensity, neither for a single leaf nor for the entire onion plant, have been done. Attempts to determine NAR as a function of light intensity in the field and under controlled conditions, therefore, appear useful.

In figs. 10a,b we have shown the relationship between NAR and relative light intensity over a growth period of 126 and 135 days (about three weeks before lifting) in the 1964 and 1965 field experiments respectively; values of NAR are means of 4 and 3 periodic harvests. It is obvious that NAR increases linearly with increase in light intensity up to full daylight. Similar results were obtained by WASSINK (1960) on Gladiolus. BLACKMAN and RUTTER (1948) and BLACKMAN and WILSON (1951a), working with different plant species, found that NAR increased linearly with the logarithm of light intensity, expressed as a fraction of full daylight. The straight line relationship between NAR and log light intensity was found to hold over a long period of the year, although NAR in full daylight varied widely (between 0.30 to 76 g/dm^2 week for sun flower). THOMAS and HILL (1937) found that for the plant as a whole, light is limiting most of the time, for even on cloudless days the photosynthesis curve follows the light curve. TAKEDA (1961), studying photosynthesis of an individual rice plant under community conditions as influenced by light intensity at different stages of growth found that in the early stages of growth, light saturation for the individual plant in a community occurred at 40 to 50 klux just like in the case of an isolated plant. However, as growth proceeds, the light requirement for full photosynthesis increases progressively and at the stage of maximal leaf area, the light saturation points disappear even under full sunlight of mid day and the trend of the curve approaches a straight line. This reaction was more manifest as the leaf area increased by nitrogen application.

A precise interpretation of the linear curve of NAR versus light intensity seems difficult. Additional difficulties may arise from the fact that the NAR values are over a long period so that their linearity is the resultant of many factors acting in one or another direction. However, the proportional increase of NAR with light intensity indicates that, on the whole, no light saturation for the individual plant in a community, unlike for a leaf or isolated small plant, occurs. Reasons for this may be as follows:

In a community, the leaf area per plant is often greater than the soil area occupied by the plant (LAI), and mutual shading is inevitable since the incident light cannot easily penetrate into the community. Accordingly, even under full light intensity, though the upper layer of the community receives sufficient light for full photosynthetic activity, a considerable part of the inner leaves will be near the compensation point, or at least in shortage of light for maximum effectivity. Moreover, even when not shaded, many leaves are not at right angles to incident radiation, therefore, are not exposed to its maximum intensity. Thus, as a whole, the community conditions are inferior in the average amount of light, received by individuals, to the isolated condition and, hence, light will remain limiting in the photosynthetic process in a plant community. However, MILTHORPE (1963) holds the opinion that the importance of light interception is often exaggerated because the shaded leaves are those less efficient in photosynthesis. DE WIT (1965), on the other hand, proved that this decrease (in photosynthesis) is more or less compensated by the otherwise more efficient use of light at lower light intensity.

In the phytotron experiment, plotting the average NAR against relative light intensity, a curvilinear relationship is obtained (fig. 31c). Some factors come into play under the controlled conditions applied and are responsible for this slight deviation in the relationship between NAR and light intensity. In the phytotron, the environmental conditions were more favourable for leaf growth, i.e., higher temperature, better water supply, probably more fertile soil of a greater water holding capacity, and delay in daylength extension for bulb induction (bulb development was arrested by growing the plants under SD conditions up to 101 days after sowing). These altogether ensured more vigorous leaf area growth in the phytotron. Considering the fact that the space available for the plant in the phytotron was smaller than in the field (100 cm^2 against 144 cm^2), one would expect a far greater LAI (leaf area per plant/soil area occupied by the plant). This higher LAI and the comparatively lower light intensity in the phytotron resulted in unfavourable light conditions for maximum photosynthesis in a larger proportion of the leaves, owing to the fact that light could not sufficiently reach them.

3. *Partial NAR's*

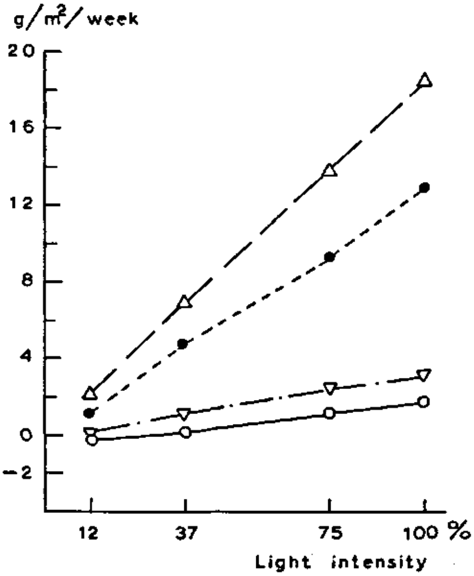
It should be noted that in almost all studies carried out on different plant species by various investigators, the rate of dry matter increase per unit area per unit time (NAR) is estimated for the plant as a whole. Considering that the agricultural yield is not usually regarded in terms of weight of the entire plant, but that of a particular organ, and, moreover, that treatments frequently have a differential effect on dry matter distribution over the various plant organs, it seems worthwhile, for complete analysis, to examine in how far the NAR for the different plant parts is influenced by a certain treatment.

In a preliminary attempt to analysis we have calculated the NAR for the various onion plant parts, based upon the gain in dry weight in the various periods. In the following sections, the partial NAR as affected by light intensity under field and phytotron conditions will be shown and discussed.

4. *Partial NAR's over 126 days (3 weeks before lifting) in the 1964 field experiment*

Fig. 41a shows the average NAR for the different onion plant organs, i.e., root, leaf, neck and bulb, plotted in relation to light intensity. At all light intensities, in general, the highest NAR values are those for the bulb followed in order by leaves, neck and root. The differences, however, between NAR$_b$ (bulb) and NAR$_l$ (leaves) on the one hand, and NAR$_n$ (neck) and NAR$_r$ (root) on the other hand are so large that the curves of the latter organs (neck, root) lag considerably behind those of the former (bulb, leaves). Thus, the shape of the NAR curve for the entire plant is mainly determined by those for the bulb and the leaves while the part played by NAR$_n$ and NAR$_r$ is relatively small.

FIG. 41a
The effect of light intensity on mean partial NAR over the period 56–126 days from sowing.
Field experiment 1964.
●- - - -● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots



Moreover, at 12% light intensity, it seems that the part of the gain in dry matter contributing to the neck is very small, and even smaller that of the roots which had amounted to a negative value. The negative value of NAR_r shows that the roots may supply other plant organs, possibly leaves, with the dry matter they had acquired before shading, since this negative value is the net result of a negative value of NAR_r recorded at the first harvest following shading and some positive values recorded at subsequent harvests. BLACKMAN and TEMPLEMAN (1940), on grasses and clover, pointed out that, at low light intensities, leaves are produced at the expense of roots, since there is a transfer of carbohydrates from the roots to the leaves when the plants are initially shaded. As light intensity increases from 12 to 37%, there is hardly a small increase in NAR_r associated with a somewhat pronounced increase for the neck.

5. *Partial NAR's over the entire growth period (147 days) in the 1964 field experiment*

Plotting the average NAR values over the entire season for the various plant organs against relative light intensities, more or less similar curves as those during 126 days (3 weeks before lifting), with some differences, are obtained (fig. 41b). It is apparent that, in general, NAR_b shifts to higher values whereas NAR_l shifts to lower ones so that NAR_l tended to be closer to NAR_n and NAR_r rather than to NAR_b, unlike in the growth period of the first 126 days. This is due to the fact that in the late stages of growth, in the distribution of dry matter gain/unit area/unit time the bulb predominates over the other plant organs. Furthermore, at all light intensities, the increase in NAR_b appears to be at the expense of the leaves, since NAR_l decreased in all cases as compared with the 126 days growth period. On the other hand, NAR_n and NAR_r remained the same at 12, 37, and 75%, while they decreased at 100%, showing that in the

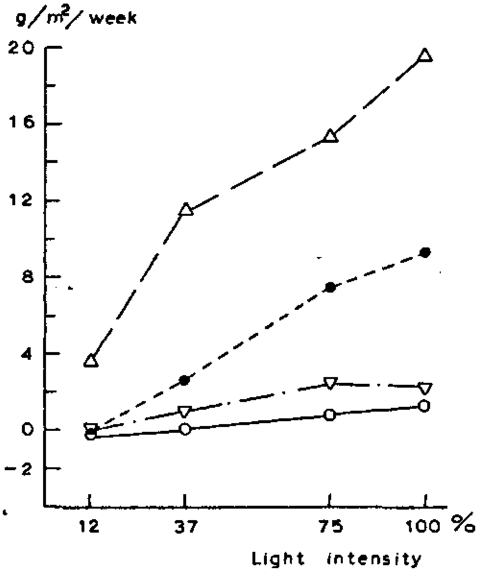


FIG. 41b
The effect of light intensity on mean partial NAR over the period 56–147 days from sowing.
Field experiment 1964.
●– – – –● : leaf blades
▽— · —▽ : neck
△— —△: bulb
○———○: roots

latter case the part of dry matter gain, which otherwise would have been distributed over neck and root, is supplied to the bulb.

6. *Partial NAR's over 135 days (two weeks before lifting) in the 1965 field experiment*

In the 1965 experiment, as shown in fig. 42a, NAR of the various plant organs appeared lower as compared with that in 1964, possibly because of the

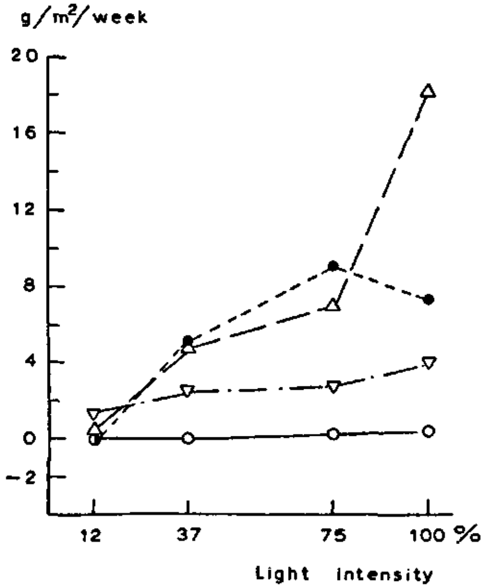


FIG. 42a
The effect of light intensity on mean partial NAR over the period 77–135 days from sowing.
Field experiment 1965.
●– – – –● : leaf blades
▽— · —▽ : neck
△— —△: bulb
○———○: roots

lower light intensity prevailing in 1965. During this season, it seems that the environmental conditions favoured the fraction of dry matter gain to the leaf and neck at the expense of the other plant organs (bulb and roots), so that NAR_l and NAR_b, except in full daylight, appeared closer together and even, in some cases, NAR_l tended to surpass NAR_b. NAR_l and NAR_b are the ones most affected by light intensity. They increased nearly regularly with increasing light intensity up to 75%, while with further increase a sharp increase in NAR_b, associated with a drop in NAR_l, is observed. The other plant organs, i.e., neck and root, and especially the latter, do not show appreciable differences at different light intensities.

7. *Partial NAR's over the entire growth period in the 1965 field experiment*

At all light intensities, NAR_b dominates over the other plant organs, so that NAR_l, NAR_n, and NAR_r, while close together, lagged behind that for the bulb (fig. 42b). Thus, the shape of the total NAR curve is mainly determined by that for the bulb and to a smaller degree by that for the leaves, while NAR_n and NAR_r played a negligible part. The NAR_b increased linearly with increasing light intensity up to 75%, while with further increase, no appreciable increase is detected. This may be explained by the fact that full light intensity speeded up leaf senescence, as a result of which the total photosynthesis by the plant was greatly reduced.

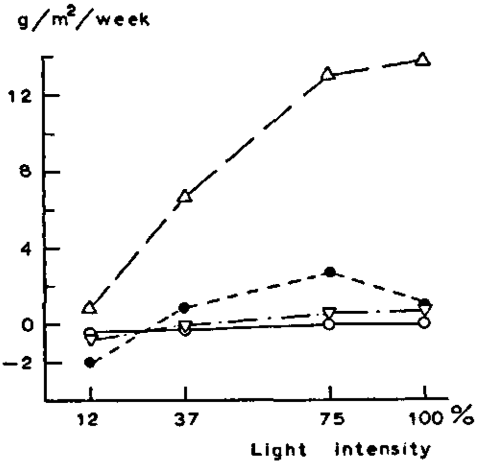


FIG. 42b
The effect of light intensity on mean partial NAR over the period 77–149 days from sowing.
Field experiment 1965.
●- - - -● : leaf blades
▽—·—▽ : neck
△— —△: bulb
○——○: roots

8. *Partial NAR's under controlled conditions over 144 days*

From fig. 43a it is apparent that most of the gain in dry weight per unit area per unit time was converted into leaves so that the highest NAR values recorded during this growth period were found for these organs; NAR-values for the other plant organs, while close together, were far below the value for the leaves. This mainly arose from the fact that bulb development was arrested by growing the plants under short day conditions (12 hrs.) for a prolonged period (about 101 days from sowing) so that a greater part of the gain in dry weight per unit

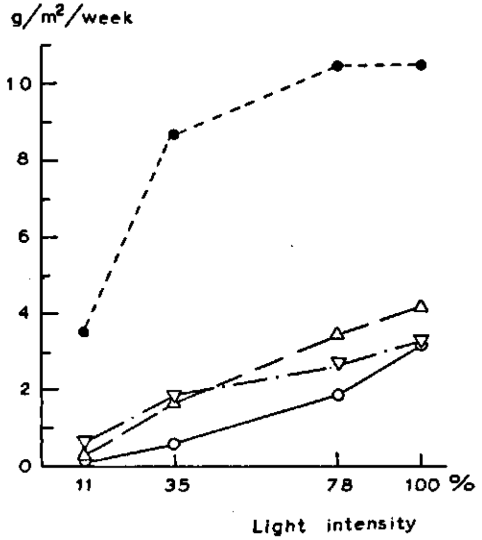


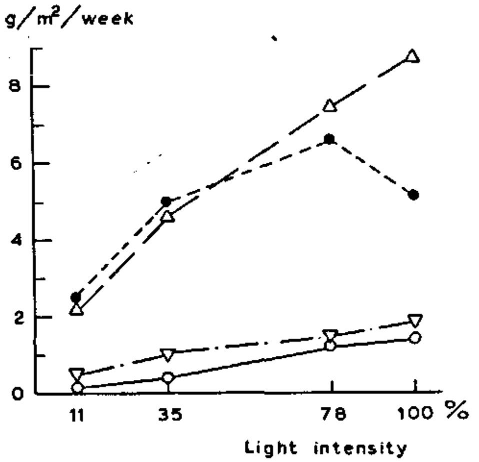
FIG. 43a
The effect of light intensity on mean partial NAR over the period 36-144 days from sowing.
Phytotron experiment 1965.
●- - - -● : leaf blades
▽—·—▽ : neck
△— —△: bulb
○——○: roots

area per unit time was used for enlarging the photosynthetic apparatus. It is interesting to note that NAR$_l$ sharply increased with increasing light intensity from 11 to 35% light, whereas with further increase a reduced increase in NAR$_l$ was observed until there was no increase with light intensity beyond 78%. On the other hand, NAR$_b$ increased linearly with increasing light intensity up to the highest intensity applied. Also ,NAR$_n$ increased as light intensity was raised to the highest value used; but the increase was relatively greater in NAR$_b$ as compared with the increase in NAR$_n$ at 78 and 100% light. It is clear also, that NAR$_r$ increased with increasing light intensity and the more so as light intensity was raised further than to 35%. Thus, it can be concluded that NAR$_b$ and NAR$_r$ contribute relatively more to the total NAR with increasing light intensity.

9. *Partial NAR's under controlled conditions over 192 days (entire growth period)*

The partial NAR values over the whole growth period in relation to relative light intensity are presented in fig. 43b. It is obvious that NAR$_b$, while remaining linear with light intensity, shifts to higher values, whereas NAR for the other plant organs shifts to lower values so that NAR$_b$ and NAR$_l$ came closer together while NAR$_n$ and NAR$_r$ lagged behind. This can be ascribed to the fact that the supply of dry matter gain/unit area/unit time to the bulb in the late stages of growth predominates over that to the other plant organs. A point worth considering is that the dry matter gain/unit area/unit time is more or less equally shared by leaves and bulb at low light intensities (11, 35%); at higher ones the supply of dry matter increase/unit area/unit time to the bulb exceeds that to the leaves, and mostly so at the highest light intensity. On the whole, it may be concluded that the curve for the total NAR in relation to relative light intensity

Fig. 43b
The effect of light intensity on mean partial NAR over the period 36–192 days from sowing.
Phytotron experiment 1965.
●- - - -● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots



is mainly determined by the NAR's for leaves and bulb, while NAR$_n$ and NAR$_r$ played a minor rôle.

What we would like to point out here, is that the entire plant NAR, as well as the partial NAR values under the phytotron conditions were lower than those under field conditions. However, the supply of dry matter gain/unit area/unit time to the leaves was relatively higher in the phytotron than in the field. Considering that the total dry matter production per plant per day at the highest light intensity in the phytotron was twice that in full daylight outside, it appears that a relatively low NAR, accompanied with a relatively large dry matter distribution per unit area/unit time over leaves, appears more efficient in total dry matter production than a higher total NAR value accompanied by a low rate of dry matter gain/unit area/unit time supplied to the leaves.

10. *Partial NAR's as % of total NAR, under controlled conditions*

In the previous sections, we have discussed light intensity effects on the rate of dry matter increase per unit area per unit time for the plant as a whole and for its various organs. In order to gain a better insight, and probably to reveal still clearer what happens, there seems much reason to express all partial NAR's values as % of total NAR at the different light intensities.

In fig. 44a we have presented the partial NAR's in percentages of total NAR in relation to light intensity over the growth period from 36 to 94 days after sowing, in the experiment under controlled conditions. During this period, in general, the percentage of total NAR of which the leaves appear to benefit is predominant over those for the other plant organs. However, distribution over the various organs differs according to treatment. As light intensity increases, NAR$_b$* and NAR$_r$ as % of total NAR also increases, while the percentage of NAR$_l$ decreass. On the other hand, the NAR$_n$ curve shows no appreciable difference at all light intensities except that it tended to be slightly higher at 100% light. A point of interest is that a striking resemblance can be observed when

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* indices indicate l(leaves), r(roots) b(bulbs) and n(necks).

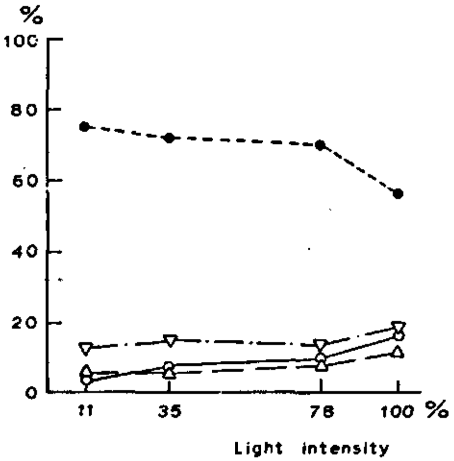


FIG. 44a
The effect of light intensity on mean partial NAR (expressed as % of NAR of the whole plant) over the period 36–94 days from sowing. Phytotron experiment 1965.
●- - - -● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots

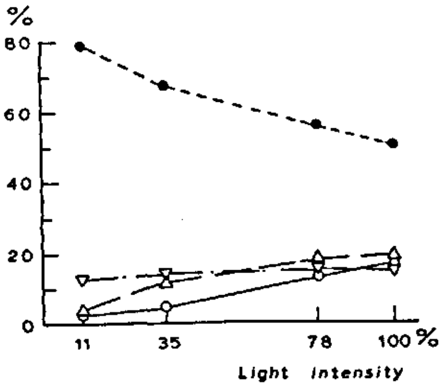


FIG. 44b
The effect of light intensity on mean partial NAR (expressed as % of NAR of the whole plant) over the period 36–144 days from *sowing*.
Phytotron experiment 1965.
●- - - -● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots

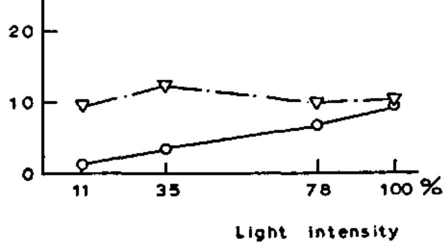


FIG. 44c
The effect of light intensity on partial NAR (expressed as % of NAR of the whole plant) over the period 36–192 days from sowing.
Phytotron experiment 1965.
●- - - -● : leaf blades
▽— · —▽ : neck
△— —△ : bulb
○———○ : roots

comparing the curves of the partial NAR's as % of total and the dry matter distribution over the various organs expressed as % of entire plant weight (fig. 40a).

More or less the same trends are obtained for the growth period from 36 to 144 days, in the phytotron experiment (fig. 44b).

Furthermore, the percentage of partial NAR's (of total NAR) as a function of light intensity over the entire growth period (192 days) is presented in fig. 44c. It is obvious that during this period, the NAR_b% becomes prevailing as compared with the preceding periods (94 and 144 days). The NAR_b and NAR_r% on one hand and the NAR_l on the other hand, like in the preceding growth periods, show opposite trends with respect to light intensity.

Moreover, also for this period there is reasonable agreement between the trends of dry weight distribution over the various organs expressed as percentage of total plant dry weight (see fig. 40b) and the trends of partial NAR's% of total NAR in their relation to light intensity.

CHAPTER VII

GROWTH AND DEVELOPMENT AS INFLUENCED BY DAYLENGTH, QUALITY OF LIGHT, INTENSITY OF SUPPLEMENTARY LIGHT AND AGE OF PLANT AT WHICH EXPOSED TO INDUCTIVE PHOTOPERIODS, RESULTS AND DISCUSSION

Extensive work has been done on photoperiodism of the onion. The dependence of bulb development on the stimulus of long days has been well established (GARNER and ALLARD, 1923; MCCLELLAND, 1928; THOMPSON and SMITH, 1938; HEATH, 1943; HEATH and HOLDSWORTH, 1948; CLARK and HEATH, 1962). Onion cultivars, however, differ markedly in their daylength requirements for bulb formation, as well as in the rate and uniformity of bulbing at daylengths that are above the minimum for the cultivar (MAGRUDER and ALLARD, 1937).

A. DAYLENGTH AND QUALITY OF SUPPLEMENTARY LIGHT EFFECTS (FIELD CONDITIONS)

In this section (1) we will deal in some detail with the growth in weight of various plant organs and with morphogenetic features developing during the growing season under daylength conditions in the field.

Among these features, bulb development is known to have pronounced relations to daylength, and moreover is of special interest from various aspects so that we have taken it apart for discussion at the beginning of this section.

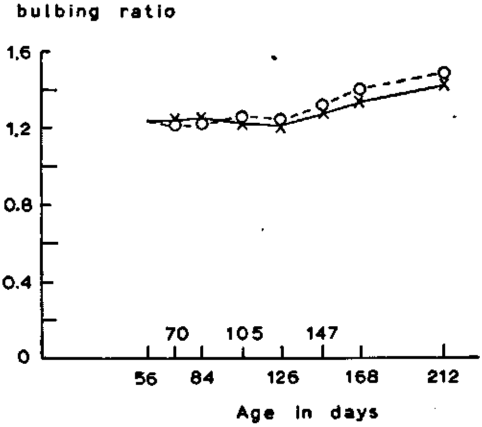
I. Preambular notion on bulb development

1. *1964 field experiment*

In an attempt to investigate the effect of daylength on bulb development of the cultivar 'Wijbo', a set of plants (grown from seeds) in the growth cabinets described by WASSINK and STOLWIJK (1953), received 8 hrs. of natural daylight only (SD treatment), while another group received 8 hrs. of natural daylight supplemented by 8 hrs. of about 700 ergs/cm^2/sec light supplied by daylight type fluorescent tubes (Philips, 55). Treatments started when the plants were 56 days old, and had two to three leaves.

In both treatments, the plants exhibited a luxuriant foliage growth more or less in the same manner. No differences could be detected between short and long day plots. The most striking result was that, although climatic conditions were fairly good to induce bulbing, as demonstrated by a full day control in natural daylight, the plants grown under 16 hrs. photoperiod (LD) like those grown under 8 hrs. photoperiod (SD), did not show any signs of bulb development and continued to produce new leaves and roots indefinitely until after 212 days old when the plants died as a result of freezing in November 1964.

FIG. 45a
The effect of daylength on bulbing ratio.
Field experiment 1964.
×———×: short day (8 hrs. natural daylight).
○- - - -○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).



Bulbing ratio. In the present work, the degree of bulb development was estimated as the 'bulbing ratio'. It can be seen from fig. 45a that up to 126 days old, the bulbing ratio was almost the same (around 1.25) for long and short day treatments. At more advanced age (between 126 and 212 days) it tended to increase slowly as the plants proceeded in age till maximum values were obtained by the end of the season. During this period, the bulbing ratio at 16 hrs. showed a slightly stronger increase than at 8 hrs. Differences, however, were not significant. The highest values found were 1.48 and 1.44 for the long and short day treatments respectively. Nevertheless, it should be emphasized here that these maximum bulbing ratios do not indicate actual bulb development. In this respect it has been reported by MANN (1952), working with garlic, that the bulbing ratio may be regarded as a reasonable measure of bulb formation and that it is largely independent of plant size. Its numerical value always lies above 1.0, but must be greater than about 2.0 to indicate definite bulb formation. Moreover, HEATH and HOLDSWORTH (1948) pointed out that even under short day conditions, the bulbing ratio increases slowly with age owing to slight swelling at the neck base. Therefore, the conclusion can be drawn that in both treatments applied no definite bulbing took place.

2. *1965 field experiment*

It was suggested that the quality of light used to extend the main photoperiod might have been a factor responsible for the failure of the plants to bulb in the long day treatment. For this reason, in the 1965 season, a third treatment in which the plants received 8 hrs. of natural daylight, supplemented by 8 hrs. of about 750 ergs/cm²/sec incandescent light supplied by 60 Watts Philips bulbs was added besides the aforementioned treatments of 1964. The plants were exposed to the different treatments when they were about 58 days old. Temperature records showed no appreciable variation between treatments, and the average daily temperature over the entire growing season was about 20°C. Periodic harvests were taken throughout the growth period.

Bulbing ratio. The question whether the plants bulbed or not in this season (1965) also can be answered from the results of the bulbing ratio presented in fig. 45b. It is apparent that up to 120 days after sowing, the bulbing ratio in all treatments did not show any marked increase and was about 1.32 at its highest value, indicating no real bulb development. Since by that time (120 days after sowing) in the plot receiving total natural daylight (intensity and duration) the plants developed definite bulbs and were about to mature (ripeness was attained 147 days from sowing, and the bulbs entered the dormant period). It was thought, therefore, that light intensity of both supplementary fluorescent and incandescent light was so low that bulbing could not be induced. For this reason, both long day cabinets were devided into two parts by a vertical black screen in the middle of the plot; in one part of each treatment the light intensity was maintained as before, whereas in the other part it was raised to about 6000 ergs/cm^2/sec for the fluorescent and incandescent light. Notwithstanding this, no signs of bulb development were detected in any of the treatments (short day, fluorescent and incandescent light extensions, irrespective of their light intensities) after 30 days from the beginning of the new treatments (152 days after sowing, see bulbing ratio). Therefore, in the period from 152 days up to the

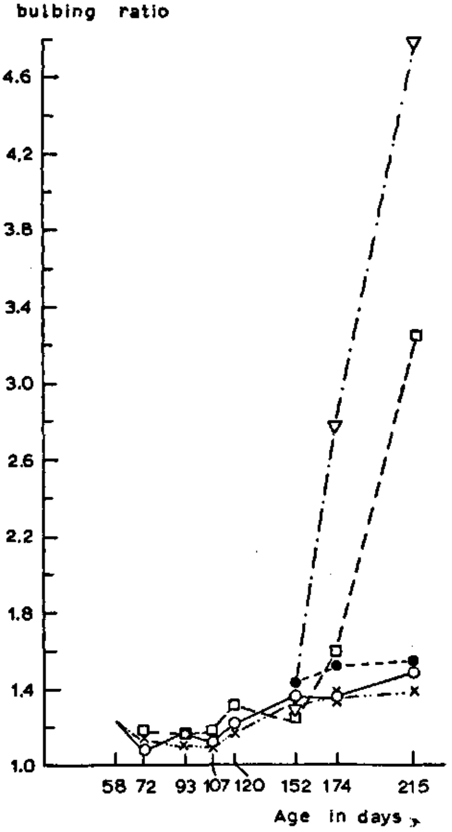


FIG. 45b
The effect of daylength, quality and intensity of supplementary light on bulbing ratio.
Field experiment 1965.

×— ·· —× : short day (8 hrs. natural day light).
●- - - -● : long day, i.e., short day + 8 hrs. fluorescent light of high intensity (6000 ergs/cm^2/sec).
○———○ : long day, i.e., short day + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
▽—· —▽ : long day, i.e., short day + 8 hrs. incandescent light of high intensity (6000 ergs/cm^2/sec).
□— —□ : long day, i.e., short day + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

end of the experiments (215 days from sowing), the period of supplementary fluorescent and incandescent low and high light intensity was extended to 16 hrs. instead of 8 hrs. Thus, the plants then received 8 hrs. of natural daylight as a basic photoperiod, supplemented by 16 hrs. of low (750 ergs/cm^2/sec) and relatively high (6000 ergs/cm^2/sec) fluorescent or incandescent light (plants thus were growing under continuous light), while the short day plot continued receiving 8 hrs. of natural daylight and then 16 hrs. darkness. Three weeks later (174 days from sowing) the bulbing ratio increased sharply at the high supplementary incandescent light treatment to reach about 2.75; in the low one it also increased, though less pronounced (bulbing ratio 1.62). In case of fluorescent high and low intensity of supplementary light and short day treatments, the bulbing ratios, although showing a slight increase especially in the high fluorescent light intensity, were lagging behind. At more advanced age (between 174 and 215 days after sowing), the bulbing ratio for supplementary high and low intensity of incandescent light treatments continued to increase rapidly to attain 4.75 and 3.22 for high and low intensity light respectively, indicating actual bulb development in both cases (bulbing ratios greater than 2.0). On the other hand, maximum bulbing ratios found by that time were about 1.38, 1.48 and 1.54 in short day, low and high intensities of supplementary fluorescent light respectively demonstrating the failure of the plants to bulb under such daylength regimes.

Apart from this, data were collected for growth in weight and some morphogenetic features induced by differences in daylength and quality of supplementary light at different developmental stages of growth. It seems worth while to mention briefly some of the results.

II. Growth in weight

1. *Entire plant dry and fresh weight*

Fig. 46a presents changes in dry weight per plant as a function of daylength and quality of supplementary light at different developmental stages. Between the first and second harvest no differences in dry weight existed between treatments. As the plants progressed in age (between 72 and 120 days from sowing), the dry weight at both long day treatments appeared to be close together, with the tendency of LD supplementary incandescent light to be always slightly higher; in short day one it was, with only one exception, lower. Differences, however, between the long day plots were insignificant. The slight decline in dry weight in LD supplementary fluorescent light observed at the third harvest is more likely due to experimental error. Since the light energy received by the plants in all cases was more or less the same (light intensity of supplementary light was too low to contribute significantly to photosynthesis), one would assume that the increase in dry weight per plant under long day conditions is primarily a consequence of speeding up the developmental growth rather than its direct effect on photosynthesis. In the period between 120 and 152 days after sowing, because of long exposure to incandescent light containing a relatively

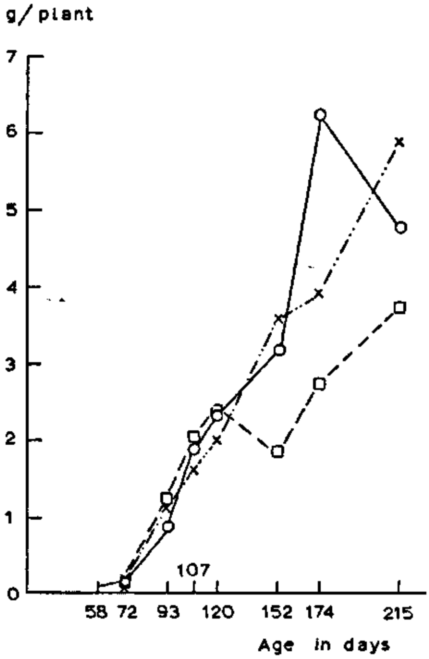


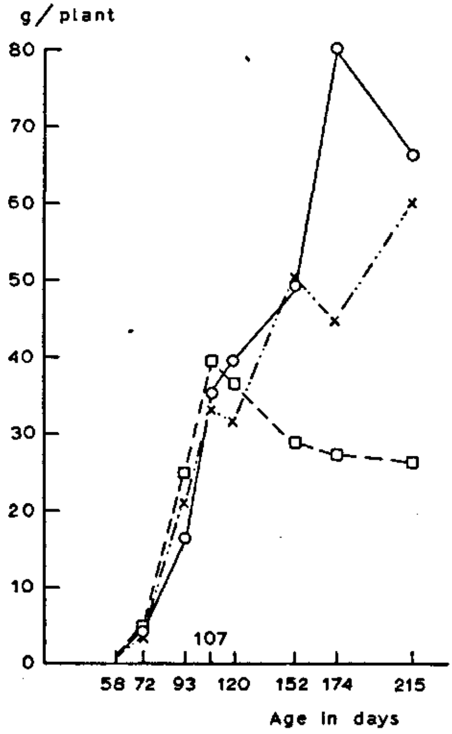
FIG. 46a
The effect of daylength and quality of supplementary light on dry weight of the whole plant.
Field experiment 1965.
×—··—×: short day (8 hrs. natural daylight).
○——○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□: long day, i.e., SD + 8 hrs, incandescent light of low intensity (750 ergs/cm²/sec).

large proportion of far-red radiation, the total plant dry weight at LD supplementary incandescent light treatment in contrast to that in other treatments (SD and LD supplementary fluorescent light) tended to decrease. Obviously, the far-red radiation promotes termination of the plant growth cycle as is especially indicated by the continuous decrease of leaf growth observed from 120 days onwards. This effect might be called 'harmful' if bulbing was not found to develop.

At more advanced age (between 152 and 215 days after sowing), due to daylength extension to become 8 hrs. of natural daylight plus 16 hrs. of incandescent or fluorescent supplementary light, the dry weight of the entire onion plant in LD supplementary incandescent light plot, contrary to the fresh weight, re-increased till a maximum was attained at the end of the growing season (see fig. 46b). This increase is mainly due to bulb development which made up the greater bulk of fresh weight as a result of exposure to inductive cycles (the dry matter content of the bulb is far greater than that of other onion plant organs i.e., blade, neck and root). In LD supplementary fluorescent light, as well as in SD treatments, owing to continuous emergence of new leaves and roots, the total dry weight per plant continued to increase; that the dry weight at the 7th harvest in LD supplementary fluorescent light exceeded that at the last harvest may be due to the fact that the former contained two split individuals out of the five plants making up the total number of the harvest.

Since the entire plant is composed of various organs, the differences in total plant weight induced by daylength and quality of supplementary light during the

FIG. 46b
The effect of daylength and quality of supplementary light on fresh weight of the whole plant.
Field experiment 1965.
×—··—×: short day (8 hrs. natural daylight).
○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).



growing season are the result of changes in the plant's constituents owing to the induced changes in the plant's cyclic development. Therefore, it seems interesting to follow the changes that may occur in the several plant parts, i.e., roots, blades, neck and bulb.

2. *Root dry and fresh weight*

As shown in fig. 47a, the dry weight of roots at the second harvest (72 days after sowing) in all treatments were more or less the same. As the plants proceeded in growth (in the period between 72 and 93 days from sowing), with only one exception, growth in root dry weight was favoured by exposure to long days particularly when the incandescent light was used to prolong the main photoperiod. In all treatments applied, root dry weight increased with time till a maximum was reached at a certain moment and then decreased. The highest dry weight value, however, was attained about two weeks earlier in the SD plot compared with long day ones. Because of bulb development (inhibitory effect of bulbing), the decline in root dry weight after its maximum was sharper in LD supplementary incandescent light. Thus the greatest dry weight of roots at the later stages of growth shifted in favour of LD supplementary fluorescent light, followed in order by the SD treatment, whereas it was lagging behind in LD supplementary incandescent light one.

We would like to point out here that new root emergence continued up to a

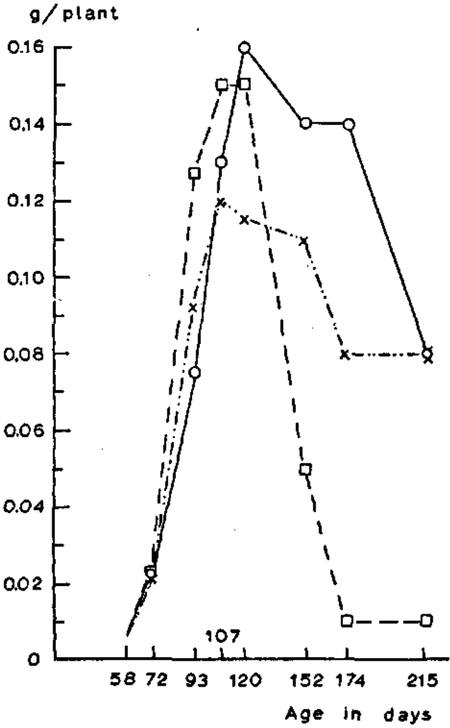


FIG. 47a
The effect of daylength and quality of supplementary light on root dry weight.
Field experiment 1965.

×—··—× : short day (8 hrs. natural daylight).

○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

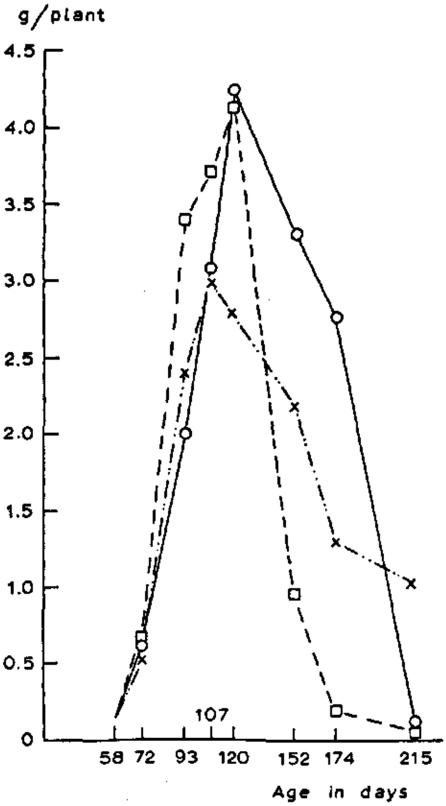


FIG. 47b
The effect of daylength and quality of supplementary light on root fresh weight.
Field experiment 1965.

×—··—× : short day (8 hrs. natural daylight).

○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

certain age after which it tended to be suppressed whether bulb development has begun or not (in the SD and LD supplementary fluorescent light treatments, although bulbing did not occur, the dry weight of roots decreased after its maximum). More or less the same trend for root fresh weight was observed (fig. 47b).

3. *Blade dry and fresh weight*

The dry weight of blades per plant as influenced by daylength and quality of supplementary light at periodic harvests is brought forward in fig. 48a. It is obvious that up to 93 days after sowing, no clear differences in blade dry weight were observed in all treatments; the decrease of blade dry weight in LD supplementary fluorescent light treatment noticed at the third harvest presumably is due to a sampling error. As the plants advanced in age (in the interval between 93 and 120 days after sowing), due to the greater specific leaf weight and/or to the increased blade size (length × diameter), blade dry weight at LD fluorescent supplementary light surpassed that at the other treatments. At more advanced age, owing to depression of new leaf emergence as a result of bulb development, the blade dry weight in case of incandescent light supplementation, in contrast to that in other treatments, tended to decrease. The sharp increase of blade dry weight with fluorescent light extension observed at the 7th harvest may be attributed to the inclusion of two split plants in the sample taken at that time.

Similar results were obtained for blade fresh weight (fig. 48b).

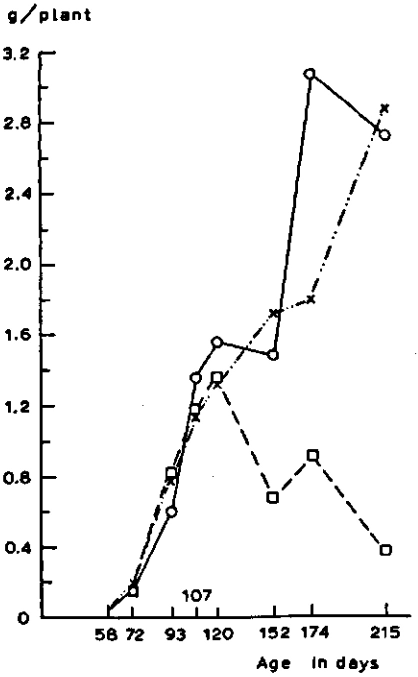


FIG. 48a
The effect of daylength and quality of supplementary light on leaf blade dry weight.
Field experiment 1965.

×— ·· —× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□ : long day, i.e.. SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

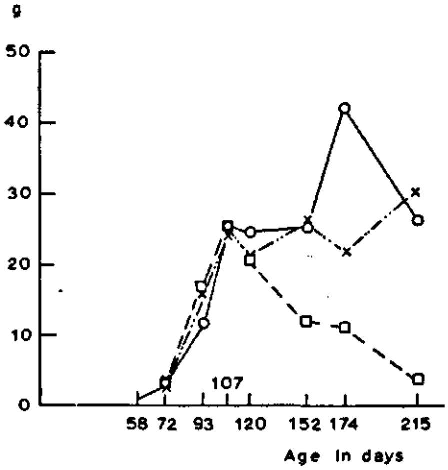


Fig. 48b
The effect of daylength and quality of supplementary light on leaf blade fresh weight.
Field experiment 1965.
×— ·· —× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

4. *Neck (pseudostem) dry and fresh weight*

Data illustrated in fig. 49a show the neck dry weight at different stages of growth as a function of daylength and quality of supplementary light. It is conceivable that up to the third harvest (93 days after sowing) no appreciable differences in neck dry weight could be detected between treatments. In the period between 93 and 120 days from sowing, owing to the elongating effect on neck length stimulated by long days in general and incandescent light extension in particular because of the high proportion of far-red light it contains, neck dry weight under long day conditions was found to exceed that in short day treatment and the more so in case of incandescent light supplementation. As the plants proceeded in age (between 120 and 174 days after sowing), neck dry weight continued to increase in all cases due to continual emergence of new leaves although the position was changed in favour of the SD and LD supple-

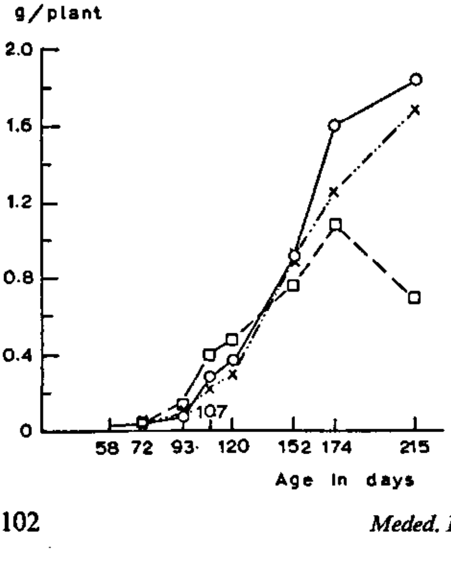


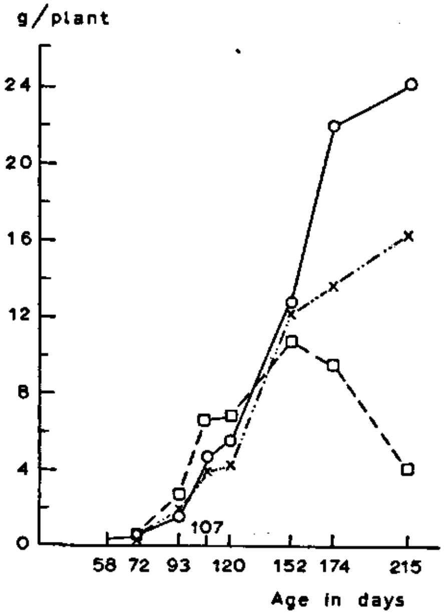
Fig. 49a
The effect of daylength and quality of supplementary light on neck dry weight.
Field experiment 1965.
×— ·· —× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

FIG. 49b
The effect of daylength and quality of supplementary light on neck fresh weight. Field experiment 1965.

×—··—×: short day (8 hrs. natural daylight).

○——○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).

□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^{2}sec).



mentary fluorescent light treatments presumably because of increased rate of old leaf death as a result of speeding up the plants' cyclic development by incandescent light. At more advanced age (between 174 and 215 days from sowing) owing to the cessation of new leaf emergence as a result of bulb development, neck dry weight in LD supplementary incandescent light, in contrast to the other treatments, tended to decrease.

The same trend was found for neck fresh weight (fig. 49b).

5. *Bulb dry and fresh weight*

The effects of daylength and light quality of supplementary light on bulb dry weight at different developmental stages are presented in fig. 50a. However, it should be emphasized here that bulb development in its proper meaning began only after 152 days from sowing; data before that time merely express dry weight of the somewhat swelling neck bases which can even occur under short day conditions or at non-inductive cycles in general. Nevertheless, it is apparent that, up to the third harvest (93 days from sowing), no marked variations in bulb dry weight were found. As the plants advanced in age (between 93 and 120 days after sowing, bulb dry weight in LD supplementary incandescent light tended to surpass that in other treatments. This increase may be attributed to increased length and thickness of swelling neck bases.

In the period between 120 and 152 days from sowing bulb dry weight in LD incandescent supplementary light, contrary to that in other treatments, did not show any increase. The reason for this remains not quite clear and may be, in part, due to sampling error. Owing to further daylength extension to 24 hrs. (continuous light) in both LD treatments (fluorescent and incandescent sup-

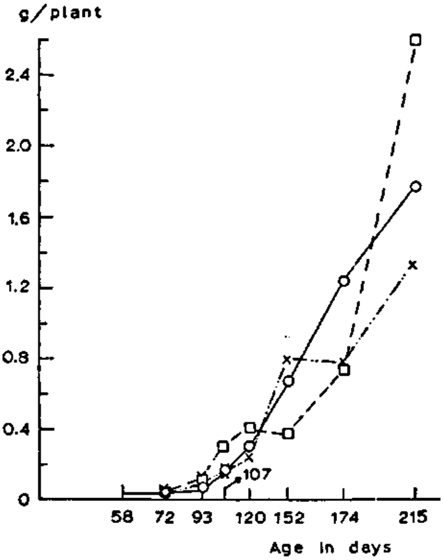


FIG. 50a
The effect of daylength and quality of supplementary light on bulb dry weight.
Field experiment 1965.
×—··—× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

plementary light) taking place in the interval between 152 days and the end of experiment, as a result of which the plants supplied with incandescent light showed actual bulb development, the dry weight of the bulb resumed its increase again and the more so in the latest stage of growth (between 174 and 215 days) so that it overtook that in the SD and LD supplementary fluorescent light plots. It should be kept in mind that the increase in bulb dry weight in LD supplementary incandescent light treatment is mainly due to actual bulb development (swelling of leaf sheaths and scale formation) as a consequence of exposure to proper cycles of daylength and light quality, whereas increase in bulb dry weight found in LD supplementary fluorescent light and SD treatments is mainly due to increased number of leaf sheaths and, to a smaller extent, to increase in their thickness without any accompanied scale formation; thus the bulb in the latter cases is a 'scallion' (a thickned neck base) and not a real bulb.

More or less the same results were obtained for bulb fresh weight (fig. 50b).

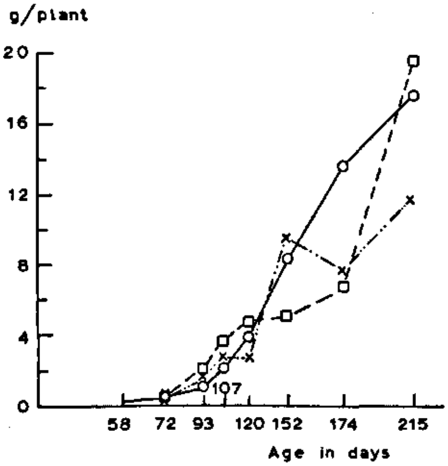


FIG. 50b
The effect of daylength and quality of supplementary light on bulb fresh weight.
Field experiment 1965.
×—··—× : short day (8 hrs. natural daylight).
○———○ : long day, i.e, SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□ : long day, i.e, SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

III. Some morphogenetic features

1. *Leaf growth*

a. Number of green blades per plant

As shown in fig. 51, up to 120 days old, the green blade number found on the plant tended to be, in most cases, slightly higher in LD treatments in general and when incandescent light was used to prolong the main photoperiod in particular. These differences, however, appeared not significant. As the plants proceeded in age (in the period between 120 and 152 days), it seems probable that the rate of leaf death especially with incandescent light extension exceeded that of new leaf emergence so that the green leaf number showed only a slight increase in some cases, or even decreased in others. At more advanced age (in the interval from 152 to 174 days after sowing), green leaf number in LD fluorescent light, contrary to that in other treatments, showed a big rise. However, this big increase in leaf number under LD fluorescent light is in part due to inclusion of two double plants out of five making up the entire sample. With still more advanced age (from 174 days to the end), because of bulb development in LD incandescent light in contrast to other treatments, leaf number in that case decreased sharply (inhibitory effect of bulbing), whereas in SD it continued to increase; in LD fluorescent light the decrease is mainly due to the fact that no double plants were included this time.

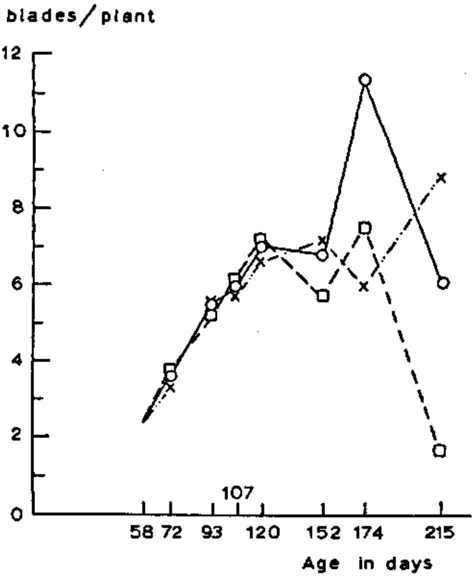


FIG. 51
The effect of daylength and quality of supplementary light on number of green leaves.
Field experiment 1965.
×— ·· —× : short day (8 hrs. natural daylight).
○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

b. Leaf length

The average length of the longest leaf at periodical harvests as influenced by daylength and quality of supplementary light is brought forward in fig. 52a. It is clear that up to the third harvest (93 days after sowing), because of the elonga-

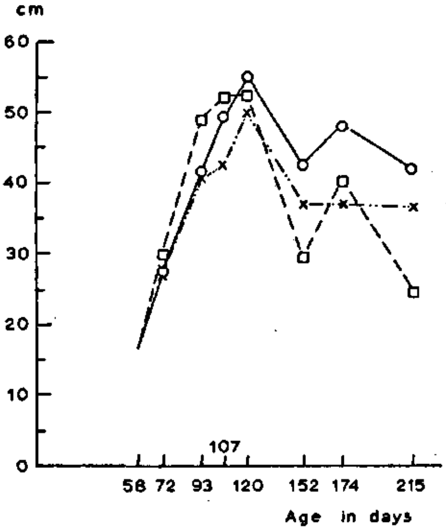


Fig. 52a
The effect of daylenght and quality of supplementary light on the length of the longest leaf blade.
Field experiment 1965.
×— ·· —×: short day (8 hrs. natural daylight.)
○———○: long day, i.e. SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/ssc).
□— —□: long day, i.e, SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

ting effect of far-red radiation which the incandescent light contains, leaf length in LD supplementary incandescent light treatment tended to surpass that obtained in LD with supplementary fluorescent light and in SD; in the latter items, leaf length was more or less the same. As the plants progressed in age (between 93 and 120 days) leaf length in all cases continued to increase and the more so in LD supplementary fluorescent light, so that it was found to exceed that in LD supplementary incandescent light plot when the plants were 120 days old. By that time maximum leaf length was attained; thereafter it decreased. The decline, however, in case of incandescent light extension seems somewhat exaggerated. That leaf length, in all treatments applied, decreased after its maximum may be attributed to the fact that every successive mature leaf is longer than its predecessor only in an actively growing plant.

The same trend was found in 1964 for SD and LD supplementary fluorescent light treatment, the only ones applied during that year (fig. 52b).

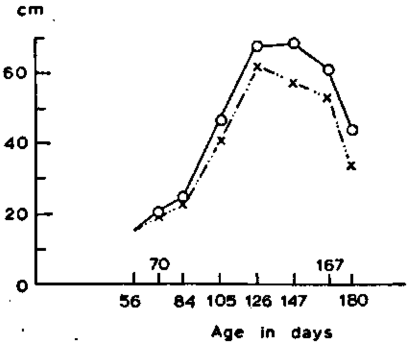


Fig. 52b
The effect of daylength on the length of the longest leaf blade.
Field experiment 1964.
×— ·· —×: short day (8 hrs. natural daylight).
○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

c. Leaf diameter

Up to 107 days old, as is obvious from fig. 53a, the average diameter of the biggest leaf in LD fluorescent light supplementation, with only one exception, always lagged behind, while in the other treatments no appreciable differences could be detected. In the period between 120 and 152 days, owing to increased rate of leaf death caused by far-red radiation, leaf diameter at the LD supplementary incandescent light plot decreased, whereas in the other treatments it continued to increase. Thus, the position was changed in favour of LD supplementary fluorescent light treatment so that leaf diameters in the latter as well as in the SD one were close together. However, the decline in the LD incandescent light treatment, recorded after 152 days from sowing, seems to be overestimated. At more advanced age (from 152 to 215 days old), leaf diameter in all treatments tended to decrease as a result of senescence in the SD and LD supplementary fluorescent light plots, and because of the depression of new leaf emergence in case of incandescent light extension owing to bulb development. In the period between 120 and 215 days, leaf diameter in the SD treatment tended to be slightly higher than in LD supplementary fluorescent light.

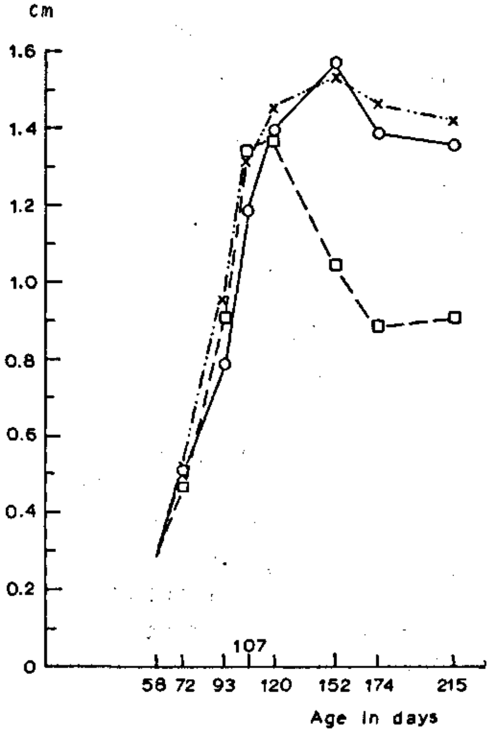


FIG. 53a

The effect of daylength and quality of supplementary light on leaf blade diameter.

The data are those of the largest leaf present on each plant at each sample.

×— ·· —× : short day (8 hrs. natural day light).

○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

Similar results were obtained in 1964 (fig. 53b).

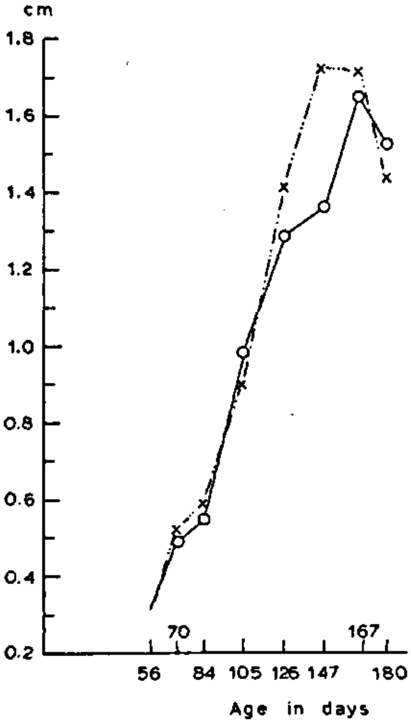


FIG. 53b
The effect of daylength on leaf blade diameter. The data are those for the largest leaf present on each plant at each sample.
Field experiment 1964.
×—··—× : short day (8 hrs. natural day light).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

d. Specific leaf weight

Data illustrated in fig. 54 indicate that, in general, the dry weight per unit leaf area in mg/cm² was greater under short day conditions than under long day conditions. Furthermore, using incandescent light for extending the main photo-

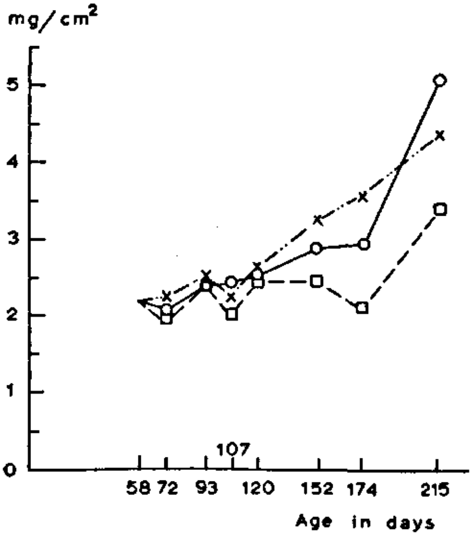


FIG. 54
The effect of day length and quality of supplementary light on specific leaf weight.
Field experiment 1965.
×—·—× : short day (8 hrs. natural day light).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

period resulted in a decline in the specific leaf weight, as compared with fluorescent light. Increased specific leaf weight in short days cannot be attributed to reduced water content under such conditions, since the dry matter content of leaves was found to increase with exposure to long days. Thus, it becomes reasonable to assume that increased cell expansion at the expense of dry matter accumulation and/or the drainage of assimilates to the other plant organs under long day conditions, especially with incandescent light extension, may be factors responsible for decreased specific leaf weight in long day conditions.

In all treatments applied, possibly owing to decreased water content with time, the specific leaf weight increased as plants advanced in age, till a maximum was attained at the end of the growing season.

e. Total blade area per plant

As apparent from fig. 55, the total plant blade area followed more or less the same trend as the green leaf number (see fig. 51).

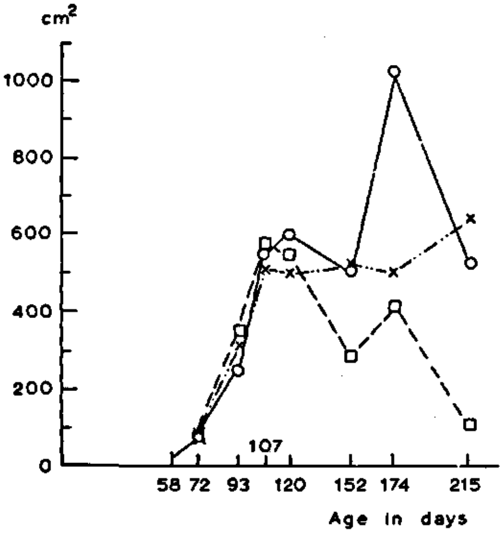


FIG. 55
The effect of daylength and quality of supplementary light on total leaf area per plant.
Field experiment 1965.

×—··—×: short day (8 hrs. natural day light).
O———O: short day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

2. *Neck (pseudostem) growth*

a. Neck (pseudostem) length

Neck length as a function of daylength and quality of supplementary light is brought forward in fig. 56a. It is clear that neck length was greater under long-day conditions. This increase is mainly due to increased length of the leaf sheaths rather than to increased number of leaves.

With incandescent light as daylength extension, the elongation effect was more pronounced than in the case of fluorescent supplementary light. This can be ascribed to the greater proportion of far-red radiation the incandescent light contains. The increase of neck length with time up to 174 days old, observed in all treatments applied, is due to the fact that each successive leaf

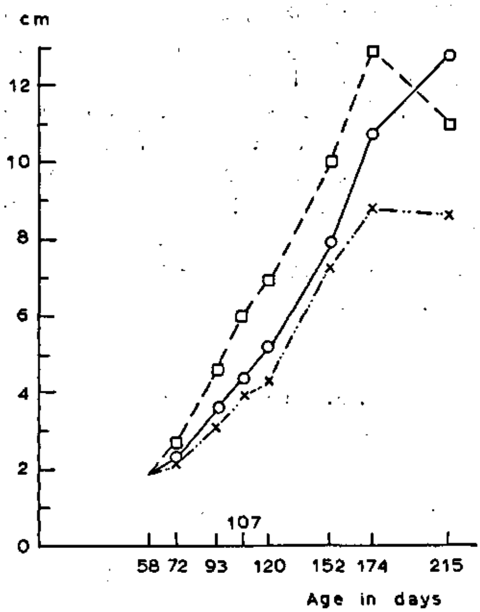


FIG. 56a
The effect of daylength and quality of supplementary light on neck length.
Field experiment 1965.
×—··—×: short day (8 hrs. natural daylight).
○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

sheath is longer than its predecessor in an actively growing plant. With more advanced age, because of bulb development in LD supplementary incandescent light, neck length in the latter tended to decrease, in contrast to that in the other treatments.

b. Neck (pseudostem) diameter

It is apparent from fig. 56b that no differences in neck diameter occurred in all treatments between the first and second harvests. As the plants proceeded in growth (between 72 and 107 days old), neck diameter for both LD supplemen-

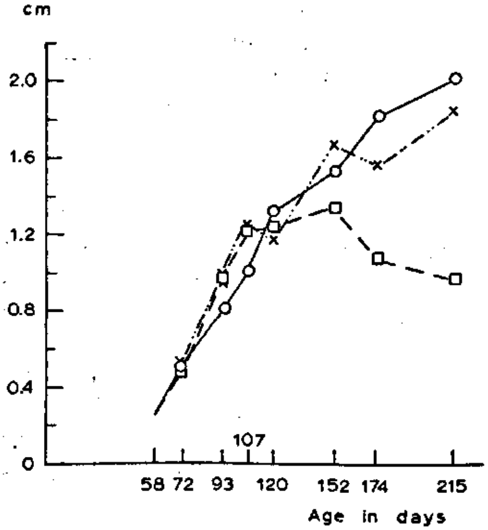


FIG. 56b
The effect of daylength and quality of supplementary light on neck diameter.
Field experiment 1965.
×—··—×: short day (8 hrs. natural daylight).
○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).
□— —□: long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

tary incandescent light and SD treatments was the same, while it lagged behind somewhat in LD supplementary fluorescent light treatment. In the period from 120 to 152 days after sowing, the position was changed in favour of the LD supplementary fluorescent light treatment, so that neck diameter in the latter exceeded that obtained with LD supplementary incandescent light, possibly because of continual new leaf emergence in case of fluorescent light extension. However, it is likely also that neck diameter in LD incandescent light recorded at 152 days from sowing was somewhat underestimated. At more advanced age (between 152 and 215 days after sowing) owing to cessation of new leaf emergence and possibly because of the passage of material from the neck to the developing bulb, neck diameter in the case of supplementary incandescent light treatment, in contrast to other treatments, tended to decrease.

3. *Bulb growth*

a. Growth in diameter

It should be noticed that real bulb development has begun only in LD supplementary incandescent light treatment after 152 days from sowing when further daylength extension (to 24 hrs.) took place; in other treatments it was absent throughout the entire season. Data recorded in the absence of actual bulbing show the diameter of the slightly swelling neck bases which effect can occur even at exposure to non-inductive cycles.

As shown in fig. 57, up to 72 days old, there were no differences in bulb dia-

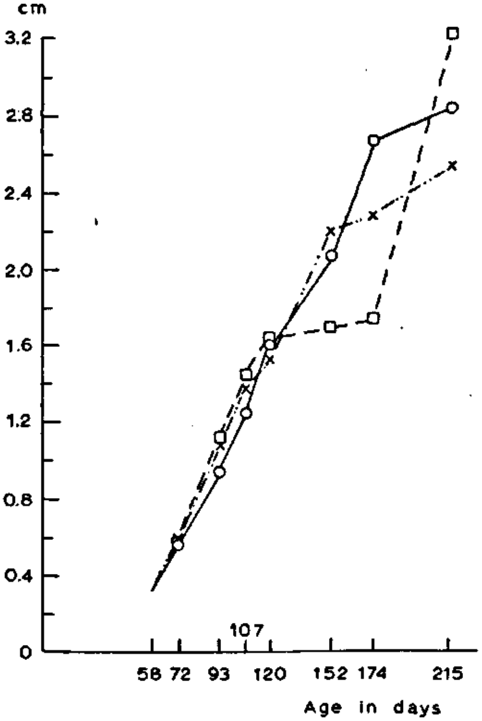


FIG. 57
The effect of daylength and quality of supplementary light on bulb diameter. Field experiment 1965.

×—··—×: short day (8 hrs. natural daylight).

○———○: long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm²/sec).

□— —□: long day, i.e, SD + 8 hrs. incandescent light of low intensity (750 ergs/cm²/sec).

meter (swelling neck base) between treatments. Between the second and fifth harvest, with only one exception, bulb diameter (neck base) was more or less the same in LD supplementary incandescent light and SD treatments while it was lower in LD supplementary fluorescent light treatment. It seems that this is a morphogenetic effect induced by daylength and quality of supplementary light. With fluorescent light extension, it was observed that relatively longer and narrower leaves were formed while the opposite was true in short day as well as with incandescent light supplement. As the plants proceeded in age (between 120 and 174 days old) the diameter of the bulb (neck base) in the incandescent light treatment continued to increase slowly and even was overtaken by that in the other treatments. Reasons for this are not quite clear, but it is likely that it is at least in part, due to sampling error. At more advanced age (in the period between 174 and 215 days), owing to rapid bulb development occurring in LD supplementary incandescent light (as a result of further daylength extension to 24 hrs. with the proper light quality), bulb diameter was found to increase so sharply that it exceeded the diameter of neck base in both LD supplementary fluorescent light and SD treatments. It appears that further daylength extension with supplementary fluorescent light (after 152 days from sowing) also stimulated swelling of neck bases so that the diameter in the latter was found to exceed its analogy in SD treatment in the priod from 174 days up to the end of the season. However, bulb development in its proper meaning was absent in both cases.

4. *Correlations*

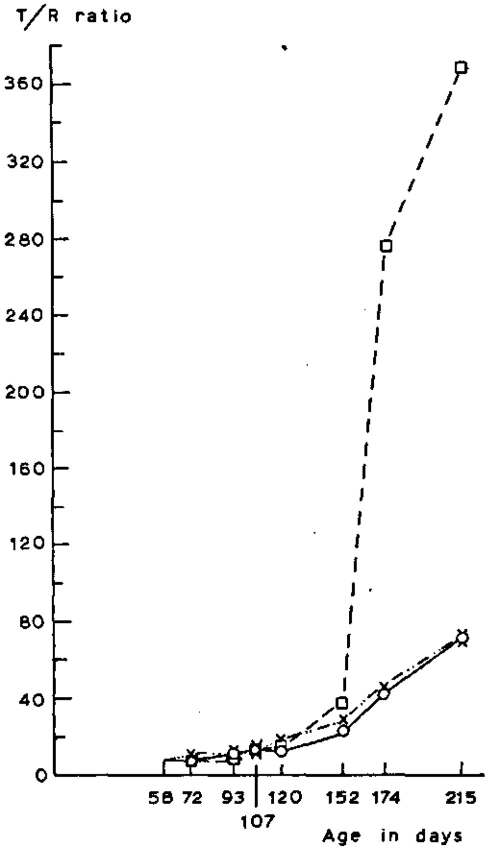
a. Top/root ratio (on dry weight basis; blades, neck and bulb included in top)

As is clear from fig. 58a, no appreciable variations between treatments were observed from the date of sowing up to 120 days old. As the plants proceeded in age (between 120 and 152 days from sowing), possibly because of bulb induction and its depressive effect on new root emergence in comparison with tops, the top/root ratio in supplementary incandescent light treatment tended to surpass that in the other treatments (both blade and root dry weight decreased during that interval, but the decrease in root dry weight was more marked). Owing to bulb development taking place in LD supplementary incandescent light treatment as a result of further daylength extension (24 hrs.) after 152 days from sowing, the top/root ratio in the latter increased very sharply whereas in the other plots it also continued to increase but less pronouncedly. This marked increase in top/root ratio is a net result of increased bulb dry weight (a part of the top) in association with a marked decrease in root dry weight (inhibitory effect of bulbing).

The time trend of the top/root ratio shows only a slight increase from the date of sowing up to 120 days, indicating more or less an equilibrium between top and root production. In the period from 120 days onwards, the top/root ratio, in all treatments, considerably increased to reach its maximum values at the end

FIG. 58a
The effect of daylength and quality of supplementary light on top/root ratio. (top = blades + neck + bulb).
Field experiment 1965.

×—··—× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).



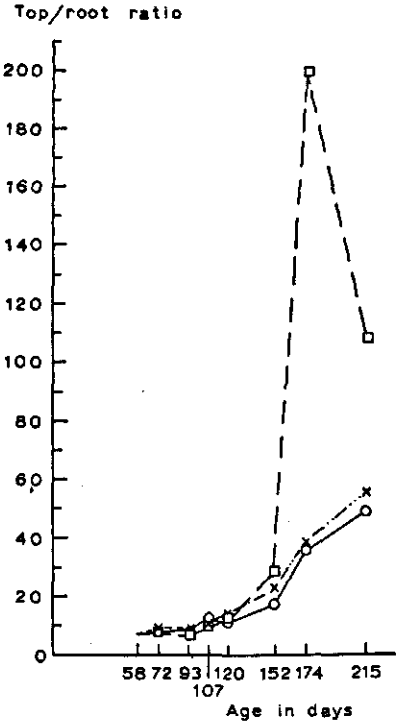


FIG. 58b
The effect of daylength and quality of supplementary light on top/root ratio.
(top = blades + neck).
Field experiment 1965.

×—··—× : short day (8 hrs. natural daylight).
○———○ : long day, i.e., SD + 8 hrs. fluorescent light of low intensity (720 ergs/cm^2/sec).
□— —□ : long day, i.e., SD + 8 hrs. incandescent light of low intensity (750 ergs/cm^2/sec).

of the growing season; this increase demonstrates that top growth gradually becomes more predominant.

Fig. 58b shows the top/root ratio when bulb dry weight is excluded. There is hardly any difference, except that, in this case, the top/root ratio under supplementary incandescent light decreased in the period between 174 and 215 days, owing to the fact that the bulb contains most of the dry weight of tops during this period in the latter treatment (supplementary incandescent light).

B. DAYLENGTH AND QUALITY OF SUPPLEMENTARY LIGHT EFFECTS (CONTROLLED CONDITIONS)

I. Effects of light quality

In a further attempt to study the effect of light quality on bulb development, 12 weeks old seedlings grown in pots under short day conditions (12 hrs.) and constant intensity and temperature (25 °C) were divided into groups and exposed to the following treatments.

1. A 24 hrs. light period (continuous light) supplied by TL 120 W/33 (56000 ergs/cm^2/sec.) at 25 °C.
2. A 24 hrs. light period consisting of a mixture of fluorescent and incandescent light (55000 ergs/cm^2/sec and 1000 ergs/cm^2/sec respectively) at 25 °C.
3. Treatments no. 1 and 2, carried out at 15 °C.
4. A 12 hrs. daily period of fluorescent light only (70000 ergs/cm^2/sec) + 12 hrs. of supplementary red light (5000 ergs/cm^2/sec) at 20 °C.
5. A 12 hrs. daily period of fluorescent light only (70000 ergs/cm^2/sec) + 12 hrs. of supplementary far-red light (5000 ergs/cm^2/sec) at 20 °C.

1. *Bulb development in continuous light at 25 °C*

Photo no. 1 shows that three weeks after the start of the treatments, bulbing was absent in plants grown under continuous fluorescent light only (treatment no. 1), on the other hand, some signs of bulb development were observed in plants exposed continually to a mixture of fluorescent and incandescent light (treatment no. 2). Two weeks later (photo no. 2), bulb development became more marked in plants – grown in gravel (GR) or soil (S) culture – and subjected continually to the mixture of fluorescent and incandescent light, whereas it still was completely absent under fluorescent light only. At more advanced age (53 days after transfer to continuous light), plants grown in a mixture of fluorescent and incandescent light, bulbs were about to mature (most of the tops collapsed); in TL light only plants started to show some signs of bulbing (photo no. 3). These signs, however, were very minor, and we will not go into probable explanation.

2. *Bulb development in continuous light at 15 °C*

These treatments were also carried out under the same conditions of light intensity, quality, and duration at 15 °C instead of 25 °C (treatment no. 3).

PHOTO 1

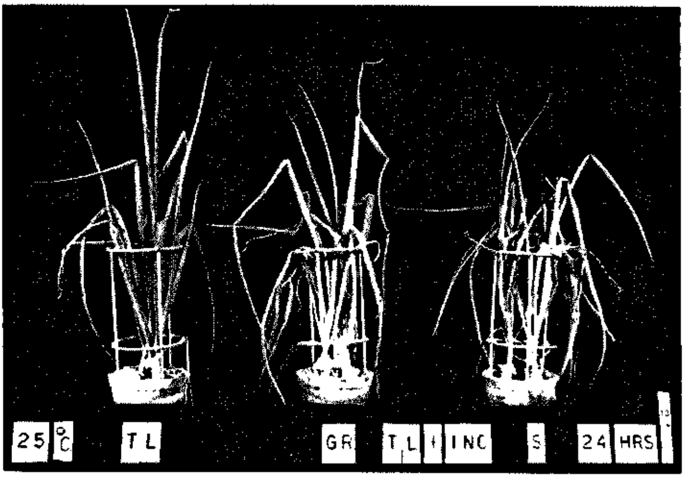


PHOTO 2

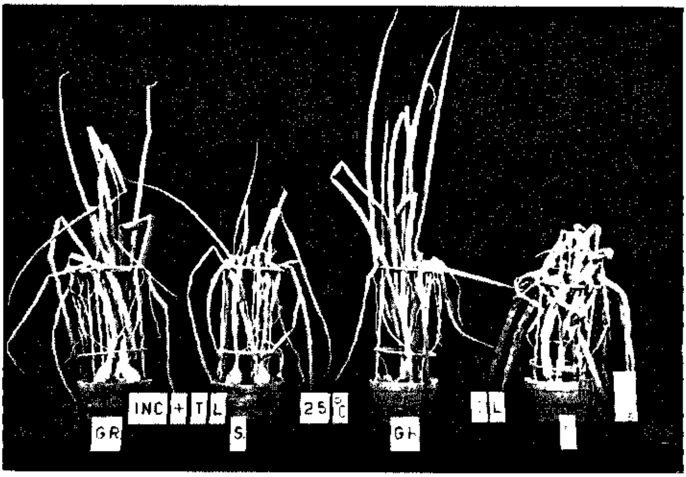
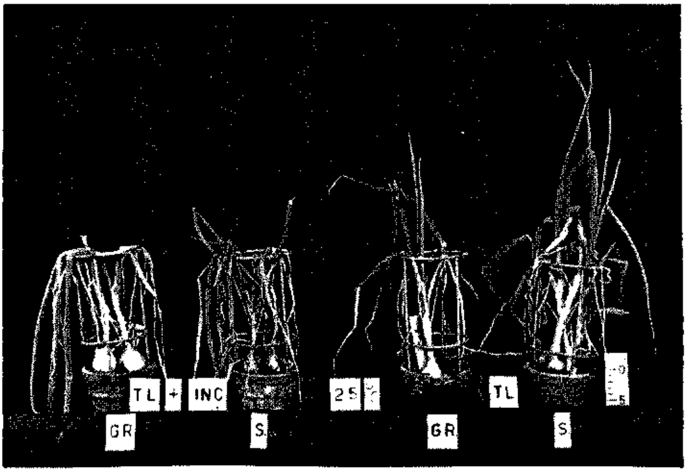


PHOTO 3



Photos 1–3
Changes in bulb development under continuous light:
TL = fluoscent light
TL + inc. = fluorescent + incandescent light.
Temperature 25 °C.

Three weeks after transfer to continuous light (photo no. 4), no signs of bulbing were apparent, neither in fluorescent light only nor in a mixture of fluorescent and incandescent light. Two weeks later, bulb development took place in plants exposed to the mixture of fluorescent and incandescent light, contrary to those grown in fluorescent light only (bulbing is still absent, photo no. 5). At more advanced age (53 days after exposure to continuous light, photo no. 6), bulb formation became much more pronounced at the mixture while it still was absent in fluorescent light only.

An observation worth mentioning here is that the bulbing plants bolted (left side of the photo), whereas the non-bulbing did not. It is generally accepted that low temperature stimulates flowering of the onion plant and this is in full agreement with our results (the plants flowered under 15 °C and did not at 25 °C). The reason why the bulbed plants only bolted while the non-bulbed did not, when grown under the same low temperature of 15 °C, is not yet clear.

These experiments (bulb development at 15 and 25 °C in continuous light) show that high temperature (25 °C) accelerated bulb formation while low temperature (15 °C) delayed it in case of continuous mixed light; in fluorescent light alone bulbing was completely absent at 15 °C and was very minor at 25 °C. What we would like to point out here is that these experiments were not designed to demonstrate a true interaction between daylength and temperature, since for this purpose the mutual interchange ability of daylength and temperature effects would have to be demonstrated. Our present type of experiment shows that the effect of an inductive daylength is realized at a higher speed at 25 °C than at 15 °C, which seems to be in good accordance with the general effect of increase in temperature on metabolic rates.

It seems to fit quite well in these results that the plants at 15 °C finally showed a bigger bulb than those at 25 °C. This is easily understood from current considerations on the relation between temperature and overall energy balance. The latter tends to be more to the positive side at lower temperatures, because of decreased respiration intensity.

In order to establish a possible, true interaction between daylength and temperature effects, the experiment should be designed so as to establish whether the critical duration of low light extension of the main photoperiod might in part be replaced by increase or decrease of temperature.

3. *Bulb development in supplementary light during 12 hrs. of red or far-red, extending a basic photoperiod of 12 hrs. fluorescent light*

With regard to the plants receiving 12 hrs. of fluorescent light alone, supplemented with 12 hrs. of either red or far-red (treatments nos. 4 and 5), it is seen from photos no. 7, 8, and 9 taken at successive intervals, that bulbing was not induced, neither by red, nor by far-red. Even when plants were maintained one month longer than the date photo no. 9 was taken, no bulbing could be detected.

PHOTO 4

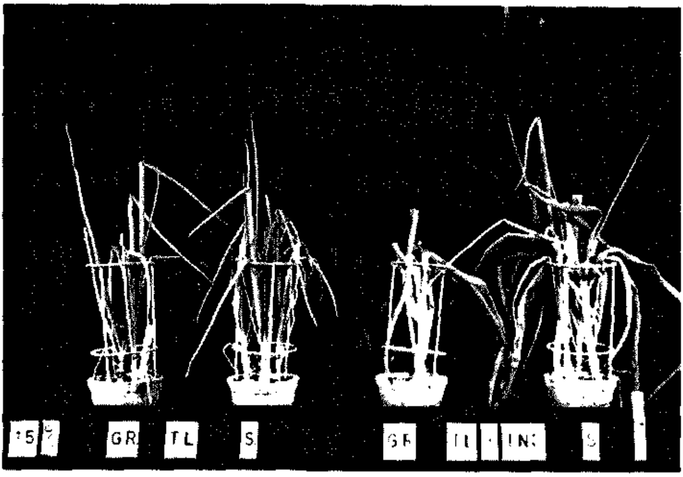


PHOTO 5

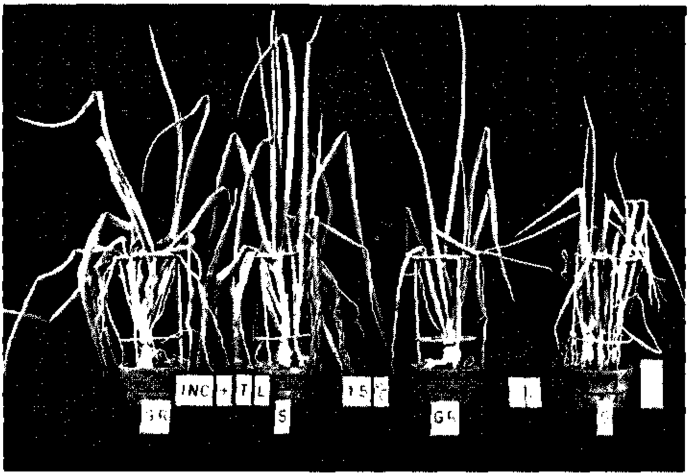
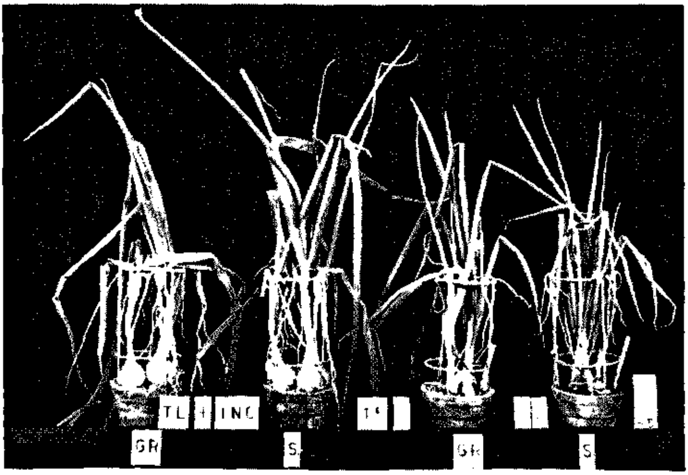


PHOTO 6



Photos 4–6
Legend as Photos
1–3.
Temperature 15 °C

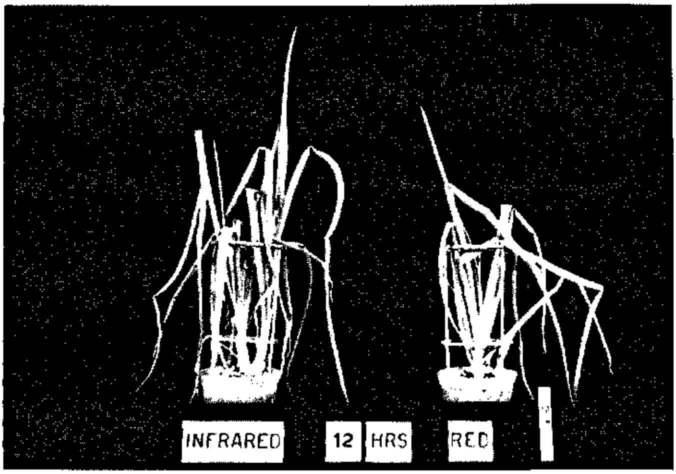


Photo 7

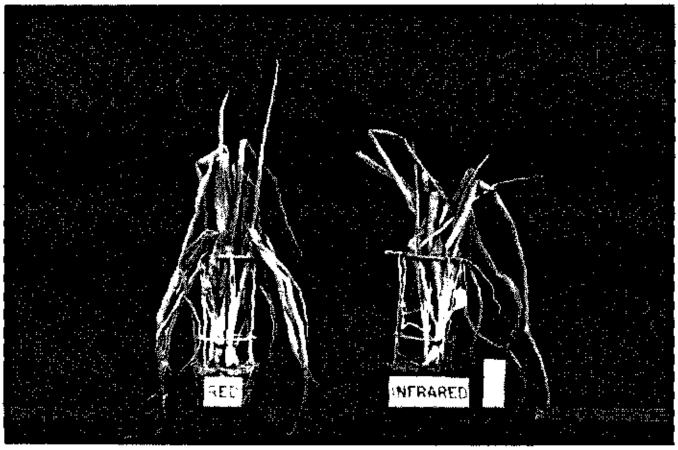


Photo 8

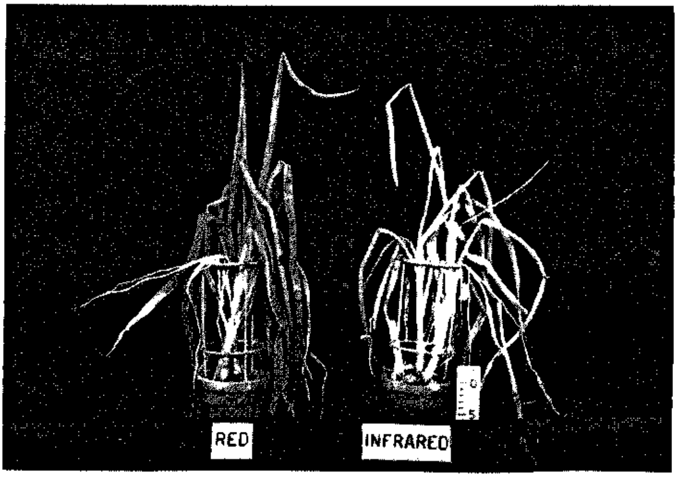


Photo 9

Photos 7–9
Changes in bulb development in supplementary 12 hrs of red or far-red light, extending 12 hrs fluorescent light. Temperature 20°C.

II. Growth and development of the onion plant as influenced by supplementary light at different intensities and durations

1. *Bulb development during 8 hrs. supplementary incandescent light of different intensities*

The degree of bulbing, expressed in the bulbing ratio, as affected by supplementary light of different intensities at successive harvests, is illustrated in fig. 59a. In this experiment, the plants received 12 hrs. of high light intensity (63000 ergs/cm^2/sec.) supplied by TL 120 W/33-tubes as a basic photoperiod, extended by 8 hrs. of incandescent light of different intensities, ranging from 730 to 8700 ergs/cm^2/sec in the visible region of the spectrum. Temperature was 25°C throughout the growing season. It can be seen from fig. 59a that 24 days after the start of the treatments (69 days old plants), the bulbing ratios for all treatments were around 1.2, indicating the absence of bulb development, irrespective of the intensity of supplementary light. In the period between 69 and 93 days after sowing, the bulbing ratios increased, and the more so as light intensity of supplementary light was raised, up to 4750 ergs/cm^2/sec. The rate of increase was more pronounced with increase of the intensity from 720 to 3200 ergs/cm^2/sec than with further increase. Thus, the ratios recorded at 93 days after sowing were about 1.32, 2.50, 2.98 and 2.84 for 720, 3200, 4750 and 8700 ergs/cm^2/sec intensities of supplementary light respectively. These ratios, however, demonstrate

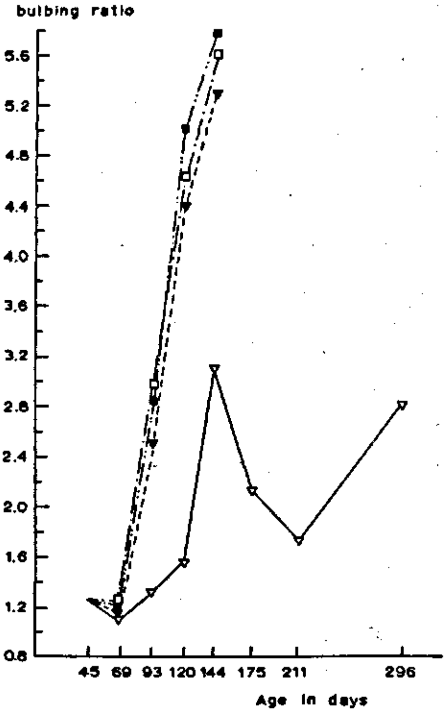


FIG. 59a
The effect of supplementary light of different intensities on bulbing ratio (12 hrs. fluorescent light + 8 hrs. of incandescent light of different intensities).
Phytotron experiment 1966.
▽——▽ : 8 hrs. at 720 ergs/cm^2/sec.
▼- - - -▼ : 8 hrs. at 3200 ergs/cm^2/sec.
□-·-·-□ : 8 hrs. at 4750 ergs/cm^2/sec.
■-··-··-■ : 8 hrs. at 8700 ergs/cm^2/sec.

the absence of bulbing at the lowest light intensity (720 ergs/cm²/sec) and the presence of actual bulb development at the other ones (bulbing ratios greater than 2.0). As the plants advanced in age (in the interval between 93 and 120 days), the bulbing ratios continued to increase in all treatments, while the higher the intensity of supplementary light, the greater the bulbing ratio was. Nevertheless, the bulbing ratio at the lowest intensity of supplementary light was only 1.56, indicating that real bulb development was still absent. At still more advanced age (between 120 and 144), the bulbing ratios, in all cases, still increased while the same relationship between treatments holds true. Ratios found after 144 days from sowing were about 3.08, 5.30, 5.70 and 5.78 for the lowest to the highest light intensities respectively. The last three ratios indicate maturity of bulbs, whereas the first one only shows that actual bulb development is taking place.

Following bulb development at 720 ergs/cm²/sec supplementary light intensity at further stages of growth, the bulbing ratio was found to decrease, followed by another increase. This irregularity of data arose from the fact that bulbing of the individuals under this condition (low intensity) was not regular, so that some plants already bulbed while others still did not. Furthermore, at the lowest intensity of supplementary light (720 ergs/cm²/sec), plants having developed mature bulbs before 144 days old, resumed their vegetative growth, forming new blades and roots at the expense of their mature bulbs when maintained growing longer. This along with the still non-bulbing plants made the ratio to drop after its peak. Briefly, the intensity of supplementary light, necessary to produce 100% normal bulbs, was found to be higher than that required to produce normal bulbs in some plants only, indicating that the cultivar used is not homozygous in its response to the applied cycles for bulb induction. On the other hand, intensities of supplementary incandescent light in the range from 3200 to 8700 ergs/cm²/sec for 8 hrs. given after a basic photoperiod of 12 hrs. at 63000 ergs/cm²/sec of fluorescent light were sufficient to obtain uniformity in bulbing.

2. *Bulb development during 4 or 6 hrs. supplementary incandescent light of different intensities*

In this experiment, 4 hrs. of different incandescent light intensities ranging from 720 to 11250 ergs/cm²/sec was used to extend the main photoperiod of 12 hrs. of the same light intensity and source as previously mentioned; temperature also being 25°C. The bulbing ratios were estimated periodically and the results are presented in fig. 59b. It is apparent that the highest values of bulbing ratio after 296 days from sowing ranged from 1.45 to 1.72 for the intensities of supplementary light applied, indicating that actual bulb development did not occur, even after a long period. This growth period is considerably longer than that necessary for production of mature bulbs under the natural conditions prevailing in the Netherlands (two times as much). Therefore, when no sign of bulb development could be detected even after 175 days from sowing, the treatments receiving 3200, 4750 and 8700 ergs/cm²/sec intensities of supplementary incandescent light were divided into two parts, one

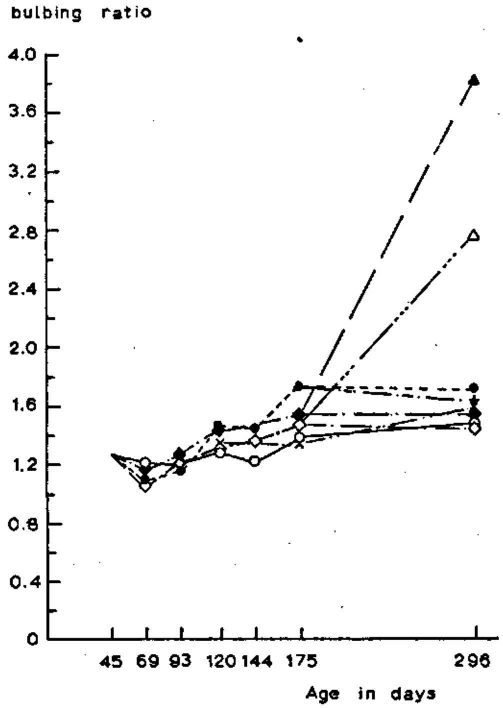


FIG. 59b
The effect of supplementary light of 4 or 6 hrs. duration at various intensities ranging from 720 to 11250 ergs/cm²/sec on bulbing ratio.
Phytotron experiment 1966.
○———○ : 4 hrs. at 720 ergs/cm²/sec.
●- - - -● : 4 hrs. at 3200 ergs/cm²/sec.
◇-·-·-·◇ : 4 hrs. at 4750 ergs/cm²/sec.
◆—·—◆ : 4 hrs. at 8700 ergs/cm²/sec.
×—··—··—× : 4 hrs. at 11250 ergs/cm²/sec.
+—·—·—+ : 6 hrd. at 3200 ergs/cm²/sec.
▽- - - -▽ : 6 hrs. at 4750 ergs/cm²/sec.
▲— —▲ : 6 hrs. at 8700 ergs/cm²/sec.

of which continued at 4 hrs. duration of supplementary light, while the other part received 6 hrs. instead of four, at the same light intensities. The bulbing ratios recorded after 121 days from the beginning of the new treatments (296 days after sowing) were 1.62, 2.78 and 3.82 for 3200, 4750 and 8700 ergs/cm²/sec of 6 hrs. extension, respectively. This shows that although the daylength was extended for two more hours (12 + 6), plants exposed to relatively low intensities of supplementary light (3200 ergs/cm²/sec) failed to bulb, while at higher intensities of supplementary light they did develop bulbs. Moreover, the higher the intensity of supplementary light, the more pronounced bulb formation was. The general time trend demonstrates, in all treatments, an increase in bulbing ratios as the plants proceeded in age. This, however, does not seem surprising since the bulbing ratio increases slowly with age, even under short day conditions, as pointed out by HEATH and HOLLIES (1963). A further point of interest is that plants of the same age, grown at the same light intensity, but provided by fluorescent and incandescent light as a continuous mixture for the entire 16 hrs. photoperiod, produced normal mature bulbs after about 150 days from sowing. The mixture used consisted of 62000 ergs/cm²/sec fluorescent light, supplied by TL 120/W/33 Philips tubes + 1000 ergs/cm²/sec of incandescent light.

3. *Growth in weight of the entire plant and its different organs during 4 or 6 hrs. supplementary light of different intensities*

The results, illustrated in figs, 60a, b, c, d, and e show that when 4 hrs. of incandescent light were used to extend a short day (12 hrs.) in fluorescent, increase of the intensity of supplementary light from 720 to 3200 ergs/cm²/sec caused an increase in the entire plant dry weight as well as in that of its various organs, i.e., blades, neck, thickened neck base, and roots. With further increase, up to 11250/cm²/sec, no significant differences were observed, neither for the entire plant dry weight nor for its different parts separately. The increase in dry weight of the whole plant or its different parts with increasing intensity of supplementary light from 720 to 3200 ergs/cm²/sec may well be attributed to increased general growth rather than to differences in development (no bulbing took place in any of the intensities of supplementary light applied).

The average leaf number, leaf size, especially leaf diameter, total green blade area/plant, neck and swollen neck base dimensions were all found to considerably increase with increasing the intensity of supplementary light from 720 to 3200 ergs/cm²/sec, which may well account for the increased general growth observed. With further increase of light intensity no appreciable increase or even a decrease of some of the previously mentioned items was observed.

The general time trend indicates an increase in the total dry weight of the plant, as well as its various organs with advanced age in all cases. This increase is mainly due to increased growth of roots, blades, neck, and to some extent swollen neck base.

Extending the duration of supplementary light of 3200, 4750 and 8700 ergs/cm²/sec to 6 hrs., 175 days after sowing, resulted in bulb development in the two latter intensities at the expense of blade and neck dry weight (the dry weight of blades and neck at 6 hrs. in contrast to 4 hrs. showed a marked decline).

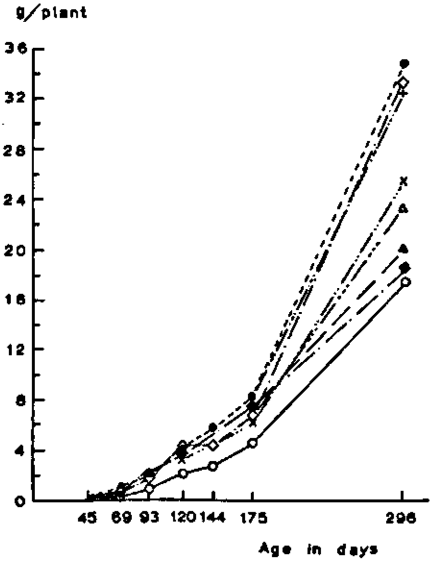
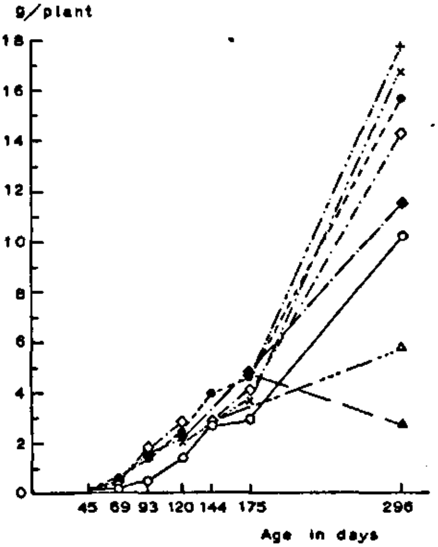


FIG. 60a
The effect of supplementary light of 4 or 6 hrs. duration at different intensities on dry weight of the whole plant.
Phytotron experiment 1966.

○———○ : 4 hrs. at 720 ergs/cm²/sec.
●– – – –● : 4 hrs. at 3200 ergs/cm²/sec.
◇–·–·–◇ : 4 hrs. at 4750 ergs/cm²/sec.
◆— · —◆ : 4 hrs. at 8700 ergs/cm²/sec.
×–··–··–× : 4 hrs. at 11250 ergs/cm²/sec.
+–·–·–+ : 6 hrs. at 3200 ergs/cm²/sec.
△– – – – –△ : 6 hrs. at 4750 ergs/cm²/sec.
▲— —▲ : 6 hrs. at 8700 ergs/cm²/sec.

FIG. 60b
The effect of supplementary light of 4 or 6 hrs. duration at various intensities on dry weight of green leaf blades.
Phytotron experiment 1966.
○———○: 4 hrs. at 720 ergs/cm^2/sec.
●- - - -●: 4 hrs. at 3200 ergs/cm^2/sec.
◇-·-·-◇: 4 hrs. at 4750 ergs/cm^2/sec.
◆—·—◆: 4 hrs. at 8700 ergs/cm^2/sec.
×-··-··-×: 4hrs. at 11250 ergs/cm^2/sec.
+-·-·-+: 6 hrs. at 3200 ergs/cm^2/sec.
△-···-△: 6 hrs. at 4750 ergs/cm^2/sec.
▲— —▲: 6 hrs. at 8700 ergs/cm^2/sec.



The higher the intensity of supplementary light for 6 hrs. duration was, the greater the decrease in neck and blade dry weight was. This seems reasonable if we suggest that the excessive energy of supplementary light is primarilary used in speeding up the developmental growth at the expense of other vegetative growth processes.

It should be emphasized that 4 hrs. extension did not lead to real bulbing in this experiment, so that the vertical sequence of points in the 4 hrs. series (figs. 60 a, b, c, d, and e) is much more arbitrary than in the 6 hrs. treatments.

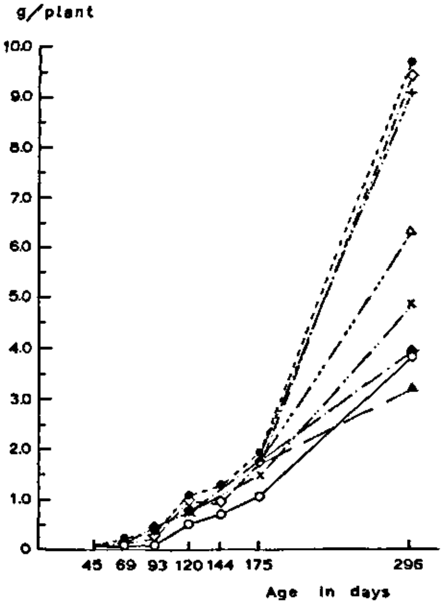


FIG. 60c
The effect of supplementary light of 4 or 6 hrs. duration at various intensities on dry weight of the neck.
Phytotron experiment 1966.
○———○: 4 hrs. at 720 ergs/cm^2/sec.
●- - - -●: 4 hrs. at 3200 ergs/cm^2/sec.
◇-·-·-◇: 4 hrs. at 4750 ergs/cm^2/sec.
◆—·—◆: 4 hrs. at 8700 ergs/cm^2/sec.
×-··-··-×: 4 hrs. at 11250 ergs/cm^2/sec.
+-·-·-+: 6 hrs. at 3200 ergs/cm^2/sec.
△-···-△: 6 hrs. at 4750 ergs/cm^2/sec.
▲— —▲: 6 hrs. at 8700 ergs/cm^2/sec.

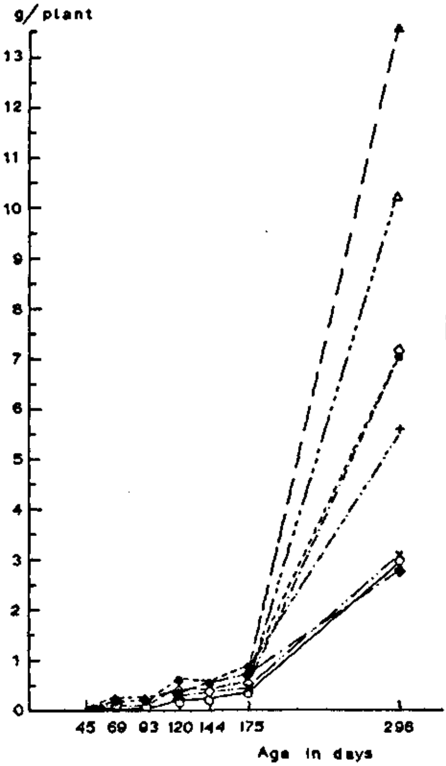


FIG. 60d
The effect of supplementary light of 4 or 6 hrs. duration at various intensities on dry weight of swollen neck base.
Phytotron experiment 1966.

○——○: 4 hrs. at 720 ergs/cm^2/sec.
●- - - -● : 4 hrs. at 3200 ergs/cm^2/sec.
◇-·-·-◇: 4 hrs. at 4750 ergs/cm^2/sec.
◆—·—◆: 4 hrs. at 8700 ergs/cm^2/sec.
×-··-··-×: 4 hrs. at 11250 ergs/cm^2/sec.
+-·-·-+: 6 hrs. at 3200 ergs/cm^2/sec.
△-····-△: 6 hrs. at 4750 ergs/cm^2/sec.
▲— —▲: 6 hrs. at 8700 ergs/cm^2/sec.

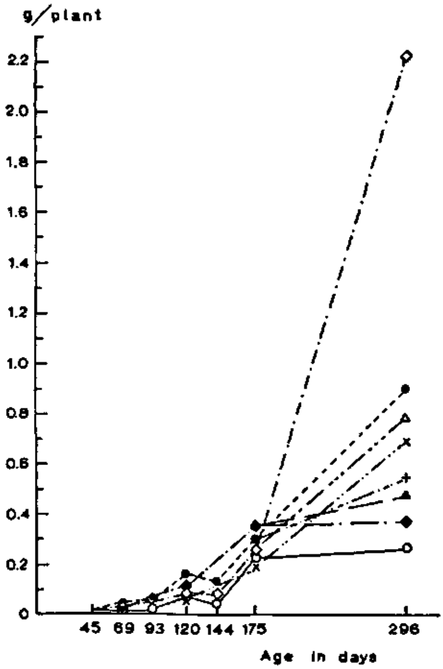


FIG. 60e
The effect of supplementary light of 4 or 6 hrs. duration at various intensities on root dry weight.
Phytotron experiment 1966.

○——○: 4 hrs. at 720 ergs/cm^2/sec.
●- - - -● : 4 hrs. at 3200 ergs/cm^2/sec.
◇-·-·-◇: 4 hrs. at 4750 ergs/cm^2/sec.
◆—·—◆: 4 hrs. at 8700 ergs/cm^2/sec.
×-··-··-×: 4 hrs. at 11250 ergs/cm^2/sec.
+-·-·-+: 6 hrs. at 3200 ergs/cm^2/sec.
△- - - -△: 6 hrs. at 4750 ergs/cm^2/sec.
▲— —▲: 6 hrs. at 8700 ergs/cm^2/sec.

4. *Growth in weight of the entire plant and its different organs during 8 hrs. supplementary light of different intensities*

When 8 hrs. of supplementary incandescent light at different intensities was used to extend a short photoperiod (12 hrs.) in fluorescent light, no considerable effect on total plant dry weight was detected 14 days after the start of the treatments (fig. 61a). As the plants advanced in age (93 days after sowing), dry weight of the entire plant in 720, 4750 and 8700 ergs/cm^2/sec intensities of supplementary light was more or less the same while it was lower in the 3200 ergs/cm^2/sec intensity of supplementary light treatment. This decrease is due to slower rate of bulb development (dry weight fig. 61b) at 3200 ergs/cm^2/sec intensity of supplementary light as well as to decreased blade and/or neck dry weight as compared with higher intensities. At the lowest intensity of supplementary light (720 ergs/cm^2/sec), though the rate of bulb development (dry weight) was much more lower than at 3200 ergs/cm^2/sec, the increase in blade and neck dry weight was enough to compensate this decline, as a net result of which an increase in the entire plant dry weight in 720 ergs/cm^2/sec treatment was observed as compared with 3200 ergs/cm^2/sec.

At more advanced age (120 days after sowing), dry weight of the entire plant was found to increase with increasing intensities of supplementary light up to

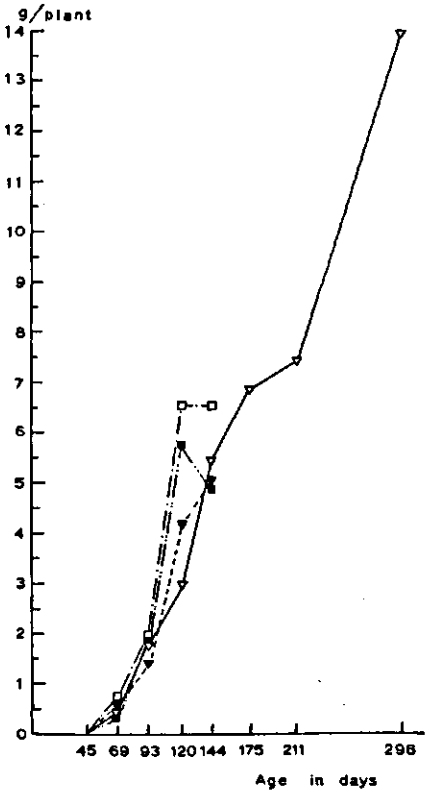


FIG. 61a
The effect of supplementary light of 8 hrs. duration at different intensities on dry weight of the whole plant.
Phytotron experiment 1966.
▽———▽ : 8 hrs. at 720 ergs/cm^2/sec.
▲- - - -▲ : 8 hrs. at 3200 ergs/cm^2/sec.
□-·-·-□: 8 hrs. at 4750 ergs/cm^2/sec.
■—··—■: 8 hrs. at 8700 ergs/cm^2/sec.

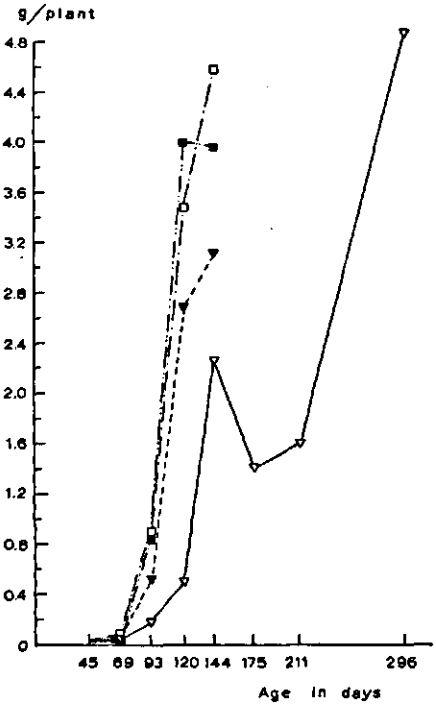


FIG. 61b
The effect of supplementary light of 8 hrs. duration at different intensities on the dry weight of the bulb.
Phytotron experiment 1966.

▽———▽ : 8 hrs. at 720 ergs/cm^2/sec.
▲- - - -▲ : 8 hrs. at 3200 ergs/cm^2/sec.
□-·-·-□: 8 hrs. at 4750 ergs/cm^2/sec.
■—··—■: 8 hrs. at 8700 ergs/cm^2/sec.

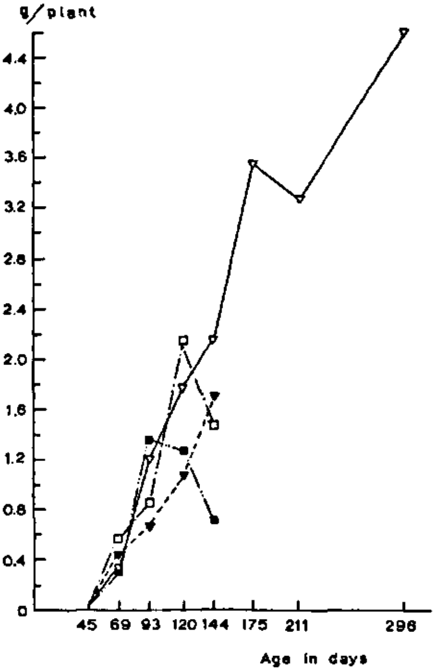
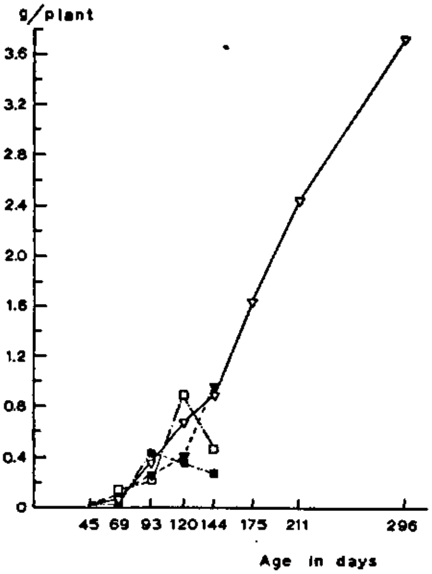


FIG. 61c
The effect of supplementary light of 8 hrs. duration at different intensities on dry weight of green leaf blades.
Phytotron experiment 1966.

▽———▽ : 8 hrs. 720 ergs/cm^2/sec.
▲- - - -▲ : 8 hrs. at 3200 ergs/cm^2/sec.
□-·-·-□: 8 hrs. at 4750 ergs/cm^2/sec.
■—··—■: 8 hrs. at 8700 ergs/cm^2/sec.

FIG. 61d
The effect of supplementary light of 8 hrs. duration at different intensities on dry weight of the neck.
Phytotron experiment 1966.
▽———▽ : 8 hrs. at 720 ergs/cm²/sec.
▲- - - -▲ : 8 hrs. at 3200 ergs/cm²/sec.
□-·-·-□: 8 hrs. at 4750 ergs/cm²/sec.
■—··—■: 8 hrs. at 8700 ergs/cm²/sec.



4750 ergs/cm²/sec; with further increase up to 8700 ergs/cm²/sec, the total plant dry weight decreased. This decrease is due to bulb development being enhanced by the excessive energy of supplementary light at the expense of other vegetative growth (see blade and neck dry weight, figs. 61c and 61d). At still more advanced age (144 days old) because of senescence being enhanced by increased energy of supplementary light, the entire plant dry weight showed a decline after its maximum, at the highest light intensity (8700 ergs/cm²/sec); at 4750 ergs/cm²/sec it came to a stand-still; with further reduction of intensity it continued to increase. At the lowest light intensity the increase was more pronounced, and the plants survived longer.

An interesting point is that maximum dry weight of blades (fig. 61c) and neck (fig. 61d) was attained at a moment which differed according to treatment, being after 93, 120, 144 and 296 days after sowing for 8700, 4750, 3200 and 720 ergs/cm²/sec intensities of supplementary light respectively, indicating that the higher the intensity the quicker the development and the earlier maturity were.

C. CONCLUSIONS

In the light of the results obtained in sections I and II of this chapter, from the series of experiments previously mentioned, the following conclusions can be drawn.

1. Although it is generally accepted that bulb development in the onion plant can only begin in response to long days, and the interactions of temperature and daylength is well established, the quality of light may greatly alter the photoperiodic response so that bulbing is not induced even at exposure to con-

tinuous light of certain wavelengths. Incandescent light proved to be most effective when admixed to fluorescent light or when used to extend a short photoperiod whereas fluorescent light alone supplied by 40/W/55 or 120/W/33 Philips tubes which lack the far-red: red radiation in adequate proportion, is not effective even at 24 hrs. daily exposure.

2. The incandescent light is effective not because of the visible red or the far-red radiation only, but because the ratio of far-red to red radiation it contains. Neither red nor far-red alone for 12 hrs. extension (5000 ergs/cm²/sec) was effective, while 8 hrs. extension of incandescent light (3200 ergs/cm²/sec or more) speeded up bulb development (the main photoperiod in all cases was 12 hrs. fluorescent light alone).
3. Bulb development strongly depends on the duration of the light period (of certain wavelengths) rather than on the energetic effect of light. When a basic photoperiod of 12 hrs. was extended by 8 hrs. of low intensity (3200 ergs/cm²/sec) the bulb developed, while 4 hrs. only of high intensity (11 250 ergs/cm² sec) did not induce bulbing.
4. When plants are exposed to inductive cycles, bulb development may be speeded up by increasing the intensity of supplementary light.
5. Intensity and duration of supplementary light may replace each other within certain limits. Eight hrs. supplementary light at 3200 ergs/cm²/sec was sufficient to stimulate bulbing; 6 hrs. at the same intensity was not, while 6 hrs. at higher intensity (4750 ergs/cm²/sec) proved effective. Thus, increase of the intensity from 3200 to 4750 ergs/cm²/sec compensated for decreasing the duration of supplementary light from 8 to 6 hrs., or lengthening the duration from 6 to 8 hrs. compensated for lowering the intensity from 4750 to 3200 ergs/cm²/sec. With further reduction of supplementary light duration to 4 hrs., increasing the intensity up to 11 250 ergs/cm²/sec. had no effect. Lengthening the duration to 8 hrs. with further reduction of the intensity of supplementary light down to 720 ergs/cm²/sec appeared to be critical for bulb development (some plants bulbed whereas others did not).
6. It seems that in order to induce bulb development, a certain minimum photoperiod in which far-red and red light occur should be maintained. A basic photoperiod of 12 hrs., supplied by fluorescent light lacking the far-red: red energy in reasonable ratio, extended by 4 hrs. of incandescent light at a range of intensities failed to stimulate bulbing; on the other hand, admixing incandescent light to fluorescent light for 16 hrs. (in total) caused bulb development.
7. Provided the temperature is low, seedstalk development may occur in the first season and then is influenced by the quality of light (plants grown under a continuous mixture of fluorescent and incandescent light (15 °C) developed seedstalks while those grown at continuous fluorescent light alone did not. Since flower initiation is temperature sensitive (favoured by low temperature), the effect of light quality (a mixture of fluorescent and incandescent light) may be in speeding up the physiological age necessary for flower induction by low temperature.

D. PHOTOPERIODIC REACTIONS AND PLANT.AGE

This experiment was conducted to determine the response of plants of different age to favourable LD cycles. A range of plants aged from 45 to 189 days, grown under SD conditions (12 hrs. at a mixture of 62000 and 8700 ergs/cm^2 sec of fluorescent and incandescent light respectively) were transferred at 4 weeks intervals to LD (16 hrs. at the same intensity and quality as in SD). In addition one group of plants was held under SD, and another under LD from the date of sowing, so as to obtain a series of plant ages from 0 to 189 days, to be exposed to LD. Temperature, in all cases, was 25 °C.

1. *Bulb development in relation to plant age*

The photoperiodic response of bulb development as influenced by plant age was expressed as the bulbing ratio (fig. 62a); bulbing ratios obtained after a period of 4 weeks exposure to long days were 1.35, 2.04, 2.02, 1.75, 1.99 and 1.51 for plant ages of 45, 74, 101, 130, 158 and 189 days. This indicates that young plants (45 days old) as well as very old ones (189 days) were much less sensitive to photoperiodic treatments as compared with those in the range from 74 to 158 days old; in the latter range, the bulbing ratios were more or less of the same magnitude (around 2.0) suggesting that plants were equally sensitive to LD treatment irrespective of their ages. After 4 weeks more in LD (8 weeks in totality), the bulbing ratios, in all cases, continued to increase. The increase of the rates was 2.23, 2.12, 2.27, 2.34, 1.86 and 0.62 for plant ages of 45, 74, 101, 130, 158 and 189 days respectively. This shows the tendency of the rate of further bulb development to be slower as plants were far more than 130 days under SD; the decrease in the rate of bulbing was, however, more pronounced in 189 days old plants than in 130 days ones. As for plants ranging from 45 to 130 days old, the rate of bulb development showed no appreciable differences among treatments, indicating that sensitivity to photoperiodic treatments was

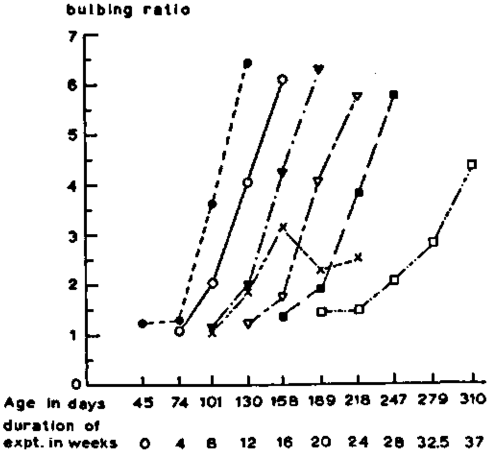


FIG. 62a
Changes in bulbing ratios of plants transferred from SD to LD at differerent ages.
Phytotron experiment 1966.
●- - - -● : 45 days 12 hrs., then 16 hrs.
○———○: 74 days 12 hrs., then 16 hrs.
▲—·—▲ : 101 days 12 hrs., then 16 hrs.
▽— - —▽ : 130 days 12 hrs., then 16 hrs.
■— —■: 158 days 12 hrs., then 16 hrs.
□-·-·-□: 189 days 12 hrs., then 16 hrs.
×—··—×: 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.

equal irrespective of plant ages within this range, while with further ageing the sensitivity decreases and the more so as plants advanced in age.

Bulb development after 12 weeks of LD treatment showd bulbing ratios from 5.70 to 6.45 for all ages from 45 to 158 days; in the oldest group (189 days) it still lagged behind (2.81). This makes it clear that bulb maturity was attained after 12 weeks exposure to LD in all treatments of plant ages in the range from 45 to 158 days old, while bulb development in still older plants progressed only slowly. Maturity in such plants was attained after 4 weeks more in LD (16.5 weeks in total). The bulbing ratio recorded was about 4.39 which is lower than the maximum bulbing ratios in other treatments at maturity (12 weeks in LD). This decrease may be a result of the production of mature bulbs with thickened necks because of long exposure to SD before transfer to long days.

As for plants, grown continually under SD conditions from the date of sowing up to 189 days, the bulbing ratio showed a slight increase as the plants advanced in age; being 1.26, 1.14, 1.26, 1.29, 1.40 and 1.50 for ages of 45, 74, 101, 130, 158 and 189 days respectively (fig. 62a, the starting points of the different curves) indicating the failure of plants to develop bulbs under such conditions. Furthermore, when onion plants, grown in SD for 101 days, were exposed to LD for 4 weeks and then transferred back to short days for the rest of the growing period, the bulbing ratio recorded at the end of 4 weeks LD treatment was about 1.90 against 1.20 immediately before shifting to LD, indicating that bulb development has begun as a result of the stimulus of 4 weeks exposure to LD. After four weeks in SD, following LD treatment, the bulbing ratio continued to increase, reaching about 3.15 and showing that bulb development was still in progress under SD conditions. Thus, it seems evident that the bulbing process became irreversible in the sense that it continued in short days, at least in part of the plants (see below). Following further bulb development in SD (4 weeks more), the bulbing ratio was found to decrease after a maximum. This decrease is due to the fact that some plants which have begun to bulb noticibly after transfer to LD, resumed their leaf and root growth in

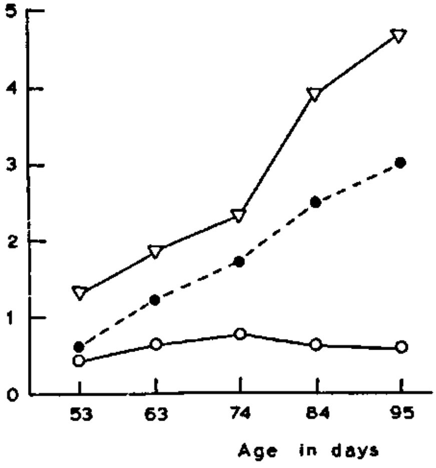


FIG. 62b
Changes in bulbing ratios of plants grown continually in LD.
Phytotron experiment 1966.
●- - - -● : average diameter of the bulb in cm.
○——○ : average diameter of the neck in cm.
▽——▽ : bulbing ratio.

SD at the expense of the bulbs. In general, the plants showed a remarkable variation in their behaviour as a result of such treatment; some plants continued bulbing and matured in short days; some began again to produce blades and roots and double necks and others even completely lost their ability to bulb. In the latter plants, evidently, the major part of the induction was not irreversible. Such variations are not surprising in a genetically heterogenous population if the transfer is made near a critical stage of development.

Concerning the plants, grown in long days (16 hrs.) from the date of sowing up to the end of growing period, the results illustrated in fig. 62b show that the bulbing ratios were 1.30, 1.80, 2.30, 3.90 and 4.65 for plant ages of 53, 63, 74, 84 and 95 days respectively. This indicates that plants did not respond to the photoperiodic treatments before they were 53 days old, after which bulb development started to take place in a regular rate up to 74 days old. In the period between 74 and 84 days, the bulbing ratio showed a marked increase; at more advanced age (from 84 to 95 days) it continued to increase, though less pronounced.

2. *Bulbing response and leaf number*

Certain plants produce a characteristic minimum leaf number before flower primordia are initiated, no matter the conditions used, while others respond immediately to favourable conditions irrespective of the number of developing leaves. The question arises whether bulb development in onions can be induced under conditions favourable to bulbing, regardless of the leaf number, or whether a certain leaf number is required. Fig. 63a presents the number of green leaves per plant in relation to its age when exposed to inductive cycles (16 hrs.) at successive harvests. The average number of green blades found on the plant at the moment of transfer of plants of 45 days old to long days, was about

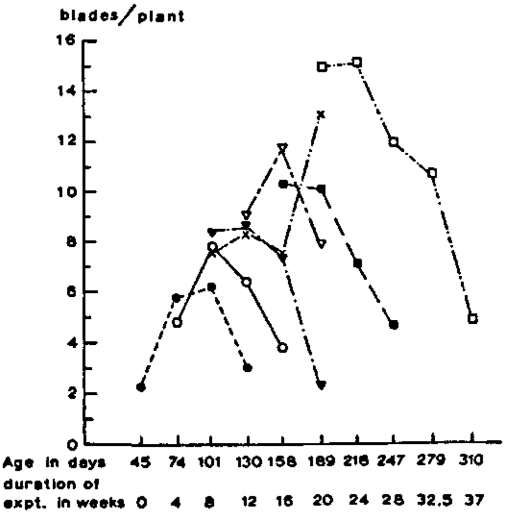


FIG. 63a
Changes in number of green leaf blades of plants transferred from SD to LD at different ages.
Phytotron experiment 1966.
●– – – –● : 45 days 12 hrs., then 16 hrs.
○———○: 74 days 12 hrs., then 16 hrs.
▲— · —▲ : 101 days 12 hrs., then 16 hrs.
▽—‚——▽ : 130 days 12 hrs., then 16 hrs.
■— —■: 158 days 12 hrs., then 16 hrs.
□-·-·-□: 189 days 12 hrs., then 16 hrs.
×—··—×: 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.

2.25. After being exposed for 4 weeks to LD, no signs of bulbing could be noticed (see bulbing ratio fig. 62a), while continual emergence of new leaves was observed so that the number reached 5.85 at the end of this period. Only as such leaf number was attained and with continued exposure to long days (4 weeks more), bulb development was noticibly taking place. However, the number of green leaves was still increasing to reach about 6.2 after which it was found to decrease sharply with still longer exposure to LD (4 weeks further). This sharp decrease in leaf number is associated with rapid bulb development, both constituting parts of the plant's reaction to long photoperiods. In plants ranging from 74 to 130 days old and subjected to long days, the emergence of new leaves continued during the first four weeks exposure to long days, so that the green leaf number reached its peak and thereafter decreased regardless of the number of green leaves at the moment when these plants were shifted to inductive cycles. In still older plants (158 to 189 days), this no longer holds true in the sense that the green leaf number found on the plant showed a negligible increase or even decreased after 4 weeks in long days only. As for 101 days old plants, when transferred to long days for a period of 4 weeks and then returned to short days (12 hrs.), the green leaf number continued to increase in long days, and thereafter decreased in the first four weeks in short days following long day treatment, while with extended exposure to non-inductive cycles (12 hrs.), the green leaf number resumed its increase, suggesting that the bulbing stimulus was destroyed by renewed and prolonged exposure to short days.

Concerning the plants, grown at inductive cycles (16 hrs.) from the date of sowing till maturity, it is clear from fig. 63b that up to 53 days old, the average number of green leaves per plant was found to be 4.15 and the corresponding bulbing ratio 1.30, indicating the absence of bulb development by that time.

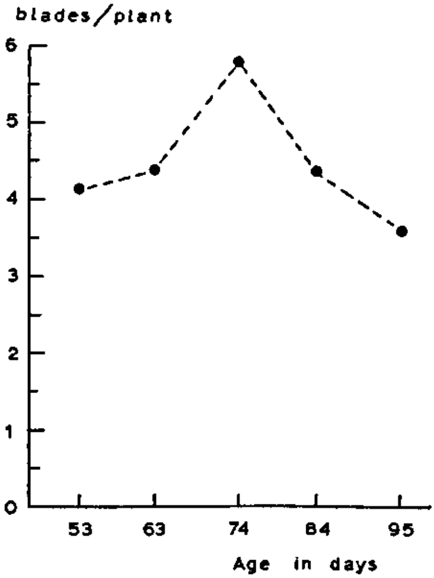


FIG. 63b
Changes in number of green leaf blades of plants grown continually in LD.
Phytotron experiment 1966.

Ten days later, green leaf number increased to 4.4 while the bulbing ratio was found to be 1.90, showing that the bulbing process during this period was in progress. As plants advanced in age (10 days more) the bulbing ratio continued to increase together with a further increase in green leaf number up to 5.80 leaves, after which it declined whereas the bulbing ratio markedly increased.

3. *Bulbing response and total leaf area*

As shown in fig. 64a, the total leaf area found at the time of transfer to long days was 16.0, 210, 975, 780, 1200, and 1995 cm^2 per plant for plants of 45, 74, 101, 130, 158 and 189 days old respectively. With exposure of such plants with different leaf area to long days, bulb development in 45 days old plants (16.0 cm^2 area) was found to be delayed until an area of about 210 cm^2 has been developed at the end of the first 4 weeks of growth in long days. Thereafter bulbing took place at an enhanced rate if the plants remained in inductive cycles. On the other hand plants having developed an area in the range from 210 to 1200 cm^2 prior to transfer to inductive photoperiods immediately responded to the stimulus of long days more or less in the same magnitude, irrespective of their leaf area. With still further increase in leaf area, up to 1995 cm^2, bulbing was greatly delayed, so that no appreciable increase in the bulbing ratio was observed after the first period of 4 weeks of inductive cycles. However, a definite conclusion cannot be drawn as to whether a minimum leaf area should develop or a certain physiological age should be attained in order that bulbing may be induced. On the other hand, the decline in bulbing response observed as the amount of leaf area exceeded a certain limit, may well be a function of meristem ageing. A point of interest is that leaf area in young plants (45 days old) con-

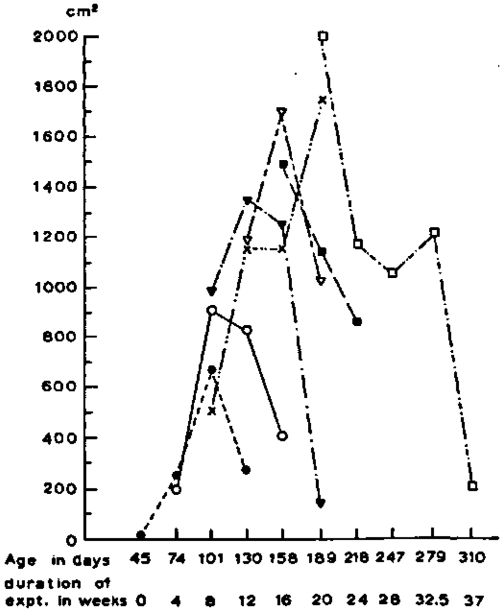


FIG. 64a
Changes in green leaf blade area of plants transferred from SD to LD at different ages.
Phytotron experiment 1966.
●- - - -● : 45 days 12 hrs., then 16 hrs.
○———○: 74 days 12 hrs., then 16 hrs.
▲— · —▲ : 101 days 12 hrs., then 16 hrs.
▽— — —▽ : 130 days 12 hrs., then 16 hrs.
■— — ■: 158 days 12 hrs., then 16 hrs.
□- · - · - □: 189 days 12 hrs., then 16 hrs.
×— ·· —× : 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.

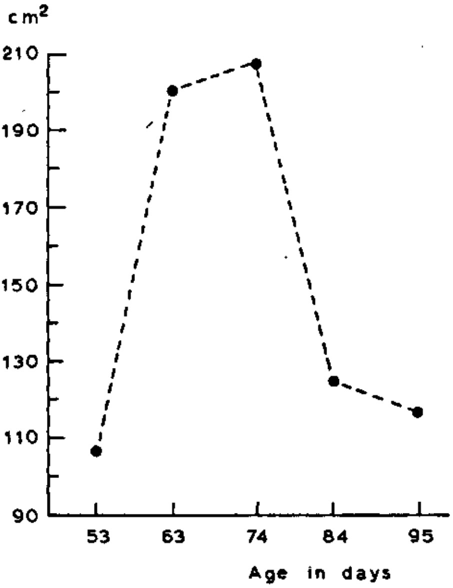


FIG. 64b
Changes in green leaf blade area of plants grown continually in LD.
Phytotron experiment 1966.

tinued to increase until after about 675 cm² was attained after 8 weeks growth in inductive photoperiods; thereafter it diminished appreciably. On the contrary, plants in the range from 74 to 130 days old, with only one exception, showed an increase in their leaf area during the first four weeks in long days after which a progressive decrease was observed up to the end of the growing period. In still older plants (158, 189 days), the total leaf area immediately decreased with exposure to long days. As to plants of 101 days old, transferred to LD for 4 weeks and then returned back to SD, the leaf area continued to increase in long days. In the first 4 weeks in short days following exposure to inductive cycles it came to a standstill; thereafter it resumed its growth as a result of renewed leaf emergence with prolonged exposure to short days.

Concerning the total leaf area in plants continually grown under long days from the date of sowing, data presented in fig. 64b show that up to 53 days after sowing, about 107.5 cm² leaf area was developed, and no signs of bulbing were observed. In the period from 53 to 63 days, the total green leaf area increased sharply (from 108 to 200 cm²), together with a marked increase in the bulbing process (bulbing ratio increasing from 1.30 to 1.90). At more advanced age (11 days later), leaf area continued to increase, though less rapidly, to attain its maximum (210 cm²), in association with increased bulb development at a similar rate as before (from 1.90 to 2.30). With still more progression in age (74 to 95 days), a marked decline in leaf area was observed, accompanied by rapid bulb bulking.

4. *Entire plant dry weight in relation to age and size when exposed to inductive photoperiods, at successive harvests*

As illustrated in fig. 65a, the longer the plants remained in short days, the greater the dry weight was at the time of transfer to long days, being 0.051, 0.614, 4.43, 6.16, 6.82 and 12.36 grams for 45, 74, 101, 130, 158 and 189 days old plants respectively. When these plants of different age and size were grown in inductive photoperiods for a period of 4 weeks, the average dry weight in all treatments, with the exception of the oldest one, was found to increase, while at the same time the dry weight was greater the older the plants, even for the oldest group (189 days). In the latter, the slight decrease in the entire plant dry weight after 4 weeks exposure to long days is mainly due to the absence of bulb development so far, simultaneously with an increased rate of foliage death because of senescence. The increase in total plant dry weight for age series from 74 to 158 days, in contrast to that in 45 days old plants, is mainly to be attributed to increase in bulb dry weight, rather than to increase in the other plant organs, i.e., blade, neck and root. It should be noticed that bulb development, in the youngest and in the oldest plants was still behind, while in intermediate age series it was already in progress (see bulbing ratio). After 4 weeks more in long days, the dry weight in all cases continued to increase, while

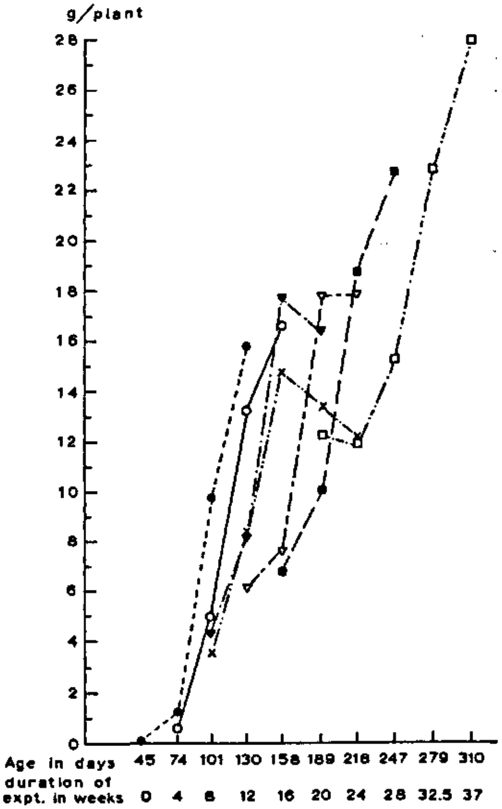


FIG. 65a
Changes in the whole plant dry weight of plants transferred from SD to LD at different ages.
Phytotron experiment 1966.

●– – – –● : 45 days 12 hrs., then 16 hrs.
○———○: 74 days 12 hrs., then 16 hrs.
▲— · —▲ : 101 days 12 hrs., then 16 hrs.
▽— – —▽ : 130 days 12 hrs., then 16 hrs.
■— —■: 158 days 12 hrs., then 16 hrs.
□–·–·–□: 189 days 12 hrs., then 16 hrs.
×—··—× : 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.

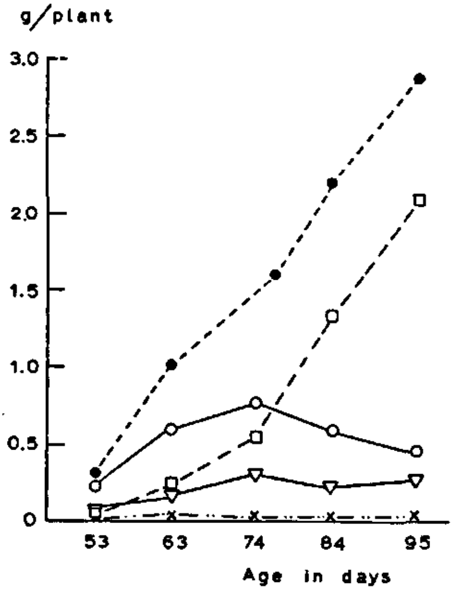
the same relationship between plant age, up to 158 days and its dry weight, still holds true, i.e., the older the plants, the greater the dry weight per plant was; with still further ageing (189 days) a marked decrease in dry weight was observed. The slower rate of bulb development in the oldest plants in comparison with other ages may fully account for the decline in total plant dry weight in the former than in the latter. With further exposure to long days (still 4 weeks more), the entire plant dry weight in all age series, with only one exception, continued to increase with the same relationship between plant age and dry weight maintaining. Also, bulb development in the oldest plants (189 days) was proceeding in an enhanced rate, so that the total dry weight per plant showed a slight increase over that in 158 days old plants after it had been lagging behind before. Bulb maturity was attained in all plant age series, except the oldest group, after 12 weeks in long days. When these old plants (189 days) were maintained for 4 weeks longer (16 weeks in total) they continued growing and the average dry weight found at the end of this period was 28.10 grams which is much greater than its analogy in 158 days old plants after 12 weeks exposure to long days. However, it is likely that this dry weight difference was somewhat exaggerated due to variation in samples.

In plants of 101 days old, transferred to the stimulus of long days for a period of 4 weeks, and then shifted back to short days, the entire plant dry weight increases, even at exposure to short days for 4 weeks following the long day treatment. This increase, for the greater part, may be attributed to increased bulb dry weight and, to a smaller degree, to increase in blade and neck dry weight (dry weight of the latter showed a slight increase in comparison with bulb dry weight), suggesting that the bulbing process became irreversible in the sense that it continued even when plants were again exposed to SD for (the first) 4 weeks following long days. With continued exposure to short days, the total dry weight declined, due to the fact that the plants renewed other organ growth, i.e., of blades, neck and roots at the expense of their bulbs.

The whole indicates a postponed readjustment of the plants, temporarily leading to a higher proportion of young leaves, probably photosynthesising at still suboptimal rate. Also the fact that light energy, in this experiment, was reduced to roughly 12:16 of that previously available (since daylength in this experiment had been extended by high light intensity), may have played a role.

With regard to the plants grown in long days from the date of sowing up to maturity (95 days after sowing), it is evident from fig. 65b that up to 53 days old, the entire plant dry weight consisted chiefly of leaves. Ten days later, total plant dry weight was found to increase, mainly as a result of increase in leaf dry weight and, to a smaller degree, to increase in bulb and neck dry weights; root dry weight seemed rather flat up to 74 days after which it tended to decrease. In the period between 63 and 74 days old, leaf and neck dry weight continued to increase together with an appreciable gain in bulb dry weight. At more advanced age (from 74 to 95 days old), the total dry weight continued to increase with bulb dry weight as the main component, while dry weight of other plant organs diminished.

FIG. 65b
Changes in dry weight of the whole plant and its various parts of plants grown continually in LD.
Phytotron experiment 1966.
○———○ : leaf blades
▽———▽ : neck
□- - - -□ : bulb
×—··—× : roots
●- - - -● : entire plant



Maximum plant dry weight was attained at the end of the growth period, no matter how long the latter was, being 2.875, 15.70, 16.63, 16.40, 17.95, 22.89 and 28.14 grams for plants subjected to long days when 0, 45, 74, 101, 130, 158 and 189 days old respectively. This indicates the importance for the onion plant of being grown in short days, at least for a short period of 45 days, before bulb induction by long days, in order to obtain a reasonable growth and subsequently a satisfactory yield.

5. *Bulb weight in relation to plant age when exposed to inductive photoperiods*

It seems interesting to see how the productivity of the onion plant is affected by its age and size when bulb development is induced by exposure to long days, since the bulb is the part of economical importance. After 4 weeks exposure to long days, as fig. 66a shows, bulb fresh weight was found to be 1.76, 6.22, 15.04, 14.02, 23.04 and 22.12 grams for 45, 74, 101, 130, 158 and 189 days old plants respectively. This indicates, in general, that up to 158 days old, the older and bigger in size the plants were when transferred to inductive photoperiods, the greater the bulb fresh weight was. With ageing further than 158 days, this seems not to hold true as the bulb fresh weight decreased. An important point is that differences in bulb fresh weight among plants ranging from 74 to 158 days old were not due to variation in bulb development as the bulbing ratios for this whole range of ages lie around 2.0 (see bulbing ratio) but rather to the more vigorous foliage growth and subsequently the increased amount of stored food in the bulb with advanced age. On the contrary, differences in bulb fresh weight between young plants (45 days) as well as very old ones (189 days) and the other age series were mainly due to differences in bulb development (in

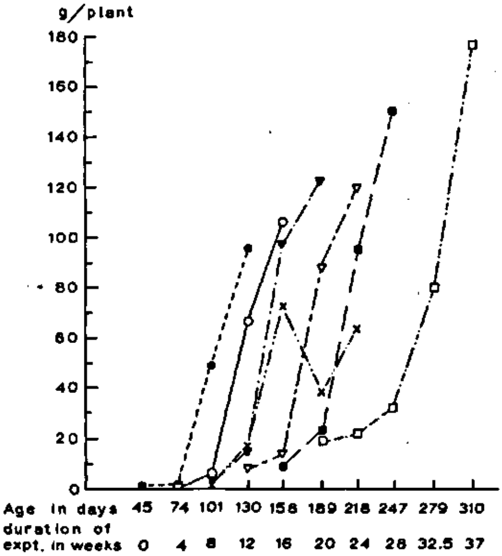


FIG. 66a
Changes in bulb fresh weight of plants transferred from SD to LD at different ages.
Phytotron experiment 1966.

●- - - -● : 45 days 12 hrs., then 16 hrs.
○———○: 74 days 12 hrs., then 16 hrs.
▲— · —▲ : 101 days 12 hrs., then 16 hrs.
▽———▽ : 130 days 12 hrs., then 16 hrs.
■— — ■: 158 days 12 hrs., then 16 hrs.
□- · - · -□: 189 days 12 hrs., then 16 hrs.
×— ·· —× : 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.

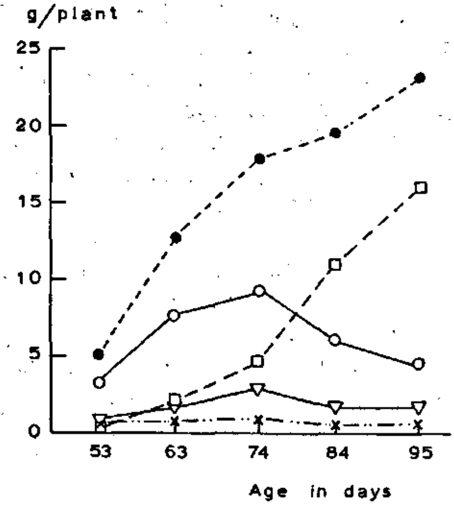
the youngest and the oldest plants bulbing was retarded as compared with the other treatments).

With longer exposure to long days, bulb fresh weight continued to increase in all cases and the more so, with only one exception, with each increase in plant age up to 158 days, while with still further ageing it decreased. This decline is mainly due to the slower rate of bulb development, possibly because of tissue ageing. It seems that this 'ageing' is specifically reflected in a delay in morphogenetic adaptation to the long day situation, since it also is very much manifest in the bulbing ratio. From fig. 65a it is evident that after 8 weeks, dry weight increase proceeds at the same rate as occurs in the plants which were transferred to long days at an earlier stage, whereas roughly the same rate of increase in bulbing ratio is attained only after 12 weeks (fig. 62a). These facts seem to mean that general ageing of the plants is not so much manifest as is ageing in the specific capacity of adaptation to the stimulus of long days.

As the plants were maintained 4 weeks more in inductive photoperiods, bulb fresh weight still increased in all age series with the same relationship between bulb fresh weight and plant age, up to 158 days; with still older plants the position was changed and bulb fresh weight was found to decrease with respect to that in 158 days old plants. In the oldest plant group, bulb fresh weight was in progress but not sufficiently rapid to keep pace with that in other treatments.

As maturity was attained in all age series, except the oldest one, after 12 weeks in long days, it was decided to keep the latter 4 weeks longer. During this period, bulb fresh weight continued to increase up to a maximum at the end of the growth period. The highest values of bulb fresh weight irrespective of the total length of the growth period were 96.40, 106.00, 122.44, 120.28, 150.00 and 176.06 grams for plants put under long days at the age of 45, 74, 101, 130,

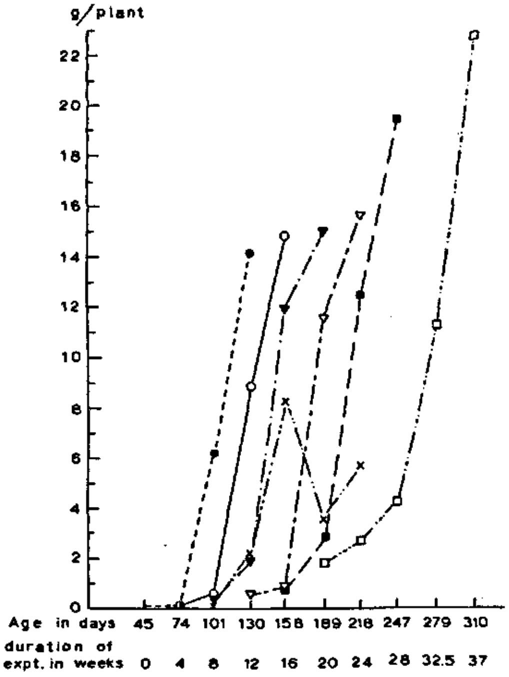
FIG. 66b
Changes in fresh weight of the whole plant and its various parts of plants grown continually in LD.
Phytotron experiment 1966.
○——○ : leaf blades
▽——▽ : neck
□- - - -□ : bulb
×—··—× : roots
●- - - -● : entire plant



158 and 189 days respectively. This indicates the existence of a positive correlation between the plant age and/or size at the time of exposure to inductive photoperiods and the final bulb fresh weight, although bulb development may be delayed as plants exceed a certain age, i.e., over 158 days).

Furthermore, in plants grown in long days immediately after sowing, the maximum bulb fresh weight, attained after 95 days, when plants matured, was

FIG. 66c
Changes in bulb fresh weight of plants transferred from SD to LD at different ages.
Phytotron experiment 1966.
●- - - -● : 45 days 12 hrs., then 16 hrs.
○——○ : 74 days 12 hrs., then 16 hrs.
▲—·—▲ : 101 days 12 hrs., then 16 hrs.
▽—·—▽ : 130 days 12 hrs., then 16 hrs.
■— —■ : 158 days 12 hrs., tehn 16 hrs.
□-·-·-□ : 189 days 12 hrs., then 16 hrs.
×—··—× : 101 days 12 hrs., then 4 weeks 16 hrs., then 12 hrs.



about 16.00 grams (fig. 66b) which is far inferior to that of plants exposed to long days at 45 days old, though the entire growth period in the latter was not much longer than in the former (16.0 grams after 95 days compared with 96.4 grams after a 130 days growth period). This in another indication of the importance of exposure to short days even for a relatively short period prior to bulb induction by the stimulus of long days.

Concerning the plants of 101 days old when transferred to long days for 4 weeks and thereafter back to short days, the bulb fresh weight was found to increase as a result of bulb induction by long day treatment and continued to increase even after 4 weeks exposure to short days, while with prolonged maintenance in short days it decreased, owing to the fact that plants renewed foliage growth at the expense of their bulbs, possibly because the bulbing stimulus was destroyed by prolonged exposure to short days.

The same results were obtained for bulb dry weight (fig. 66c and fig. 65b).

CHAPTER VIII

TEMPERATURE EFFECTS, RESULTS AND DISCUSSION

A. GROWTH IN WEIGHT

1. *Entire plant fresh weight*

The total plant fresh weight as influenced by air temperature at different stages of growth is presented in fig. 67a and table 1. In the early stages of growth (between 36 and 54 days after sowing), though differences were not yet marked, 15 °C seems to be the most favourable for growth in fresh weight. Each 5 °C rise from the optimum, up to 30 °C, was associated with a decline in the entire plant fresh weight. This decrease, however, was more pronounced as the temperature increased from 25 to 30 °C than if it increased from 15 to 20 °C or from 20 to 25 °C. Moreover, lowering the air temperature to 10 °C greatly checked plant growth, so that the minimum fresh weight was found at this temperature. At 10 °C, the reduction in the total plant fresh weight is a consequence of suppression of growth of the various plant organs, viz., roots, neck, swollen neck base and blades, while the reduction at 30 °C was mainly due to depression of root growth, and to a smaller extent to blade growth. As the plants proceeded in growth (in the period between 54 and 101 days after sowing) the temperature optima shifted to higher values so that the maximum fresh weight during this period was found at 20 °C. Increasing or decreasing the air temperature from 20 °C resulted in a decrease in the entire plant fresh weight. Due to the fact that 15 and 25 °C were on both sides the optimum, the decline at these temperatures was less than that at the two extremes (10, 30 °C). Furthermore, the growth was more checked at the lowest temperature than at the highest one, so that plant fresh weight at 10 °C lagged behind. It should be noticed that, up to 101 days after sowing, differences in fresh weight between treatments were due to variations in root, blade and neck growths, as bulbing was absent, owing to the fact that plants were grown under short days (12 hrs.) during this period, after which daylength was extended to 15.5 hrs. Twenty six days following daylength extension (127 days after sowing) differences in the entire plant fresh weight became pronounced while the relationships between fresh weight and temperature were more or less the same. At later stages of growth (from 127 to 164 days after sowing), the optimum temperature shifted to a higher value so that maximum plant fresh weight was obtained at 25 °C. During this period, variations in the entire plant fresh weight as brought about by changes in temperature may well be attributed chiefly to differences in bulb fresh weight. It was observed that bulb development at 10 and 15 °C was still absent whereas at higher temperatures it was proceeding rapidly, and the more so as the temperature increased within the range studied. This indicates that the decline in total plant fresh weight at 30 °C is not to be accounted for by a slower

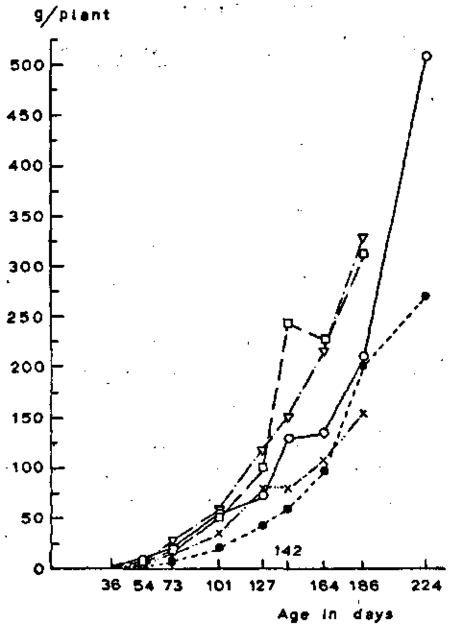


FIG. 67a
The effect of temperature on fresh weight of the whole plant.
●– – – –● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×–·–·–×: 30°C

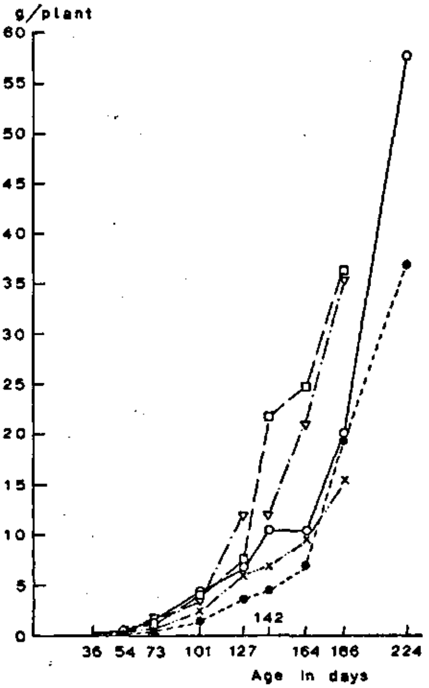


FIG. 67b
The effect of temperature on dry weight of the whole plant.
●– – – –● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×–·–·–×: 30°C

rate of bulb development at this temperature but rather by reduction in general growth. At more advanced age (between 164 and 186 days after sowing), because of earlier tissue senescence induced by the highest temperature – and also owing to about 2°C rise in air temperature occurring in the 10°C room as a result of some damage in the air cooling system in the period between 142 and 164 days from sowing – the entire plant fresh weight at 10°C exceeded that at 30°C. With further ageing (between 186 and 224 days after sowing) the entire plant fresh weight at 10 and 15°C continued to increase, to reach its highest value at the end of the experiment. The highest fresh weight at 15°C was twice that at 10°C. This increase was mainly due to seedstalk development which contributed much to the gain in total plant fresh weight, and to a smaller degree to bulb development. It should be noticed that all the plants developed seedstalks at 15 and 10°C. However, this development was enhanced by the former temperature as compared with the latter so that the seedstalks at 15°C were well beyond the bulb while only seen by dissection at 10°C. A point of interest is that, although at all stages of growth the entire plant fresh weight was depressed by either the lowest or the highest temperatures, the cause of this depression seems quite different in both cases. At 10 °C, the rate of photosynthesis might have been temperature limited, while at 30 °C an increased ratio of respiration over photosynthesis may be involved. In this respect, HEATH (1950) pointed out that raising the temperature above 25 °C, causes marked stomatal closure, due to the CO_2 of respiration of the guard cells being re-inforced by that of the bulky non chlorophyllous tissue in the leaf as a consequence of which accumulation of CO_2 in the leaf cavity results.

2. *Entire plant dry weight*

As shown in fig. 67b, the entire plant dry weight in relation to temperature and time followed, with few exceptions, the same trend as total plant fresh weight.

In the early stages of growth (up to 101 days after sowing), the optimal temperature for dry matter accumulation, in contrast to fresh weight, appeared to be 15 °C in most cases. It seems that 15 °C is less favourable for cell division and elongation than higher temperatures, up to 25 °C, so that assimilates that can be used for growth (cell division and extension) at the higher temperatures accumulate, resulting in an increase in dry matter content which was large enough to compensate for or even surpass the small reduction in fresh weight. In this respect, probably the balance between photosynthesis and respiration also is important, especially since photosynthesis goes on in the leaves only whereas respiration occurs in the entire plant. At 10 °C, although dry matter content was higher than at 15 °C, the increase failed to compensate for the great reduction in overall growth at this low temperature. However, the increase in dry matter content reduced the differences in dry weight values between 10 °C and other temperatures so that the total plant dry weights, in contrast to fresh weights, appeared to be more closely together. Moreover, contrary to fresh weight, dry weight at 25 °C in the interval between 142 and 164 days after sowing was found to increase. This is due to the fact that the bulb which contains less water was the major component of the plant at 164 days so that upon drying, it yielded greater dry weight. A point worthy of notice is that the highest dry weight value at 10 °C recorded at the end of the experiment (224 days) was approximately two-thirds of that at 15 °C, whereas fresh weight was only one-half. This indicates the greater accumulation of assimilates (mostly carbohydrates, as will follow) at 10 as compared with 15 °C, owing to the fact that the growth rate is curtailed much more at 10 than at 15 °C.

Apart from these considerations there is still the question in how far the different onion plant organs, viz., root, blades, neck, and bulb are influenced by air temperature.

A point to consider is that light intensity probably influences the sequence of the temperature curves; the higher the light intensity the more favourably the high temperature will probably come out, a fact which has been found by many investigators, e.g., MITCHEL and LUCANUS (1962) and ALBERDA (1965). These authors, however, applied different light duration in order to obtain varying daily

Table 1. The effect of temperature on fresh and dry weight of the whole plant and its various parts.

10 °C

Age in Days	Blade weight		Neck weight		Bulb weight		Root weight		Total weight	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
54	0.846	0.062	0.215	0.018	0.125	0.011	0.372	0.017	1.558	0.108
73	4.100	0.326	0.972	0.085	0.639	0.069	1.820	0.084	7.531	0.565
101	13.820	0.990	3.600	0.250	1.600	0.160	2 830	0.100	21.850	1.500

15 °C

Age in Day	Blade weight		Neck weihgt		Bulb weight		Root weight		Total weight	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
54	4.820	0.285	0.826	0.057	0.408	0.036	1.400	0.056	7.453	0.435
73	14.880	0.994	0.765	0.215	1.583	0.143	5.556	0.208	22.780	1.560
101	26.880	2.240	7.370	0.760	6.190	0.770	15.320	0.650	55.760	4.420

20 °C

Age in Days	Blade weight		Neck weight		Bulb weight		Root weight		Total weight	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
54	4.624	0.252	0.942	0.057	0.370	0.027	0.814	0.033	6.750	0.369
73	19.200	1.140	1.811	0.266	1.517	0.125	3.720	0.126	26.250	1.658
101	34.320	2.190	7.910	0.640	3.250	0.300	12.840	0.420	58.320	3.550

25 °C

Age in Day	Blade weight		Neck weight		Bulb weihgt		Root weight		Total weight	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
54	4.220	0.226	0.804	0.043	0.350	0.022	0.630	0.021	6.003	0.312
73	14.660	0.860	0.985	0.196	1.113	0.086	0.970	0.035	17.730	1.177
101	39.430	2.470	8.840	0.680	4.380	0.380	1.460	0.060	54.110	3.590

30 °C

Age in Days	Blade weight		Neck weight		Bulb weight		Root weihgt		Total weight	
	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry	Fresh	Dry
54	3.316	0.185	0.596	0.037	0.225	0.017	0.288	0.011	4.425	0.251
73	10.540	0.616	1.976	0.134	0.735	0.056	1.480	0.055	14.730	0.861
101	24.890	1.640	6.210	0.530	3.240	0.300	2.380	0.090	36.710	2.560

light energy and did not change the light intensity. So, it will be important to keep in mind that the temperature relations discussed should be considered valid only in relation to the other prevailing experimental conditions.

3. *Root fresh weight per plant*

Data, illustrated in fig. 68a show, in general, that root growth and development was more or less optimal at 15°C. Increase or decrease in air temperature from 15°C resulted in a decline in root fresh weight. At 20°C, however, the decrease was less marked as compared with that at other temperatures. Although it is highly probable that growth of roots and tops is influenced by movement of hormones from shoot to root and vice versa, the environmental factors, one of which is the air temperature, may also affect root growth. Roots can make none of their carbohydrate requirements, but depend on tops for supply. Thus, it seems possible that the carbohydrate distribution over roots and tops may be greatly influenced by changes in air temperature. In the onion plant temperatures higher than 20°C apparently result in monopolization of most of the available assimilates by the tops while only a small proportion is translocated to the roots, thus limiting their growth and development. The possibility that shortage of oxygen, which is important for root growth and function, at temperatures higher than 20°C may also be responsible for decreased root growth is not excluded. This has been proven by KHALIL (1956) who found that root growth of wheat at 30°C was favoured by external supply of O_2 as compared with that without any supply. Furthermore, the author showed that oxygen requirement for root growth increases with increased temperature. However, this seems not to be the only explanation (l.c., p. 143), as root growth was also checked when temperature was lowered to 10°C. Under such conditions, it is likely that the metabolic processes are depressed as a result of low activity of the enzymatic

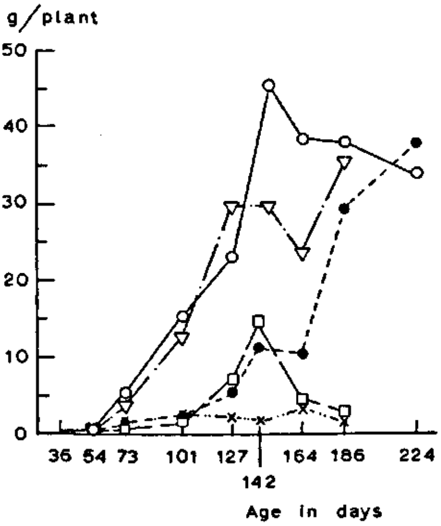


FIG. 68a
The effect of temperature on root fresh weight.
●- - - -● : 10°C
○———○ : 15°C
▽— · —▽ : 20°C
□— —□ : 25°C
×—··—× : 30°C

systems so that all growth aspects, one of which is root growth, are restricted. At all temperatures applied, in general, and at 15 and 20 °C in particular, fresh weight of roots increased with time up to a maximum and then, with few exceptions, decreased. Increased root fresh weight observed in the early stages of growth was due to continuous new root emergence and branching, whereas at the latter stages of development, due to inhibitory effect of bulbing on new root development together with increased rate of root senescence, root fresh weight declined after its maximum. The continual increase in root fresh weight up to the end of experiment at 10 °C may be due to slower rate of bulb development, while at 20 °C this increase is more likely due to sampling errors.

4. *Root dry weight*

With few exceptions, root dry weight in relation to temperature and age followed more or less the same trend as root fresh weight (fig. 68b). Variations in root dry weight at 15 and 20 °C were somewhat more pronounced than those of fresh weight of the same sample, which may be brought into connections with the observation we made that the dry matter content of roots at 15 °C is greater than at 20 °C. For the same reason, root dry weight, in contrast to fresh weight, after 127 days from sowing was equal at 15 and 20 °C. The rise in water content of roots at 25 in comparison with that at 10 °C in the period between 101 and 142 days after sowing may also account for the more marked differences in root fresh weight at these temperatures than in root dry weight. Also, due to greater sugar accumulation in roots at 10 than at 15 °C, root dry weight at

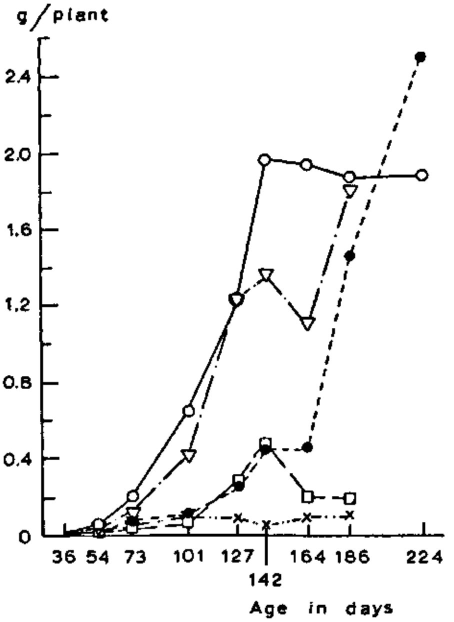


FIG. 68b
The effect of temperature on root dry weight.
●- - - -● : 10 °C
○———○ : 15 °C
▽— · —▽ : 20 °C
□— —□ : 25 °C
×-·-·-× : 30 °C

10 °C, contrary to root fresh weight, considerably exceeded that at 15 °C after 224 days from sowing.

5. *Blade fresh weight*

It is apparent from fig. 69a that up to 54 days after sowing (18 days after the start of the different treatments), no appreciable differences in blade fresh weight at 15, 20 and 25 °C could be detected. On the other hand, increase or decrease of temperature beyond this range caused a decline in blade fresh weight; the decrease, however, was more marked at the lowest temperature than at the highest one (30 °C). At 10 °C, the decreased leaf number, at 30 °C the reduced leaf dimensions, viz., length and diameter, are the main factors responsible for this decline. As the plants advanced in age (in the period between 54 and 73 days after sowing) the fresh weight of blades at all temperatures increased, owing to increased leaf number and size with time. During this period leaf growth seemed most favoured by 20 °C; 5 °C on both sides of the latter caused an equal decline in blade fresh weight. It is interesting to note that the latter similarity is to be attributed to different factors. At 15 °C the greater specific leaf weight (weight of 1 cm^2 leaf area) compensated for the reduction in total blade area, while at 25 °C the reverse was true. Deviating further from the optimum (20 °C) to either sides increases these effects. With increasing temperature, up to 30 °C or decrease down to 10 °C, a marked decline in blade fresh weight resulted. In the former case (30 °C) decreased leaf size (length × diameter) and not the reduction in leaf number was a factor responsible for the observed decline, while in the latter (10 °C) both factors were involved, making the fresh weight value at 10 °C to lag behind. In the period between 73 and 101 days after sowing, the blade fresh weight, in all cases, continued to increase with the tendency of blades fresh weight at 25 to be slightly higher than 20 °C. This difference, however, does not seem significant. At temperatures other than those mentioned, the fresh weight of blades appears reduced. At the two extremes (10, 30 °C) a decline in leaf number and size was found in both cases as compared with 20 or 25 °C, and very much largest at 10 °C. In the interval between 101 and 127 days after sowing, the fresh weight values at all temperatureswere still increasing whilst the relationships between fresh weight and temperature were, with few exceptions, the same. Because of a more rapid increase in leaf production at the highest temperature (30 °C) than at 15 and 10 °C, total blade fresh weight at 30 °C exceeded that at the latter temperatures. Between 127 and 142 days after sowing, owing to earlier bulb initiation at the highest temperature, and its depressive effect on new leaf emergence, the blade fresh weight at 30 °C decreased in contrast to that at other temperatures. Furthermore, owing to the daylength extension, having taken place after 101 days from sowing, as a result of which the total daily light energy was increased, a shift in temperature optima to higher value (25 °C) occurred so that the highest fresh weight value was obtained at 25 °C for which we refer to the general statement, p. 143. Increase or decrease of temperature from 25 °C, resulted in a decrease in blade fresh weight, and the more so as the temperature decreased further, mainly due to the reduction in leaf

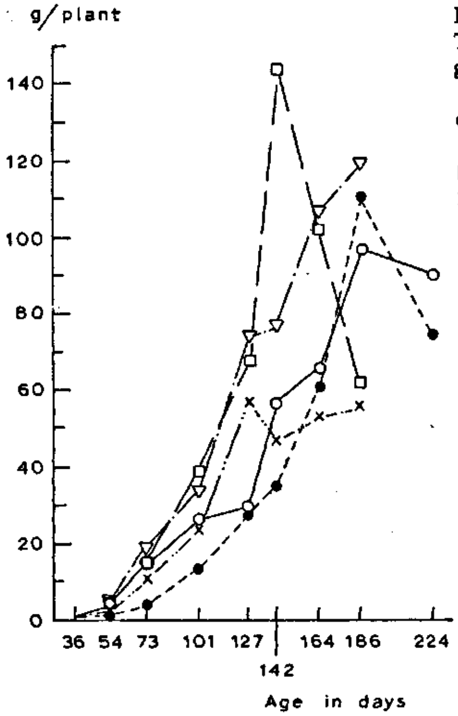


FIG. 69a
The effect of temperature on fresh weight of green leaf blades.

●- - - -● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×-·-·-× : 30°C

number, while at the highest temperature the decline in blade fresh weight was chiefly due to reduced leaf size. Owing to rapid bulb bulking, especially favoured at 25°C in the period between 142 and 164 days after sowing, accompanied by the drainage of assimilates from the blades to the developing bulb, the blade fresh weight at 25°C diminished sharply, contrary to what happened at lower temperatures. At still more advanced age (between 164 and 186 days) the blade fresh weight at 20, 15, and 10°C continued to increase and the more so as the temperature was lower, while at 25°C it was still sharply diminishing. The continual increase in blade fresh weight at 15 and 10°C may well be attributed to the absence of bulb development, whereas the unexpected continuous rise at 20°C may be due to the fact that the last harvest included a double onion plant with about 35 leaves without which the blades fresh weight would have decreased here as well. With further ageing (between 186 and 224 days), presumably because of bulbing and/or flowering and its depressive effect on leaf growth and production, fresh weight of blades at 10 and 15°C decreased. This decrease, however, was more pronounced at 10 than at 15°C. Moreover, it should be noticed that the increase in blade fresh weight at 10 over 15°C found after 186 days from sowing must not be attributed to increased leaf number and total blade area, but rather to higher specific leaf weight as a result of greater sugar accumulation at 10 than at 15°C.

Why blade fresh weight at 30°C in the period between 142 and 186 days after sowing tended to level off is obscure, but it seems likely that further leaf emergence is only depressed at the most favourable temperatures for rapid bulb formation (here, e.g., 25 °C). At temperatures higher or lower than the optimum, new leaf emergence may continue longer. HEATH (1943) pointed out that onion sets, grown at high temperature (30 °C), tended to produce distorted leaves and such new leaf emergence was continued longer than in plants grown at lower temperatures. In our present experiment, the leaves were not distorted; they were rather small, but healthy and rich in chlorophyll. This seems to suggest that, unlike at 25, at 30 °C the dominance of bulb formation is far less evident.

6. *Blade dry weight*

The blade dry weight as a function of temperature and age showed much the same type as the fresh weight (fig. 69b). Up to 101 days after sowing, the blade dry weight at 15, 20 and 25 °C, tended to be close together. Increased dry matter content with decreased temperature, within the latter range, reduced the differences in dry weight between these temperatures. Furthermore, because of increased specific leaf weight at 10 and 15 °C at the last harvest compared with the preceding one, the blade dry weight during this period levelled off, while blade fresh weight at both temperatures decreased. Also, due to increased sugar accumulation at 10 as compared with 15°C, the blade dry weight in the former in contrast to fresh weight, surpassed that at 15 °C at the last harvest.

Apart from these considerations, we would like to point out that maximum blade dry weight was attained at a moment which differed according to treatment; being after 127, 142, 164*, 186 and 224 days after sowing for 30, 25, 20,

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[*] For 20 °C, the higher value at 186 days probably was due to one particularly large plant, see above

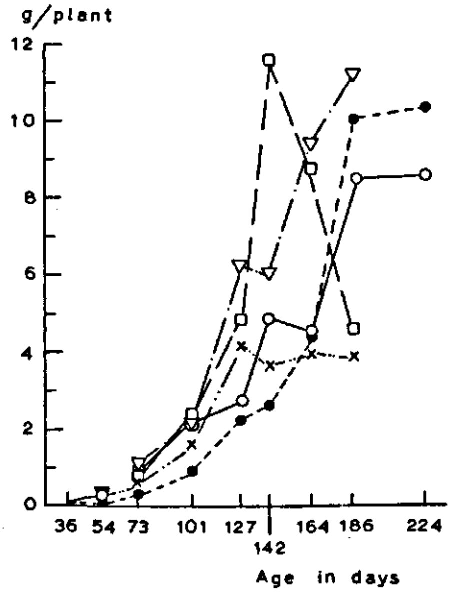


FIG. 69b
The effect of temperature on dry weight of green leaf blades.
●- - - -● : 10 °C
○———○: 15 °C
▽—·—▽ : 20 °C
□— —□: 25 °C
×—··—×: 30 °C

15, and 10 °C respectively, indicating that the higher the temperature, the earlier tissue senescence occurred.

7. *Blade dry matter content*

The percentages of blade dry matter content as related to temperature and age are presented in fig. 69c. Up to 127 days after sowing, temperatures lower than 20 °C showed a pronounced rise in the blade dry matter content. Conversely, temperature rise above 20 °C had a slight effect though a tendency towards increased water content of blades at 25 °C as compared with 20 or 30 °C can be detected. The fact that temperatures lower than 20 °C showed increased dry matter content of blades is perhaps surprising when viewed against the background of basic physiological knowledge, as transpiration may be much stronger at high temperatures. Nevertheless, it seems likely that the dry matter percentage of blades is determined by a complex of physiological processes rather than by actual rates of water uptake and transpiration only. The dry matter content of blades is greatly influenced by photosynthesis, respiration, utilization in growth or accumulation and translocation to other plant organs of which rates may well be affected to different degrees by changes in temperature, e.g., respiration increases relatively more than photosynthesis with rising temperature.

In this respect, WENT (1953) pointed out that at lower temperatures the ratio of photosynthesis to respiration is over 10, while at higher temperatures low ratios are observed. Thus, it appears reasonable if one suggests that increased ratio of photosynthesis/respiration may be an important factor responsible for the rise in dry matter content of blades at 15 °C. Another possible explanation is that at optimal or near-optimal temperatures for growth, a relatively greater proportion of assimilates is used in building up new tissues, i.e., increase in the cellular mass (number and size), and since water is the major component of the cell, a decrease in the dry matter content, perhaps in contrast to the absolute dry weight, would be expected. At temperatures far beyond the optimal,

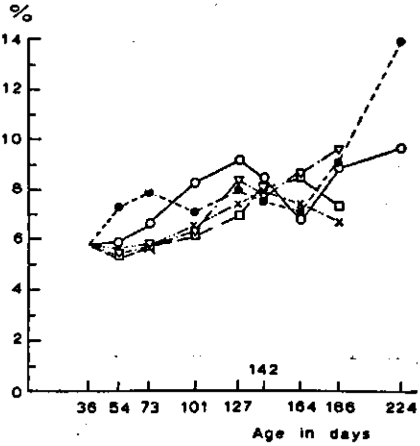


FIG. 69c
The effect of temperature on the ratio of dry to fresh weight of green leaf blades expressed as a percentage.

●– – – –● : 10 °C
○———○ : 15 °C
▽— · —▽ : 20 °C
□— —□ : 25 °C
×— ·· —× : 30 °C

the opposite is true, i.e., the growth rate it greatly checked, causing the assimilates to accumulate. However, a definite conclusion whether these factors were the only ones operating, or others, cannot be drawn.

At temperatures in the range from 15 to 30 °C, the time trend of blades dry matter content showed an increase up to a certain time and then decreased in some cases or continued to increase up to the end of the experiment in others. This increase is largely due to increased carbohydrate accumulation in blades with time (as will follow) and/or decreased water content as the plants progressed in age. That the dry matter content in the later stages of growth (after 142 and 164 days from sowing for 30 and 25 °C respectively) decreased at higher temperatures (30, 25 °C), in contrast to that at lower ones, may be attributed to increased rate of drainage of assimilates to the bulb at the higher temperatures as compared with the lower ones. The reason for decline in dry matter content at 15 and 10 °C, observed in the period between 142 and 164 days from sowing is not quite clear. It may be linked with an increased rate of leaf growth (expansion), owing to the unexpected rise in air temperature of about 2 °C during this period, owing to a failure in the air cooling system. The dry matter content at 10 °C in relation to that at other temperatures, and with time, up to 164 days after sowing, cannot be explained on the basis of carbohydrate accumulation, since the total soluble sugar content at 10 °C showed the opposite behaviour of that of the dry matter content in relation to other temperatures and with time (see fig. 79a). This suggests that factors other than those determining sugar content have been responsible for this behaviour. Contrary to this, the increased dry matter content at 10 °C in the period between 164 and 224 days after sowing goes in line with total soluble sugar content, and may well be explained on this basis.

8. *Neck (pseudostem) fresh weight*

Variations in neck fresh weight as a function of temperature and age are presented in fig. 70a. It is obvious that up to 101 days after sowing, though differences were not yet pronounced, neck growth tended to be most favoured by 20 °C, so that the highest fresh weight values were obtained at this temperature. Temperatures higher or lower than 20 °C resulted in a decrease in neck fresh weight. The decrease on both sides near the optimum was less marked than that at the extreme temperatures. However, the lowest temperature caused a more pronounced reduction in neck fresh weight than the highest one. In the latter, the decrease was mainly due to the depression in leaf sheath size, whereas at the lower temperatures the reduction in both leaf sheath number and size were involved. At later stages of growth, differences in neck fresh weight became pronounced, with the highest value at 20 °C, followed by 25, 30, 15, and 10 °C. Higher neck fresh weights at 20 °C than at 25 °C may be primarily attributed to differences in leaf sheath size and swelling, and not to their number, since the latter was greater at 25 °C. Conversely, decreased leaf sheath numbers at 10, 15 and 30 °C as compared with 25 °C may chiefly account for the decline in neck fresh weight observed in the former temperatures as compared with the

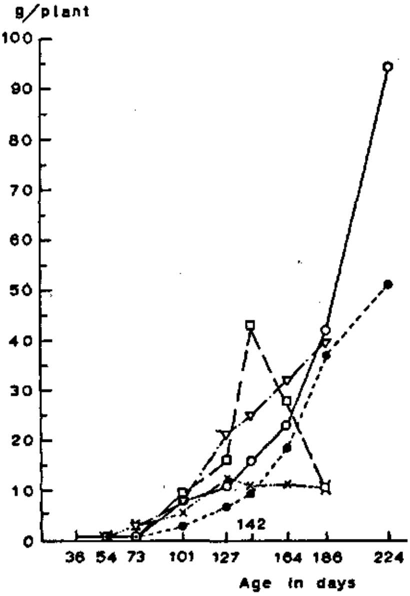


FIG. 70a
The effect of temperature on neck fresh weight.
●- - - -● : 10°C
O———O: 15°C
▽—·—△: 20°C
□— —□: 25°C
×—··—×: 30°C

latter (25°C). As the plants progressed in age (142 days from sowing), each 5°C rise from 10 up to 25°C resulted in a marked increase in neck fresh weight, mainly owing to increased leaf sheath number and swelling.

Further increase in temperature caused a so marked decline in neck fresh weight that the latter at 30°C was lower than that at all temperatures applied, except that at 10°C which was the lowest. The greater reduction in leaf sheath size at 30°C than at 15 and 20°C may account for the decrease in neck fresh weight at the former temperature, while compared with 25°C both reduced leaf sheath number and size were involved. At still more advanced age (between 142 and 186 days after sowing), because of bulb development being induced earlier at high temperature and its depressing effect on new leaf emergence, neck fresh weight at 30 and 25°C, in contrast to that at other temperatures, showed no further increase. At 25°C, neck fresh weight actually decreased, while at 30°C it came to a stand still, presumably owing to continual leaf emergence at 30°C which did not seem to be as favourable as 25°C for bulb formation. Also, the drainage of assimilates to the developing bulb may, in part, account for the decline observed. With further ageing (from 186 to 224 days after sowing), owing to seedstalk development, neck fresh weight at 10 and 15°C continued to increase, attaining its peak value at the end of the experiment.

The fact that fresh weight of neck at 25°C reached its peak value after 142 days from sowing, though it may be somewhat exaggerated, is real. Top growth of the onion plant is most favoured by this temperature as a result of which neck size, especially neck diameter, was found to increase due to increased leaf sheath number and dimension.

Considering the entire set of curves, we would like to remark that at 30°C neck fresh weight flattens off after 127 days, at 25 °C after 142 days, and taking into consideration footnote p. 149, at 20 °C probably after 164 days, whereas this tendency does not occur, contrarily even showing a steeper increase, at 15 and 10 °C owing to initial development of a flower stalk inside the neck. Bulbing in the latter cases is delayed.

9. *Neck (pseudostem) dry weight*

As shown in fig. 70b, neck dry weight, with some exceptions, followed the same trend in relation to temperature and time as neck fresh weight. In the early stages of growth (up to 101 days after sowing) it seems that neck dry weight was favoured by relatively lower temperatures than neck fresh weight so that the greatest values were found to fluctuate between 15 and 20 °C, while for fresh weight the optimal temperature fluctuated between 20 and 25 °C. Furthermore, because of greater sugar accumulation at 10 °C than at 15 °C, at the last harvest neck dry weight at 15 °C was only 1.45 times that at 10 °C, as compared with 1.85 times for fresh weight.

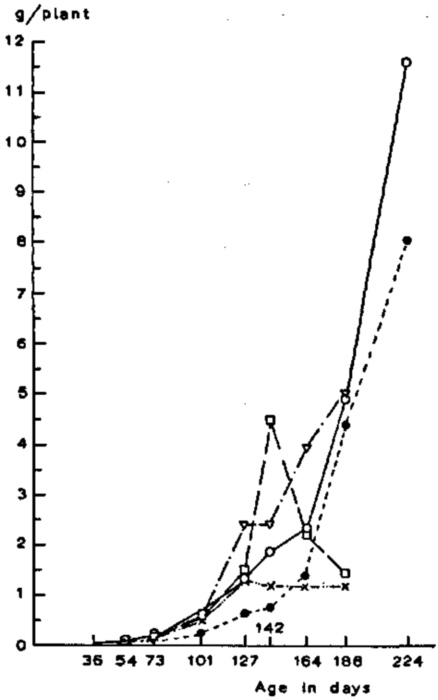


FIG. 70b
The effect of temperature on neck dry weight.
●- - - -● : 10 °C
○———○ : 15 °C
▽— · —▽ : 20 °C
□— —□ : 25 °C
×— ·· —× : 30 °C

10. *Bulb fresh weight* .

The effect of temperature on bulb fresh weight per plant at periodic harvests is presented in fig. 71a. It should be observed that up to 101 days after sowing, the plants were grown under short day conditions (12 hrs.). Consequently, no bulbing took place at all temperatures applied, untill after the daylength was extended to 15.5 hrs. Thus data illustrated in fig. 71a, up to 101 days express only the fresh weight of slight swelling in neck base which can even occur in short days. During this period, though differences were still small, 15°C seemed to be optimal for swelling in neck bases so that fresh weight values at this temperature tended to exceed those at all other temperatures. The decline at the two temperature extremes was more marked, as compared with that at 20 and 25°C. However, due to reduced leaf sheath number and perhaps thickening, the decrease in fresh weight at 10°C was greater than at 30°C in which case reduced leaf sheath size was the only cause. Twenty six days following daylength extension (127 days after sowing) the fresh weight of swelling neck base, in all treatments, tended to increase, with the highest value at 20 and the minimum at 10°C, while at other temperatures no appreciable differences could yet be detected. The increase at 20°C, however, even seems somewhat exaggerated. Since the bulbing ratio recorded by that time was more or less the same at 15, 20, 25 and 30°C, the tendency of fresh weight of swelling neck base to be slightly higher at 20°C must not be attributed to increased rate of bulb development, but rather to increased general growth which may have been favoured by the relatively high temperature (20°C) and as a result of daylength prolongation and, consequently, increased total daily light energy. In the period between 127 and 142 days from sowing, bulb fresh weight at temperatures higher than 10°C continued to increase. The highest bulb fresh weight value was obtained at 25°C, followed in order by those at 20 and 30, at 15 and 10°C. Enhanced rate of bulb development at 25°C, as compared with lower temperatures, may well account for increased bulb fresh weight at this temperature (25°C), whereas decreased general growth at higher temperature (30°C) was the chief

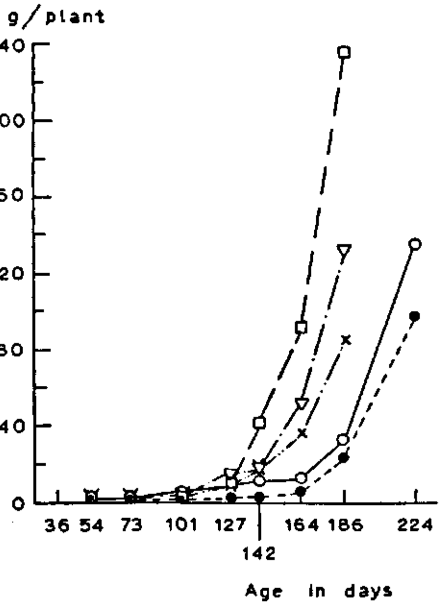
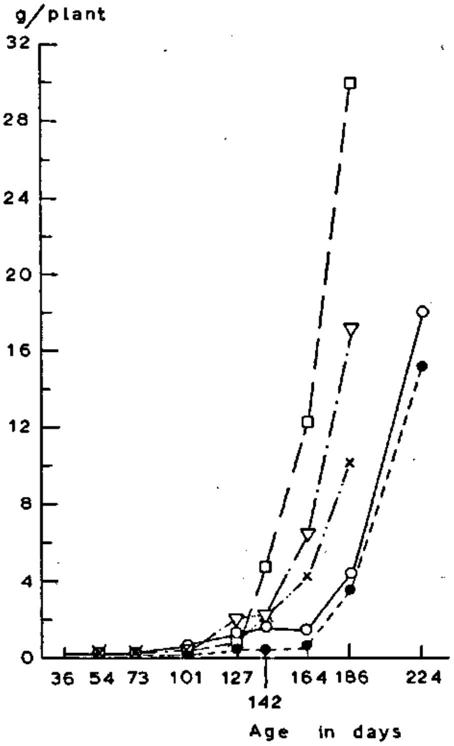


FIG. 71a
The effect of temperature on bulb fresh weight.

●- - - -● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—×: 30°C

FIG. 71b
The effect of temperature on bulb dry weight.

●- - - -● : 10°C
○———○: 15°C
▽— · —▽ : 20°C
□— —□: 25°C
×— ·· —× : 30°C



cause for lower bulb fresh weight at 30 than at 25°C and its equality to that at 20°C as the bulbing ratio at 30°C was greater than that at lower temperatures. At more advanced age (between 142 and 164 days after sowing), bulb fresh weight at temperatures in the range from 20 to 30°C increased considerably, while at lower temperatures, due to the absence of bulbing, no appreciable increase was observed. The highest bulb fresh weight occurred at 25°C; 5°C on both sides of the optimum resulted in a marked decrease which was more pronounced at the higher temperature (30°C) than at the lower one. The slower rate of bulb development at 20°C as compared with 25°C may account for the smaller increase in bulb fresh weight observed at 20°C. On the other hand, reduced general growth at 30°C may mainly account for lower bulb fresh weight at this temperature as compared with that at 25 and 20°C. At still more advanced age (between 164 and 186 days after sowing), bulb fresh weight at 20, 25, and 30°C continued to increase, attaining its peak value whilst the same relationships as before still exist. During this period, though actual bulb development (with bulbing ratio of 2.0 or higher) was still absent, the fresh weight of the swelling neck base showed a pronounced increase at 10 and 15°C. With further ageing (from 186 to 224 days after sowing), bulb fresh weight at 10 and 15°C continued to increase and the more so at the latter to reach its highest value.

An important point we would like to refer to here is that, although the bulbing ratios recorded after 224 days from sowing ranged from 2.25 to 2.75, indicating actual bulb development, all the plants grown at 10 and 15°C bolted.

11. *Bulb dry weight*

The dry weight of the bulb as a function of temperature and time (fig. 71b) followed closely, with only one exception, bulb fresh weight. At the last harvest (224 days after sowing) because of higher water content of the bulb at 15 than that at 10°C, difference in dry weight between these temperatures was not as marked as in fresh weight.

B. SOME MORPHOGENETIC FEATURES

1. *Leaf growth*

a. Leaf number per plant. Variations in green blade number per plant, as brought about by temperature at periodic harvests, are presented in fig. 72a. It is evident that, up to 73 days after sowing, the green blade number increased with increase in temperature up to the highest one applied. The increase, however, was more pronounced as the temperature was raised from 10 to 15°C than that caused by further increase. Presumably, increased rates of leaf initiation as well as expansion (emergence) with rising temperatures may account for the greater leaf number observed. As the plants progressed in growth (in the interval between 73 and 142 days after sowing)*, with the only exception at

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* It should be remembered that, in this experiment, after 101 days, daylength was extended (at full light intensity) from 12 to 16 hrs.

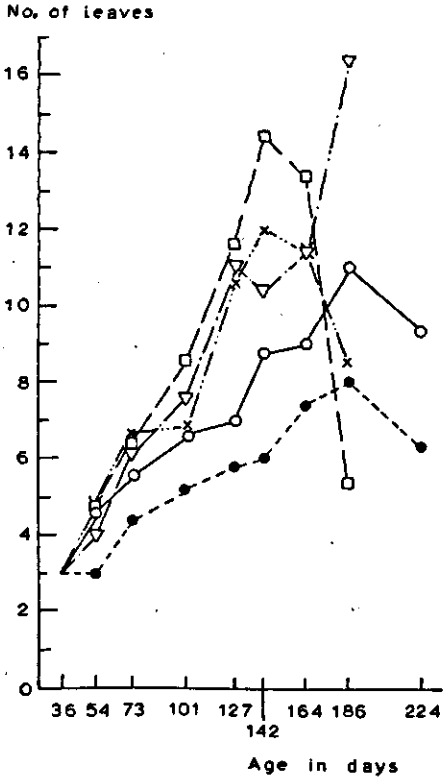


FIG. 72a
The effect of temperature on the number of green leaf blades.
●- - - -● : 10°C
○——○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—×: 30°C

20°C between 127 and 142 days after sowing, the green leaf number, in all cases, continued to increase, the highest value being at 25°C followed in order by those at 20, 30, 15 and 10°C. This implies that a 5°C shift from the temperature optimum towards higher values resulted in a relatively greater reduction in leaf number than a 5°C shift towards lower values. In both cases, the cause for this decrease appears quite different; at 20°C the lower rate of leaf emergence and/or initiation is the main factor, whereas at 30°C, the increased rate of senescence appears as the main factor responsible for decreased leaf number. Decrease of temperature further than to 20°C greatly suppressed new leaf emergence and probably initiation, and the more so with further reduction so that the minimum value was obtained at 10°C. It should be noticed that longevity of the leaves was found to increase as the temperature decreased. At more advanced age (between 142 and 186 days from sowing), owing to the depressing effect of bulb development on new leaf emergence, enhanced by high temperature, the green leaf number at 30 and 25°C, in contrast to that at lower temperatures, decreased. The continual rise in leaf number observed at 20°C in the period between 164 and 186 days after sowing, however, is due to the inclusion of one plant having 35 leaves in the last harvest, while the rest of plants making up the sample averaged approximately 11 leaves. After having reached a maximum at a relatively advanced age (186 days from sowing) because of the absence of bulbing, the green leaf number at 10 and 15°C decreased when the plants were kept growing longer (up to 224 days after sowing). This decrease may be attributed to bulb development and/or to flower stalk emergence taking place during the period from 186 to 224 days.

b. Leaf length. From fig. 72b, it is obvious that up to 101 days after sowing, the optimum temperatures for growth in leaf length were 20 and 25°C so that leaf length at these temperatures, while close together, exceeded that at other ones. However, the decline at 30°C was more pronounced than that at 15°C. Still further reduction of temperature greatly checked growth in length so that the minimum values were found at 10°C. At later stages of growth (from 101 to 127 days after sowing), with one irregularity, leaf length at all temperatures continued to increase, the highest values still being at 20 and 25°C followed by 30, 10, and 15°C (the latter obviously showing reversed order). That leaf length at 30°C during this period tended to surpass that at 15°C may be due to increased rate of leaf growth at 30°C as a result of increased total daily light energy by daylength extension after the 101st day. With advanced age (between 142 and 164 days), owing to earlier bulb development induced by the higher temperature, and its suppressing effect on leaf growth, leaf length at 30°C, contrary to that at other temperatures, decreased to become lowest of all. Meanwhile, more or less the same relationships between leaf lengths at other temperatures still hold true while the increase in leaf length observed at 25°C at 142 days seems somewhat exaggerated. Owing to rapid bulb bulking occurring at 25°C in the interval between 142 and 164 days after sowing, leaf length at this temperature fell off rapidly; at 20 and 30°C it tended to level off, whereas at lower temperatures, whilst close together, it continued to in-

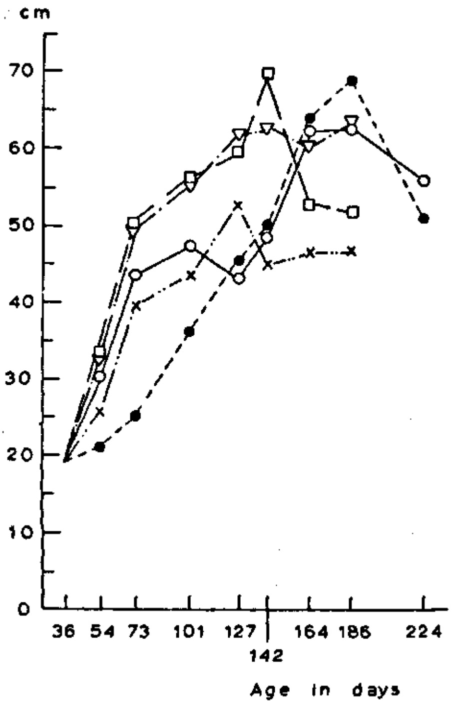


FIG. 72b
The effect of temperature on the length of the longest green leaf blade.

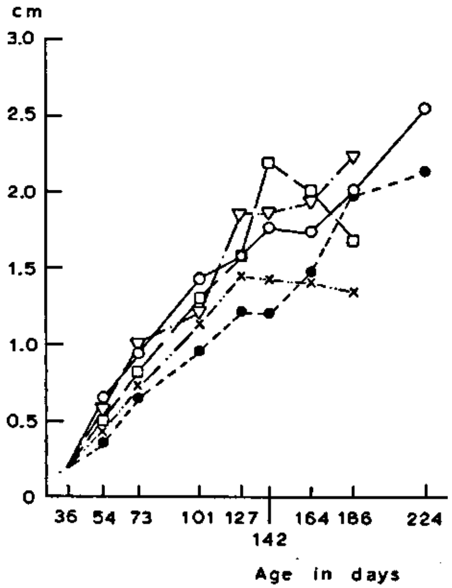
●– – – –● : 10 °C
○———○: 15 °C
▽— · —▽ : 20 °C
□— —□: 25 °C
×— ·· —× : 30 °C

crease. With further ageing (in the period from 164 to 186 days after sowing) leaf length at 10 °C, because of delay in seedstalk development, was still increasing, while at 15 °C it came to a stand still. When the plants were maintained longer (up to 224 days after sowing) leaf length at both temperatures decreased, possibly due to bulb development and/or to seedstalk emergence.

c. **Leaf diameter.** Unlike length, variations in leaf diameter brought about by temperature were less pronounced (fig. 72c). After 54 days from sowing, leaf diameters at 15, 20 and 25 °C, while tending to be more or less the same, surpassed those at lower or higher temperatures. As the plants advanced in age (between 54 and 73 days after sowing) leaf diameter, at all temperatures, increased and differences became more pronounced. The greatest leaf diameter was found at 15 °C; higher or lower temperatures resulted in a decline in leaf diameter. This decrease, however, was more marked at the temperature extremes, than at 20 and 25 °C. Between the third and fifth harvest (between 73 and 127 days after sowing) leaf diameter, in all cases continued to increase, with a shift in the temperature optimum for growth in leaf diameter towards higher values. Thus, the highest values during this period were found at 20°C; 5 °C on both sides of the optimum causing a decrease in leaf diameter. This decrease, however, was less pronounced at the lower side (15 °C) than at the higher one (25 °C). It seems that with temperatures beyond the range from 15 to 20 °C, growth in leaf diameter was greatly curtailed so that the minimum values were obtained at 10 and 30 °C with the tendency of leaf diameter in the former to

FIG. 72c
The effect of temperature on the diameter of the largest green leaf blade.

●- - - -● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—×: 30°C



be slightly lower than that in the latter. At later stages of growth (in the period between 127 and 164 days after sowing) presumably because of increased total daily light energy as a consequence of daylength extension, the temperature optima for growth in leaf diameter shifted to a higher value once more, so that leaf diameter at 25°C increased rapidly, to exceed those at other temperatures. Meanwhile, because of leaf growth cessation induced by earlier bulb development, leaf diameter at 30°C came to a stand still, while at 10°C it continued to increase, exceeding that at 30°C. At still more advanced age (between 142 and 186 days) owing to bulb development at temperatures from 20 to 30°C and its depressing effect on leaf growth, leaf diameter at these temperatures tended to decrease; at lower temperatures it continued to increase, especially at the lowest one, so that leaf diameter at 10°C exceeded that at all temperatures at the 8th harvest (after 186 days from sowing). With further ageing (between 186 and 224 days after sowing) leaf diameter at 10 and 15°C continued to increase, to attain its highest value at the end of the experiment, illustrating again the increase in life span of the leaves at the lower temperatures (see also fig. 72b).

d. Total leaf blade area per plant. Fig. 73a shows total blade area per plant as influenced by temperature at successive harvests. In the early stages of growth, up to 101 days from sowing, growth in leaf area was largest at 20 and 25°C while the values obtained at these temperatures were close together. Due to the reduction in leaf number as well as in leaf size (length × diameter), the decline in leaf area at 10°C was more marked than at 30°C, in which the reduction in leaf size was the only factor. The depression of leaf production also was the main factor responsible for decreased total leaf area at 15°C as compared with 20 and 25°C. During this period, although leaf number at 30°C was higher than that at 15°C, the greater leaf size in the latter was sufficient to

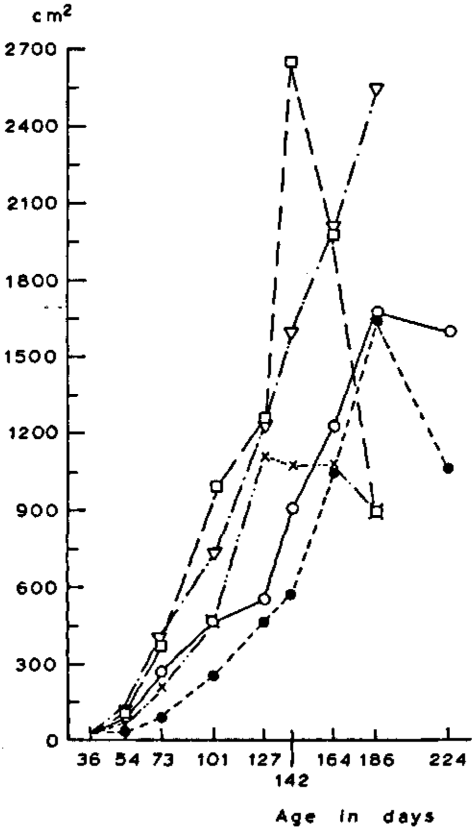


FIG. 73a
The effect of temperature on green leaf area/plant.

●- - - -● : 10°C
○——○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—× : 30°C

result in a slight increase in leaf area at this temperature as compared with that at 30°C. At later stages of growth (between 101 and 127 days from sowing), the total blade area, in all treatments, continued to increase, whilst the relationships between blade area and temperature, with only one exception, remained the same. Because of greater leaf number and length, the total blade area at 30°C exceeded that at 15°C. It must be noticed also, that similarity of total blade area at 20 and 25°C was due to different factors. At 25°C, the higher rate of leaf production compensated for the reduction in leaf diameter, whereas the opposite was true at 20°C, so that equality was obtained. As the plants advanced in age (between 127 and 142 days old), the greatest blade area per plant was found at 25°C followed in order by that at 20, 30, 15, and 10°C. Owing to the depressing effect on leaf growth by bulb development, induced earlier at the highest temperature, the total blade area at 30°C, in contrast to other temperatures, tended to level off. At more advanced age (between 142 and 186 days from sowing), because of the increased rate of leaf senescence as a result of bulbing, the total blade area at 25 and 30°C continually decreased, while at lower temperatures it continued to increase and attained the highest values. However, because the effect of bulbing on leaf production was less dominant (new leaves still continuing to appear), the decrease at 30°C was less pronounced than that at 25°C. The continuous increase in total blade area at 20°C in the interval from 164 to 186 days seems surprising, since bulb development at this temperature was in progress. However, probably this increase was due to the presence of one odd plant bearing about 35 blades without which it would have decreased. At still more advanced stages of development (between 186 and 224 days from sowing) because of bulb formation and/or seedstalk development, the total blades area at 10 and 15°C decreased.

It should be kept in mind that the total green leaf area (fig. 73a) is not merely the net product of leaf length and diameter shown in figs. 72b and 72c respectively, since the values indicate length and diameter of the largest leaf and not the average length or diameter of the total blades number. Furthermore, one would not forget the average leaf number (fig. 72a) which comes into play in determining total green leaf area presented in fig. 73a.

2. *Leaf area ratio*

The ratio of the leaf area to the total plant dry weight (leaf area ratio) as a function of temperature and time is presented in fig. 73b. First of all, it should be borne in mind that the leaf area ratio does not lend itself to simple interpretation as this ratio is the resultant of the interrelationships between many phyiological processes, the rates of which are differently affected by temperature. However, using this growth function, it may serve to increase our understanding of variation in yield and responses of the onion plant to the environment in which it is grown. From fig. 73b, it can be seen that up to 127 days from sowing, the highest value for the leaf area ratio was obtained at 25°C, while a reduction in this ratio occurred with decrease or increase in temperature. This may be due to two different causes; first, at 25°C, a relatively greater proportion of the gain in dry weight may be utilized in building up the photosynthetic apparatus (higher LWR values), secondly it can mean that leaves at 25°C have the lowest specific leaf weight (or the highest specific leaf area or leaf expansion). In the following, evidence is presented that both these possibilities cooperate. First, it is shown that the LWR in percent (dry weight of leaves/entire plant dry weight, in percents) during the growth period from 36 to 127 days after sowing increased with increasing temperature from 15 to 25°C. The values of LWR in percents amounted to 60.5, 55.3, 62.7, 69.4 and 68.4 for 10, 15, 20, 25 and 30°C respectively. Secondly, the corresponding specific leaf weights (the weight in mg of 1 cm^2) were 3.6, 4.2, 3.2, 2.8 and 3.0 indicating a decrease in specific leaf weight or an increase in leaf expansion with increase in temperature from 15 to 25°C. This, altogether, demonstrates that leaf weight ratio (LWR) as well as leaf expansion (leaf area/ leaf weight) played a role in determining the LAR curves obtained (see also further below). Thus, during this period, 25°C seems to be optimal for both LWR and leaf expansion (the highest value of LWR and the lowest one for specific leaf weight were found at 25°C); these components are factors responsible for the highest LAR observed at 25°C. At higher temperature (30°C) the dry weight proportion converted into leaves (LWR) as well as

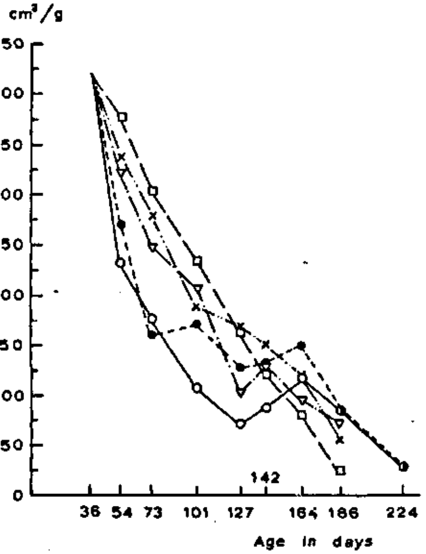


FIG. 73b
The effect of temperature on leaf area ratio.
●- - - -● : 10 °C
O———O: 15 °C
▽—·—▽ : 20 °C
□— —□: 25 °C
×—··—×: 30 °C

leaf expansion tended to be slightly lower than at 25 °C. This may account for the decline in LAR at 30 °C as compared with that at 25 °C. The same reasoning may apply for increased LAR at 10 °C as compared with 15 °C, i.e., that it is due to higher LWR as well as to lower specific leaf weight at 10 °C than at 15 °C.

Specifying this last case still a little further, we may state that the decrease in specific leaf weight may be due to depression in, e.g., carbohydrate content at 10 as compared with 15 °C and/or to increased leaf expansion at 10 °C as compared with 15 °C. Comparison of figs. 69b and 73a shows that both leaf weight and leaf area are lower at 10 than at 15 °C. The behaviour, evident in fig. 73b, thus is to be explained by the fact that the decrease in leaf weight is somewhat larger than that in leaf area.

At later stages of growth, (i.e., in the period between 127 and 186 days from sowing), besides leaf expansion, bulb development comes into play in determining the LAR curves through its effect on leaf weight ratio. During this growth period the LWR values amounted to 59, 44.4, 44.5, 31.1 and 39.5% for 10, 15, 20, 25 and 30 °C respectively. This implies that 25 °C is most favourable for dry matter distribution over useful organs, as the bulb, aside of leaf production. A shift in temperature from the optimum to lower or higher value increases the proportion converted into leaves. However, the increase towards the lower side is larger than that towards the higher one. The specific leaf weights (weight in mg of 1 cm²) during this period were 5.0, 4.7, 4.3, 4.6 and 3.7 for 10, 15, 20, 25 and 30 °C respectively. Up to 25 °C, differences in specific leaf weight between temperatures are less pronounced than differences in LWR. Thus, LAR values for temperatures ranging from 10 to 25 °C were mainly governed by LWR and to a slight degree by leaf expansion. The highest LAR at 10 and 15 °C is due chiefly to increased LWR, owing to the fact that these temperatures were less favourable for bulb formation. On the other hand, higher

LAR at 30°C than at 20 and 25°C is mainly due to increased leaf expansion at 30°C as compared with 20 and 25°C.

It appears useful to pay some attention to the time course of some of the derived quantities under consideration at the various temperatures. As such, we will consider the LWR (dry weight green leaves/dry weight plant, in percent), the specific leaf area (SLA, i.e., total surface area/dry weight of leaves) and the LAR (leaf area ratio, i.e., total leaf surface/dry weight per plant). Clearly, if two of these relations are known, the third one can be derived.

It is well-known that, in general, in early phases of development, plants mainly develop leaves, later on the photosynthetic factory in the leaves produce material for the production of other plant organs, and reserves. Thus, it is to be expected that, in the course of time, the part, leaf weight contributes to plant weight, tends to decrease. The LWR shows this in a similar way for all temperatures (fig. 74a). Generally, the decrease in the first part is less steep than later on, viz., the total weight predominates over the (as such also increasing) leaf wight more and more. LWR, e.g., decreases in the period between 54 and 127 days from an average (over all temperatures) of 67.6 to 56.4%, yielding a ratio LWR_{54}: LWR_{127} = 1.20 (we will confine ourselves in first instance to this period). LAR shows a somewhat different course, the decline in the first period being much steeper, viz., from 306 to 126 cm²/g, i.e., a factor of 2.43.

The discrepancy between the two values, obviously, has to be correlated with

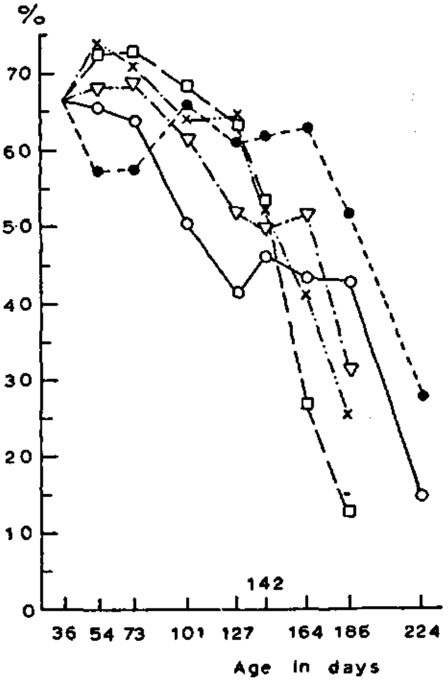


FIG. 74a
The effect of temperature on leaf weight ratio.

●- -·- -● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—× : 30°C

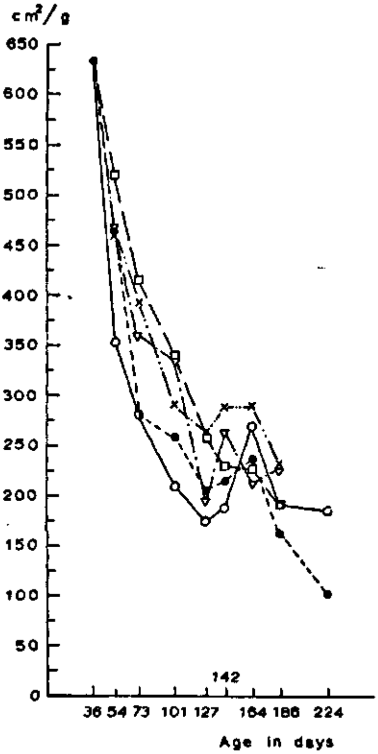


FIG. 74b
The effect of temperature on specific leaf area.
●- - - -● : 10°C
○———○ : 15°C
▽— · —▽ : 20°C
□— —□ : 25°C
×— ·· —× : 30°C

the area/weight relationship for the leaves, in which, in the onion, the peculiar cylindrical shape of the leaves will be expressed.

Indeed, looking for the leaf area/weight relationship (SLA) we find that, between the 54th and the 127th day, it decreses from 450 to 220 = 2.06 (fig. 74b). It thus appears that there is a satisfactory agreement between the three curves discussed, since 1.20 × 2.06 = 2.47, in reasonable agreement with the LAR decrease value of 2.43.

It is of interest to look into weight and size development of the leaves in the period considered. Leaf area increases from an average of 90 cm^2/plant at the 54th day to 910 cm^2 at the 127th day, thus, a 10-fold increase. In the same period the leaf dry weight increases from 0.20 g/plant to 4.11 gram/plant, thus, a 20-fold increase. Taking into consideration the rather 3-dimensional (± cylindrical) shape of the leaves, it seems logical that, with increases of the dimensions, the surface should increase in a lower proportion than the weight, since the surface roughly grows with the 2nd, the weight with the 3rd potence of the linear dimensions. Taking the 10-fold increase of the area as a second potence increase, one would expect a weight increase of roughly 30-fold. The 20-fold increase actually found, lags behind this figure. To this lag two factors may contribute; viz., 1) the possibility that part of the leaf expansion is due to one-dimensional (length) increase without appreciable increase in diameter, 2) that part of the surface expansion may not be 'translated' into dry weight because of: α cell expansion with uptake of much water and production of little dry weight, β) decrease of productive (photosynthetic) overall efficiency owing to: αα) decrease in efficiency of photosynthesis by ageing, ββ) mutual shading of leaves.

The latter phenomena probably become more dominant after the 127th day, causing differences in slopes in the various curves discussed above. An analysis along similar lines as the one given above could be applied to demonstrate this.

For a more profound analysis of the whole picture, more extensive morphological data and gas exchange data will have to be collected, and certainly offer a fascinating field of research for the plant physiologist and ecologist.

3. *Neck growth (pseudostem diameter)*

It is obvious from fig. 75a that up to 101 days after sowing, growth in neck diameter is most favoured by 15 and 20°C so that the largest neck diameter, with only one exception, was obtained at these temperatures. This increase was mainly due to increased leaf sheath size and thickness, and not to leaf sheaths number since the latter was greater at 25 than at 15 and 20°C. As the temperature increased beyond 20°C, neck diameter decreased, and the more so at higher temperatures so that neck diameter at 30°C was inferior to that at 25°C. Furthermore, due to the reduction in leaf sheaths number and size, neck diameter at 10°C was lagging behind. As the plants advanced in age (between 101 and 127 days), presumably owing to increased total daily light energy as a consequence of daylength extension, the temperature optima for neck growth shifted to higher values, so that neck diameter at 20°C surpassed that at 15°C. The latter was similar to that at 25°C, followed in descending order by those at 30 and 10°C. However, similarity between 15 and 25°C was due to different factors. At 25°C, increased leaf sheaths number was sufficient to compensate for reduced leaf sheath size and thickness whereas at 15°C the opposite was true. At later stages of growth (in the interval between 127 and 142 days after sowing), the optimum

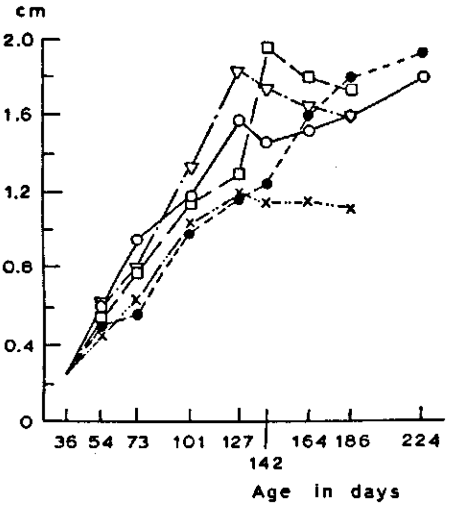


Fig. 75a
The effect of temperature on neck diameter.
●- - - -● : 10°C
○———○: 15°C
▽—·—▽ : 20°C
□— —□: 25°C
×—··—×: 30°C

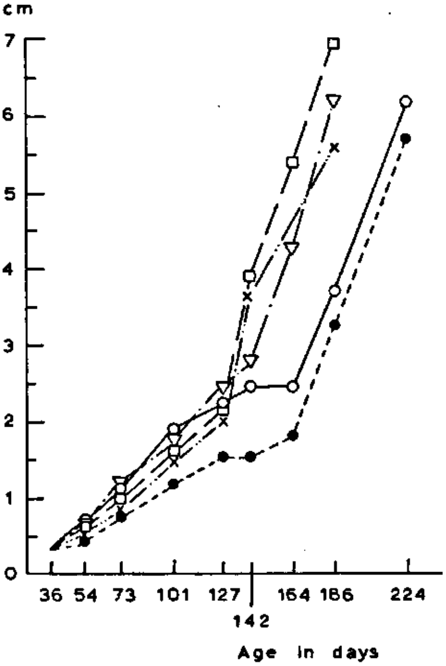
temperature shifted to a higher value once more. Thus, maximum neck diameter occurred at 25°C, chiefly because of increased rate of leaf sheath formation. Owing to the depressing effect on new leaf emergence of bulb development induced earlier at high temperature, the decline in neck diameter caused by 5°C rise above the optimum was greater than that caused by 5°C lowering. At still more advanced stages of development (between 142 and 186 days) because of rapid bulb bulking and its depressing effect on new leaf emergence, and due to the drainage of assimilates to the bulb, neck diameter at 25°C, in contrast to other temperatures, diminished; at 30°C it levelled off owing to the fact that bulb formation was not completely predominant on leaf production as at 25°C. With further ageing, neck diameter at 15 and 10°C continued to increase and attained its highest value at the end of the experiment, which, however, was due to seedstalk emergence.

Owing to increased leaf sheaths number and thickening, neck diameter, in all cases, increased with time up to a maximum attained at a certain moment which differed according to treatment, being after 127, 142, 186 and 224 days from sowing for 30, 25, 20, 15, and 10°C respectively. This indicates that, the higher the temperature, the earlier maturity was reached, which, as such, is characterized by a decrease in neck diameter.

4. *Bulb growth*

a. Bulb diameter. The influence of temperature on bulb diameter at different stages of growth is presented in fig. 75b. It should be remembered that up to 101 days after sowing, the plants were grown under short day conditions after which daylength was extended to 15.5 hrs. Thus, data illustrated in fig. 75b up to 101 days merely express the slights swelling in neck bases that can even occur under short days. Hence, it is not surprising that swelling of the neck bases in relation to temperature and age, up to 127 days, followed closely the same trend as neck diameter. Furthermore, the same interpretation previously given for differences in neck diameter, induced by temperature and time, also apply for thickening of neck bases. In the period between 127 and 142 days from sowing, variations in bulb diameter became pronounced. During this period, increasing temperatures, up to 25°C, resulted in an increase in bulb diameter, owing to an increased rate of bulb development (thickening of leaf sheath bases and scale formation) with rising temperature. At still higher temperatures (up to 30°C), bulb diameter tended to decrease. This decline may not be attributed to a reduced rate of bulb development at 30°C as compared with that at lower temperatures, but rather to the depressing effect on the general plant growth caused by this high temperature (the bulbing ratio at 30°C by that time exceeded those at all other temperatures). As the plants proceeded in growth (between 142 and 164 days old), bulb diameter in all cases continued to increase, whilst the interrelationship between bulb diameter and temperature still was the same so that the maximum value was obtained at 25°C and a decline in bulb diameter resulted at both sides of this optimum. The decrease, however, at temperatures on both sides near the optimum was less marked than that at 15 and 10°C. This

FIG. 75b
The effect of temperature on bulb diameter.
●- - - -● : 10°C
○——○: 15°C
▽—·—△: 20°C
□— —□: 25°C
×—··—×: 30°C



may be due to the fact that actual bulb development at the latter temperatures was still absent so that no appreciable increase in bulb diameter was found. At more advanced age (between 164 and 186 days) bulb diameter, at all temperatures, continued to increase. Because of earlier tissue senescence induced by high temperature, bulb diameter at 20°C tended to surpass that at 30°C. During this period, though bulb diameter at 10 and 15°C showed a pronounced increase, actual bulb development (with bulbing ratios of 2.0 or higher) was still absent, causing bulb diameter at these temperatures to be in the rear. It should be noticed that the increase in bulb diameter observed at 10 and 15°C was chiefly due to swelling of leaf sheath bases and not to scale development while at higher temperatures both factors were involved. At further stages of development (in the period between 186 and 224 days after sowing), bulb diameter at 10 and 15°C rapidly increased to reach its highest value. It is worth notice that all plants at these temperatures developed seedstalks, spoiling the bulb from the economical point of view.

b. Bulbing ratio. The development of a bulb in the onion plant may be assessed by the relation between the maximum diameter at the base to the minimum diameter at the neck, the 'bulbing ratio'. It is generally accepted that bulb development (swelling of the neck base, and scale formation) can only begin in response to the stimulus of long days, but thee is a strong interaction between the effects of daylength and temperature in the sense that bulbing is enhanced by high temperature as long as the daylength is sufficient to induce bulbing. High temperature alone has no effect on the initiation of bulbing (THOMPSON and

Smith, 1938). Fig. 75c shows the bulbing ratio as influenced by temperature under short day conditions (12 hrs.), up to 101 days from sowing, as well as under long days (15.5 hrs.), from 101 days onwards. Under short days, it is not surprising to find no differences in bulbing ratio caused by temperature so that the values are close together. Moreover, the time trend of the bulbing ratio, up to 101 days, showed no appreciable increase, indicating the absence of actual bulb development at all temperatures applied. Twenty-six days following daylength extension (in the period between 101 and 127 days), the bulbing ratio, in all treatments, tended to increase. The increase was slightly more pronounced at temperatures ranging from 20 to 30 °C as compared with that at lower ones. Owing to the tendency of the bulbing ratio at 15 °C to be slightly higher from the beginning (after 101 days from sowing) the values at 15, 20, 25 and 30 °C were similar, while that at 10 °C lagged behind. As the plants proceeded in growth (between 127 and 142 days), the bulbing ratio at temperatures in the range from 20 to 30 °C increased, and the more so as the temperature was raised within this range so that the highest value was attained at 30 °C. At lower temperatures, the bulbing ratio seemed to level off. This indicates that bulb

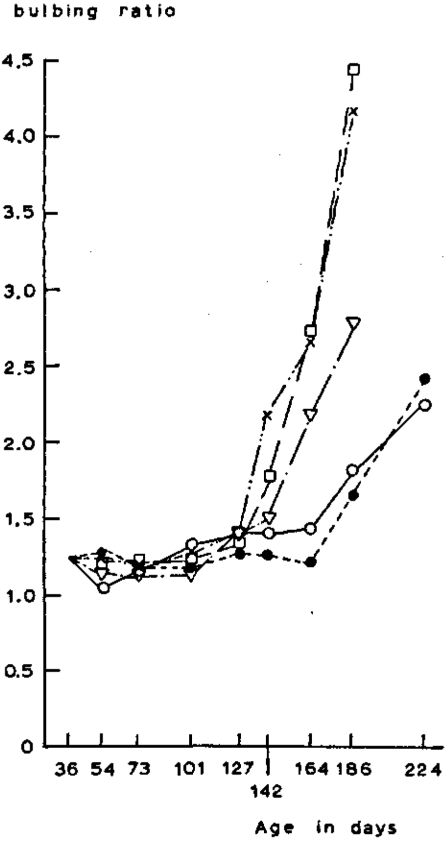


Fig. 75c
The effect of temperature on bulbing ratio.
●- - - -● : 10 °C
○——○ : 15 °C
▽—·—▽ : 20 °C
□— —□ : 25 °C
×—··—× : 30 °C

development was progressively speeded up by rising temperature in the range from 20 to 30 °C, while no bulbing was observed at lower temperature. At later stages of growth (between 142 and 164 days), bulb development at 20, 25 and 30 °C was proceeding, whereas at 10 and 15 °C it was still absent. At more advanced age (between 164 and 186 days old), the bulbing ratio, in all cases, continued to increase, reaching its highest value at 30, 25 and 20 °C. Due to rapid bulb bulking being most favoured by 25 °C, the bulbing ratio at the latter overtook that at 30 °C. However, it should be noticed that the continuous increase of bulbing ratio at 30 and 25 °C during this late stage of bulbing in part was due to shrivelling of the older leaves and the cessation of new leaf emergence which together reduce the diameter of the neck. With further ageing, the bulbing ratio at 10 and 15 °C continued to increase, reaching values higher than 2.0 which indicate actual bulb development. That the bulbing ratio at 10 °C exceeded that at 15 °C is not to be attributed to greater increase in bulb diameter at 10 °C, than at 15 °C since the reverse was true, but rather to the greater neck diameter at 15 °C, owing to seedstalk emergence beyond the bulb.

5. *Top/root ratio (on dry weight basis)*

The relationship between top and root growth over the growth period from 36 to 101 days after sowing as influenced by temperature is brought out in fig. 76. It is evident that this growth correlation increased with increased temperature from 15 to 25°C. The increase was greater upon temperature increase from 20 to 25 °C than upon increase from 15 to 20 °C. This indicates that top growth predominates over root growth with rising temperature in general, and in particular as the temperature increases from 20 to 25 °C. With further increase from the latter (25°C), the top/root ratio decreases. The reason for that may lie in the fact that at 30 °C not only root growth is greatly curtailed but also top growth, since 25 °C seems to be most favourable for top growth. On the other hand, 15 °C proved to be optimal for root growth as the lowest top/root ratio was obtained at this temperature. Five degrees on both sides of the optimum (15 °C) resulted in an increase in top/root ratio. The increase at the higher side (20 °C) is due to the fact that this temperature promoted root as well as

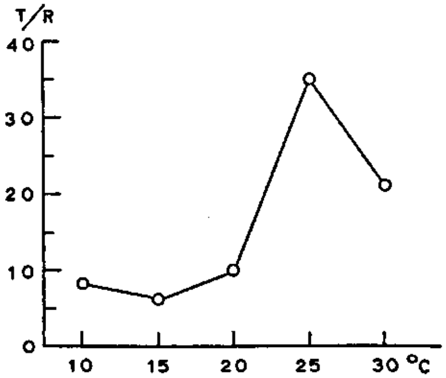


FIG. 76
The effect of temperature on top/root ratio over the period 36 to 101 days from sowing (means of 3 harvest values). Top = leaves + neck + swollen neck base.

top growth, but increase in the latter (top) was relatively greater than at 15 °C. At 10 °C, both top and root growth were checked as compared with 15 °C, but root weight decreased relatively more, making the top/root ratio to be slightly higher than at 15 °C (for example, root weight at 15 °C was 4.4 times that at 10 °C, while top weight was only 3 times as high).

6. *Net assimilation rate (NAR), leaf area ratio (LAR) and relative growth rate (RGR) relationship as a function of temperature*

Temperature affects growth through its effect on the metabolic processes within the plant. Like enzyme activities, growth activities are more than doubled by a 10 °C rise in temperature within the physiological range, and this rate of temperature response in many cases declines in the higher temperature ranges. The growth rate depends on the excess of assimilates produced by the photosynthetic system over losses through respiration in the entire plant. Respiration usually increases strongly with the temperature while, at the usual atmospheric CO_2 concentration there is hardly any increase in the gross photosynthesis (GAASTRA, 1962). Throughout our investigation, neither the rate of photosynthesis, nor the rate of respiration was measured, but we computed NAR which is the net result of the rates of photosynthesis minus those of respiration. In 1920, BRIGGS, KIDD and WEST defined the relative growth rate (dry matter increase per unit dry weight present, per unit time) as the product of the net assimilation rate and the ratio of leaf area to total plant weight (leaf area ratio). It follows that any change in weight brought about by changes in temperature will be dependent on the changes induced in the net assimilation rate and in the leaf area ratio. In fig. 77 we present the relationship between these three growth characteristics as a function of temperature over 101 days from sowing. It is interesting to note that the relative growth rate curve at 10 and 15 °C follows the NAR curve, while at higher temperatures the relative growth rate curve appears closer to LAR one. This indicates that changes in weight at lower tem-

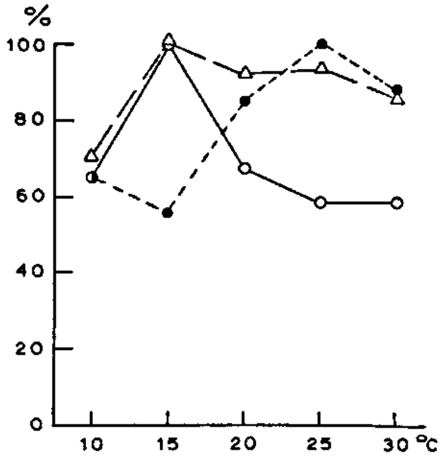


FIG. 77
The effect of temperature on mean RGR, NAR and LAR over the period 36 to 101 days from sowing. RGR, NAR at 15 °C and LAR at 25 °C = 100.
△— —△: RGR
○——○: NAR
●- - - -● : LAR

peratures (10, 15 °C) are mainly determined by the NAR; at higher temperature (20 to 30 °C) the leaf area ratio is the chief determinant.

Not only dry matter production but also dry weight distribution over the various plant organs is influenced by temperature. In fig. 78a, the percentage dry matter distribution over roots, blades, neck and swollen neck base is presented; values are means of three periodic harvests from 36 to 101 days after sowing. It is clear that leaves and roots are most affected by temperature. They show opposite trends in their response to temperature in that the dry weight percentage distributed over leaves increases with increasing temperature, while in roots it tends to increase as temperature declines. The curve of the neck is nearly flat, whereas that for swollen neck bases is slightly higher at 10 and 15 °C. A point of special interest is that temperatures higher than 25 °C or lower than 15 °C did not bring about any change in root or blade dry weight percentage. In general, most of the dry weight gain during these early stages of growth is converted into leaves, while the part distributed over the other organs is very small. Under long day conditions, the picture is quite different (fig. 78b). Bulb dry weight percentage becomes predominant mainly at the expense of leaves and the more so as temperature increased up to 30 °C. However, at 25 °C, bulb dry weight percentage is the most dominant. During this growth period, no large differences in the percentages of dry weight of the bulb at 10 and 15 °C as compared with the first period are observed.

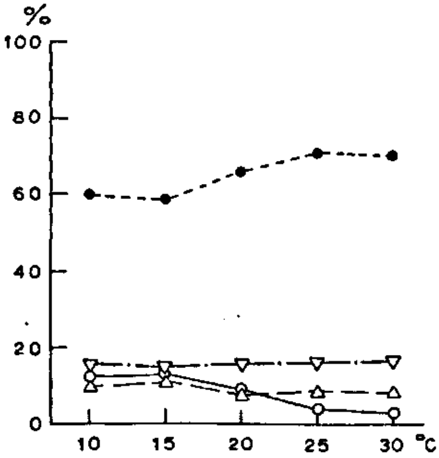


FIG. 78a
The effect of temperature on mean dry matter distribution between the various plant parts over the period 36 to 101 days from sowing.
●- - - -● : leaf blades
▽—·—▽ : neck
△— —△: bulb (swollen neck)
○———○: roots

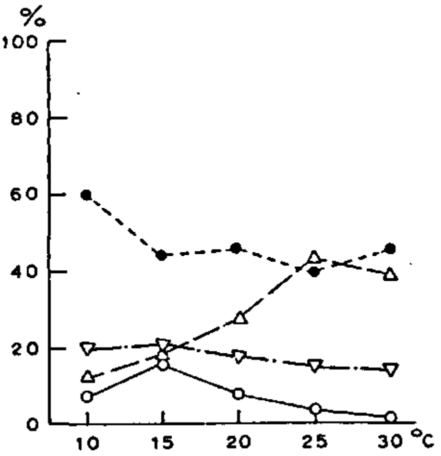


FIG. 78b
The effect of temperature on mean dry matter distribution between the various plant parts over the period 127 to 186 days from sowing.
●- - - -● : leaf blades
▽—·—▽ : neck
△— —△: bulb
○———○: roots

C. TOTAL SOLUBLE SUGAR CONTENT

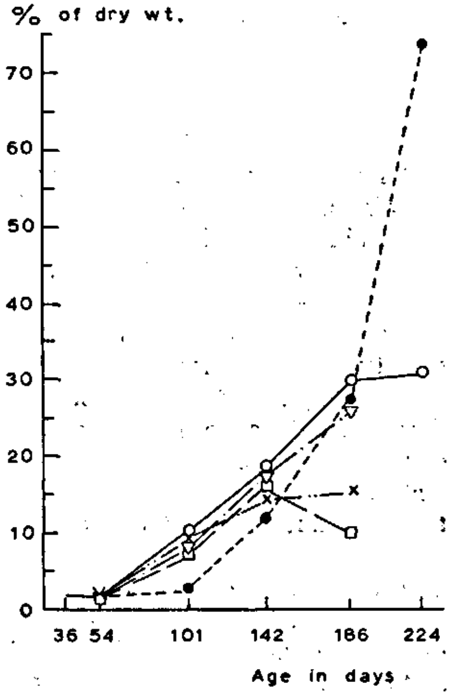
1. *Blade sugar content*

The sugar content of blades, expressed as percentage of dry weight, as a function of air temperature at different stages of growth is shown in fig. 79a. It can be seen that, up to 54 days from sowing, no differences in the sugar content could be detected. As the plants advanced in growth (in the interval between 54 and 101 days after sowing) the soluble carbohydrate content, at all temperatures, increased with the highest value at 15°C. Temperatures beyond the latter (lower or higher) resulted in a decline in the sugar concentration of the blades. This decline, however, was more pronounced at 10°C than at temperatures in the range from 20 to 30°C so that the sugar content at 10°C former was lagging behind that at the other temperatures. The sugar content of blades is a net result of the rate of sugar synthesis through photosynthesis and its rate of consumption through respiration, utilization in growth, and translocation to the other plant organs. During this period, although the growth rate of the entire plant was greatly curtailed at 10°C as compared with other temperatures, it seems possible that the rate of sugar formation at this temperature was hardly adequate to keep pace with sugar consumption and export so that no appreciable increase in the sugar level of the blades was observed. Though the photosynthetic rate at 15°C may have been lower than that at 20 or 25°C, it seems likely that the ratio of photosynthesis over respiration decreases with increased temperature, since the respiration rate probably increases relatively more. This along with relative decreases in the rate of carbohydrate utilization in growth with decrease in air temperature from 25 to 15°C, makes the sugar reserves in the blades rise as the temperature was lowered to 15°C. It should be remembered that after 101 days from sowing, the entire plant fresh weight at 20°C was highest; at 15 and 25°C it was more or less the same. On the other hand, the entire plant dry weight was highest at 15°C, while at 20°C it equalled that at 25°C. Moreover, the number of green blades per plant, the total green blades area, the fresh weight of blades as well as the fresh weight of neck were found to increase with increased temperature from 15 up to 25°C. This indicates that a rise of temperature in the latter range stimulated plant growth, and consequently resulted in an increase in the rate of sugar utilization. That the sugar content at 15°C in blades tended to be slightly higher than that at 20 and 25°C may well be attributed to the decreased rate of growth at 20°C, as compared with 25°C. At more advanced age (between 101 and 142 days after sowing) the carbohydrate content, in all cases, continued to increase, whilst the same relationships between the sugar content and temperature still, with one exception, remained the same. The only exception was that the sugar concentration at 30°C tended to be slightly lower than that at 25 and 20°C. This decline may be due to increased loss of sugars through respiration because of increased C/F ratio (the ratio of non-photosynthetic tissues to the photosynthetic system) caused by this high temperature and/or to the export of sugars from the blades to the developing bulb. At still more advanced age (in the period between 142

FIG. 79a

The effect of temperature on total soluble sugar content of green leaf blades.

●- - - -● : 10°C
○———○ : 15°C
▽—·—▽ : 20°C
□— —□ : 25°C
×—··—× : 30°C



and 186 days), owing to rapid bulb bulking being most favoured by 25°C, and the drainage of assimilates at an enhanced rate, the sugar concentration of blades at 25°C markedly diminished; at other temperatures it continued to increase and the more so as the temperature decreased, so that the sugar content at 10°C now surpassed that at all other temperatures, except 15°C. The continual rise in the sugar content at 10, 15, and 20°C may be a result of the extension of the growth period during which photosynthesis continues, induced by these low temperatures. Furthermore, the absence of bulbing or at least its progress in a very slow rate at 15 and 10°C in general, and at the latter temperature in particular, may be a factor responsible for sugar accumulation in the blades at these temperatures. With further ageing (from 186 to 224 days after sowing) the sugar content of blades at 10 and 15°C was still increasing to reach its peak at the end of experiment. The rate of increase, however, was much more pronounced at 10 than at 15°C, so that the sugar level in the former was twice as high as in the latter. The continual supply of sugars through the photosynthetic process, while the rate of its consumption was not sufficiently rapid to keep pace with the sugar formation, especially at 10°C, owing to the fact that this temperature was the least favourable for growth may account for the rise in the sugar content observed. In this respect it should be noticed that the entire plant fresh weight attained after 224 days from sowing at 10°C was only about half that at 15°C (230.13 and 475.34 grams respectively), while the entire plant dry weight at 10°C was two thirds that at 15°C. Moreover, the total blades area, as well as the fresh weight of blades, were far greater at 15 than at 10°C, whereas the opposite was true for blade dry weight. This may indicate the greater extent of carbohydrate utilization in building up new tissues at 15°C as compared with 10°C and, accordingly, the increased sugar accumulation in the latter.

2. *Neck (pseudostem) sugar content*

It seems that the onion neck serves as a temporary storage organ for carbohydrates. As the neck is incapable of carrying out photosynthesis owing to the absence of chlorophyll, and even if it contains some, it would be very little to contribute to photosynthesis, due to the fact that every successive leaf sheath is covered by its predecessors which become dry with time. Therefore, the neck is largely dependent on the blades for the sugar supply, either for consumption or accumulation as a transitory stage to the bulb or the roots. Thus, it is not surprising that the neck sugar content in relation to temperature and time followed more or less the same trend as that in the blades (fig. 79b). In the early stages of growth (between 36 and 54 days from sowing) neck sugar content at all temperatures tended to decrease, apparently because the photosynthetic apparatus was not yet well developed and presumably also because the amount of sugars formed may have been preferentially utilized in the synthesis of new photosynthesising tissue so that only a small proportion of the carbohydrate was available for translocation. Owing to the fact that the growth rate of the entire plant fresh weight increased with decrease in temperature from 30 to 15°C, the decline in the sugar concentration became smaller with rising temperature up to 30°C. At the lowest temperature, although the growth rate was least of all, the sugar content of the neck also lagged behind that at 20°C, possibly owing to the rate of photosynthesis being greatly checked by the lower temperature. At a later stage (in the interval between 54 and 101 days after so-

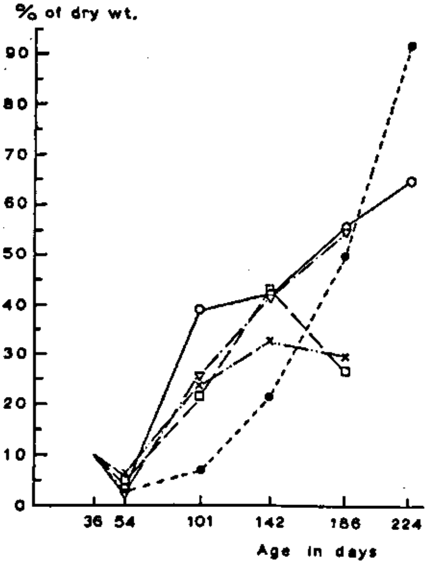


FIG. 79b
The effect of temperature on total soluble sugar content of neck.
●- - - -● : 10°C
○———○: 15°C
▽—・—△: 20°C
□— —□: 25°C
×—‥—×: 30°C

wing), the sugar content of the neck, in all cases, increased, presumably because of the increase in capacity of the photosynthetic system so that the sugar export to the neck was greater than its consumption in the different physiological processes. Owing to the fact that leaf growth (emergence and expansion) was greatly reduced at 15 °C, as compared with higher temperatures up to 25 °C, the rise in sugar content of the neck at 15 °C was more pronounced than that at 20 and 25 °C, and it may be suggested that carbohydrate which would otherwise have been used for leaf growth was translocated to the neck, and made the reserves in the latter increase. At 30 °C, though the leaf area was more or less the same as at 15 °C, the rate of photosynthesis/rate of respiration ratio apparently was lower at 30 °C, as presumably the respiration rate increases relatively more with rising temperature. This may account for the decline in the sugar content of the neck at 30 °C as compared with 15 °C. It seems that lowering the temperature from 15 to 10 °C greatly curtailed the rate of photosynthesis, in addition to all other growth aspects, so that no appreciable increase in the sugar content at 10 °C was observed, making its value lag behind. That no marked differences in the sugar level were found between 20, 25, and 30 °C, may be explained by the fact that 20 and 30 °C are on both sides of the optimum (25 °C). As the plants advanced in age (between 101 and 142 days after sowing), the sugar content of the neck, at all temperatures, continued to increase at different rates, so that the values at 15, 20, and 25 °C were the same; that at 30 °C was lower and still more that at 10 °C. The sugar concentration in the blades after 142 days from sowing was found to increase with decrease in temperature from 25 to 15 °C, whilst in the neck it was equal at these temperatures. By that time, the growth rate increased with rising temperature in the range from 15 to 25 °C, indicating an increase in the rate of sugar consumption in growth as the temperature rises from 15 to 25 °C. Thus, it appears not misleading to suggest that the rate of sugar transport from the blades to the neck increased with increased temperature within this range. The decline in sugar content of the neck at 30 °C, as compared with that in the range from 15 to 25 °C, may be due to increased rate of sugar export to the developing bulb, which is induced earlier at this high temperature; it may be assumed that the sugar supply to the neck was not sufficiently rapid to keep pace with its consumption, possibly since the rate of respiration is likely to be increased more than that of photosynthesis (at 30 °C). At more advanced age (between 142 and 186 days after sowing), because of rapid bulb bulking during this period, involving drainage of assimilates towards the bulb, the sugar content of the neck at 25 and 30 °C, in contrast to that at other temperatures, fell off, and the more so at 25 °C, which was more favourable than 30 °C for bulb growth. At still more advanced age (in the interval from 186 to 224 days after sowing), with continued sugar synthesis owing to the extended growth period during which photosynthesis can continue, a situation induced by low temperature, the sugar level in the neck at 10 and 15 °C continued to increase. Because a relatively larger fraction of carbohydrate was utilized for growth of the developing seedstalks at 15 °C, the sugar concentration of the neck in the latter was far lower than that at 10 °C in which scape development was greatly retarded.

3. *Bulb sugar content*

The total soluble carbohydrate content in the bulb as influenced by air temperature at different stages of growth is presented in fig. 79c. In the early stages of growth (after 54 days from sowing), no appreciable differences in the sugar content of the bulb were detected. At a later stage (between 54 and 101 days after sowing), the sugar content, in all cases, increased and differences became more pronounced with the highest value at 15 °C. Temperatures lower or higher than 15 °C resulted in a marked decrease in sugar content. This decrease was greater at 10 °C than in the range from 20 to 30 °C, so that the sugar level at 10 °C was lower. Since the combined blades and neck fresh weights recorded 101 days from sowing were 34.25, 42.23, 48.27 and 31.10 grams per plant for 15, 20, 25, and 30 °C respectively, it seems reasonable to assume that temperatures which promote leaf growth and hence the utilization of a larger proportion of sugars in their growth, tend to lower the carbohydrate content of the bulb. The low value of the sugar content of the bulb at 10 °C, though the combined blades and neck fresh weight was the least of all (17.42 grams), may be explained by a larger reduction in the rate of photosynthesis as a result of the low temperature.

At more advanced age, i.e., in the period between 101 and 142 days after sowing, the sugar content in the bulb, at all temperatures, continued to increase.

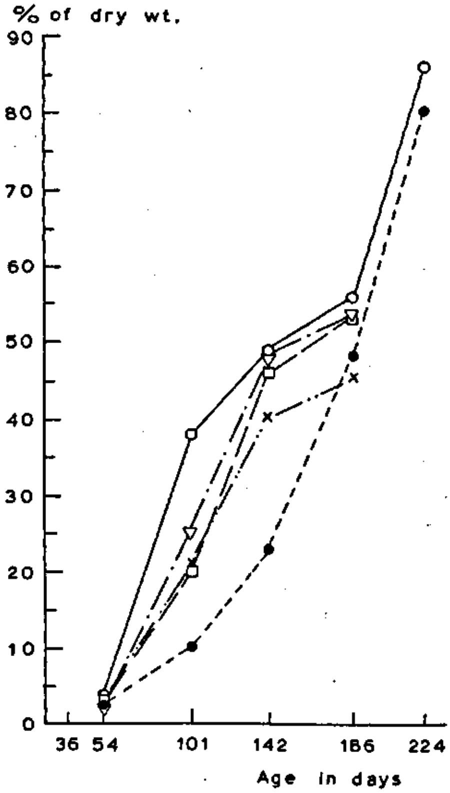


FIG. 79c
The effect of temperature on total soluble sugar content of bulb.

●- - - -● : 10 °C
○———○ : 15 °C
▽—·—▽ : 20 °C
□— —□ : 25 °C
×—··—× : 30 °C

The rate of increase, however, was favoured by increase of temperature in the range from 15 to 25 °C, so that bulb sugar contents at 15, 20, and 25 °C at 142 days from sowing, in contrast to the situation at the preceding harvest (101 days after sowing), were close together. This may be due to the fact that the photosynthetic system has reached its peak of development and capacity at 25 °C, while at lower temperatures it was still progressively increasing; consequently, the sugar consumption in leaf growth was also in progress so that a relatively decreasing fraction of the sugar was available for export to the bulb with a decrease in temperature from 25 to 15 °C. At 30 °C, presumably owing to increased rate of respiration, the sugar content in the bulb was even lower than that at 15 °C. At 10 °C, the sugar concentration was still lower.

At still more advanced age (from 142 to 186 days after sowing), the sugar level, at all temperatures, continued to increase, while the same relationship between sugar content and temperature, with one exception, was maintained. Because of the continued sugar supply through photosynthesis at 10 °C, the concentration in the bulb at 10 °C tended to surpass that at 30 °C.

With further ageing (between 186 and 224 days old), possibly due to progression of bulb development in a very slow rate at 10 and 15 °C, the sugar content at these temperatures rapidly increased to attain the highest values so far recorded in this experiment.

4. *Root sugar content*

The sugar content of the roots in relation to air temperature and time is illustrated in fig. 79d. It is obvious that in the early stages of growth (between 36 and 54 days after sowing), the sugar content of the roots tended to decrease, and the more so as the temperature was increased beyond 15 °C, so that the highest values were obtained at 10 and 15 °C, while at higher temperatures it was lower. As the top/root ratio was found to increase with rising temperature during this period, it seems possible that most of the carbohydrate was monopolized by the tops, promoting their growth, and the more so as the temperature increased. Thus, only a small fraction of sugars was available for export to the roots, so that a restriction of their growth, as well as a decrease in the sugar level resulted.

At a later stage (in the interval from 54 and 101 days from sowing), the sugar concentration at 15 and 20 °C increased; at higher temperatures it levelled off, while at 10 °C it continued to decrease in the order 15, 20 °C and other temperatures. This implies that, at relatively low temperatures (15, 20 °C), the roots were generously supplied with sugar so that vigorous root growth as well as increase in their sugar content resulted; at higher temperatures (25, 30 °C), the rate of sugar supply to the roots was just enough to cope with its poor utilization in growth, while at the lowest temperature (10 °C), presumably owing to restricted photosynthesis at this temperature, the sugar supply to the roots dropped more markedly than its rate of consumption.

At more advanced age (from 101 to 142 days after sowing), the root sugar level continued to increase at 15 °C; at 20 °C it came to a standstill, while at 30 and 10°C it showed a slight increase. The photosynthetic apparatus reached its full capacity at 25°C, so that a larger proportion was transported to the roots, and the sugar content at this temperature tended to surpass that at 20°C.

At still more advanced age (between 142 and 186 days after sowing), the root sugar content in all cases still increased. Perhaps due to the absence of bulbing which serves as an intense sink for carbohydrate accumulation whilst the photosynthetic system has attained its full size, the sugar content of the roots at 10°C during this period increased so rapidly that it exceeded that at all other temperatures.

With further ageing (in the period from 186 and 224 days after sowing), owing to continuous sugar supply to the roots as a result of the continuation of leaf growth, and thus photosynthesis, as induced by low temperatures, the carbohydrate level in the roots continued to increase at 10 and 15°C. The rise at 10°C, however, was far greater than that at 15°C, so that the maximum value in the former was four times as high as that in the latter. An interesting point is that, when the development of the bulb was slowed down or prevented, for example by low temperature as in this case, the other plant organs, i.e., root, neck, and blades serve as storage organs for carbohydrates that would otherwise have been used for bulb development, and may now be diverted to the other

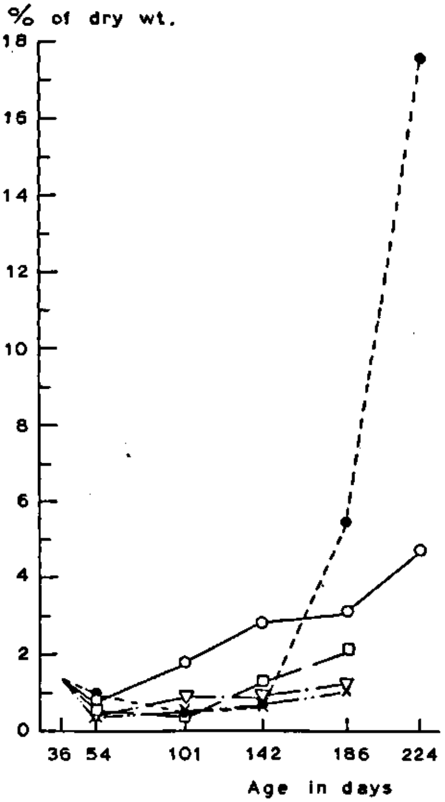


FIG. 79d
The effect of temperature on total soluble sugar content of roots.
●- - - -● : 10°C
○——○ : 15°C
▽—· —▽ : 20°C
□— —□ : 25°C
×—··—× : 30°C

organs, causing a great rise in their sugar contents. However, the bulb appears to be a more efficient sink than the other organs because it obviously can store more carbohydrate. In this respect, NÖSBERGER and HUMPHRIES (1965) found that the removal of tubers in the potato plant caused the carbohydrate to accumulate in leaves and stems instead. It is worth notice also that sugar supply to the roots continues even after their growth has ceased. This is indicated by the fact that root sugar content at 15, 20, 25, and 30 °C continued to rise in the later stages of growth, while root fresh weight decreased.

CHAPTER IX

GENERAL DISCUSSION

In this discussion, our aim will be to review, against the background of previous work, the results of the present investigation which may throw some light on the growth and development of the onion plant in relation to light and temperature. It should be borne in mind that conclusions drawn here need not necessarily be applicable to other cultivars, or to the same cultivar under other experimental conditions.

A. EFFECTS OF LIGHT AND TEMPERATURE ON GROWTH AND MORPHOGENESIS IN GENERAL

The development and reactions of an organism are the result of the coordinated interplay of hereditary factors and environmental conditions upon the physiological processes of that organism. Light and temperature are the general ecological factors, long known to affect plant growth and development. A considerable amount of work has been done on the influence of light intensity on growth and development of various plant species. Data relating to the onion growth, however, are conspicuously deficient, and even where onion growth has been studied, observations have usually been qualitative and subsidiary to the main interest which was confined to bulb development only. The present study contains information on onion growth and correlations as a function of light and temperature under field conditions and controlled conditions throughout the entire growth period, i.e., from sowing up to bulb maturity.

It has been established from our shading experiments in the field and from those with varied light intensity in the phytotron that growth in weight of the entire plant and its various organs, viz., root, blade, neck and bulb was greatly influenced, being higher with increasing light intensity up to the highest one applied. These results are in accordance with those obtained by other investigators, in majority with open habitat plants. For example, ROSÉ (1913) on several plant species; CLEMENTS et al. (1929) on *Helianthus annuus*, MILTHORPE (1945) on flax; KAMEL (1959) on barley, and DEINUM (1966) on grass obtained the highest dry weight at light intensities equal to full daylight.

Apart from the fraction consumed in respiration, the dry weight yield is the product of photosynthetic capacity and efficiency. The relationship between photosynthesis, light intensity and CO_2-concentration has been established by various authors (e.g., BLACKMAN and MATTHAEI 1905, and GAASTRA, 1959). Furthermore, the maximum rate of photosynthesis, the compensation point, and the value of light saturation differ with the plant species and the conditions under which they have previously been grown (BOYSEN-JENSEN and MÜLLER, 1929 and WASSINK et al., 1956). At the usual atmospheric CO_2-

concentration, the maximum photosynthetic rate is attained when leaves are exposed to light intensities considerably lower than full sunlight intensity. In leaves of cotton, sunflower, tomato, for example, maximum photosynthetic rates are reached at light intensities of one-fourth to one-third of full sunlight (MEYER and ANDERSON, 1965). When the effect of light intensity on photosynthesis is considered in terms of an entire plant in a community, a different relationship holds. The rate of photosynthesis in an individual plant in a canopy, unlike a solitary plant or a single leaf, increases progressively with increasing light intensity up to full daylight. According to some investigators, competition for other factors, affecting photosynthesis, e.g, water and nutrient supply can be greatly reduced or even ceases when these factors are in ample supply. For light this is not so. Light is available in a passing stream which must be intercepted by the leaves if it is not to be permenantly lost to the plant. In a natural vegetation, usually a total leaf area far greater than the soil surface is available for absorbing the incident light. The upper leaves only receive full light, while the basal leaves will be heavily shaded and much reduced in photosynthetic activity; they will perhaps be below or near their compensation point. Even when not shaded, many leaves are not at right angles to incident radiation and, therefore, do not receive full incident intensity. These unfavourable conditions seem to predominate in a plant community. Thus, competition for light remains a factor of major importance for the plant as a whole, and the photosynthetic curve follows the light curve (THOMAS and HILL, 1937). Our results from field experiments also point into this direction. The average NAR over 126 and 135 days of growth increased linearly with increasing light intensity up to full day light, indicating that for the plant as a whole, no light saturation occurs. In the phytotron, a curvilinear relationship was obtained. This, undoubtedly, because the LAI at high light intensities was far greater in the phytotron than in the field experiments, tending to increase mutual shading effects. It should be observed, that, moreover, incident light in the phytotron was inferior to that under natural conditions. Moreover, the rate of dry matter increase per unit surface area per unit time under phytotron conditions was lower than that under field conditions. Nevertheless, the total dry matter gain per plant in the phytotron was far superior to that in the field, owing to the fact that the photosynthetic system extensively developed in the former (phytotron). This suggests that a greater assimilatory apparatus accompanied with a lower rate of dry matter increase per unit area per unit time may be more effective in total dry matter production than a smaller photosynthetic apparatus with a higher NAR. In the latter case the average cm^2 leaf area receives more light. Thus, within the limits set by natural climates to the length of the growth period, improvement of onion yield in existing onion cultivars is likely to be brought about by increasing total photosynthetic capacity rather than by increasing efficiency of photosynthesis, as also suggested already by WATSON (1958).

Along with changes in weight, light intensity induces changes in morphogenesis. In most studies with various plant species, leaf production was found to increase with increasing light intensity, see, e.g., CLEMENTS et al. (1929) with sunflower; MILTHORPE (1945) with flax. This was also proven to hold true for the onion plant. Whether under field or phytotron conditions, leaf number was positively correlated with light intensity (Chapters IV and V). Not only leaf number, but also leaf shape was influenced by light intensity; relatively longer and narrower leaves indicated by greater leaf length/diameter ratio were found with decreasing light intensity (Chapter V). Such formative effect of light intensity was also shown by BENSINK (1960) on lettuce. Similar results were obtained by FRIEND et al. (1962) who showed that light intensity differently affected length and breadth of 'Marquis' wheat leaves; the broadest leaves were produced at 2500 ft.c. and the longest at 200 to 500 ft.c. According to the authors, these effects were due to a change in cell dimensions rather than by changes in the number of cells.

The amount of leaf area/plant is the outcome of leaf number and leaf size, and any changes in leaf area will depend on how far light intensity affects these components.

It seems that growth in area in relation to light intensity differs with plant species. GREGORY *(1921, 1928) on cucumber;* MITCHELL *(1953, 1954) on Lolium perenne*; MILTHORPE (1945) on flax found an increase in leaf area with increasing light intensity. By contrast, potatoes, *Scilla non-scripta* and *Citrus* seedlings respond to shading by increase in leaf area. In the onion plant under natural conditions, in 1964, total green leaf area increased with increasing light intensity and this relationship was maintained throughout the growth season. In 1965, in field and phytotron experiments leaf area was higher as light intensity increased in the early stages of growth, while later on leaf area at 37% light intensity tended to surpass that at higher ones, mainly owing to increase in leaf size and particularly in leaf length. Reasons for difference in leaf area behaviour in relation to light intensity under the 1964 field condition on the one hand, and in the 1965 field and phytotron experiments on the other hand, are not quite clear. Perhaps, they may be due to differences in the prevailing environmental conditions, viz., temperature, nutrient supply, and amount of rainfall. The possibility also that longer pretreatment at 100% light intensity in 1965 than in 1964 may be a factor involved, is not excluded.

When growth in leaf area is considered in terms of the ratio of total leaf area per plant to entire plant weight (leaf area ratio), it was found that this ratio progressively increased with reduction in light intensity. This change in LAR with shading in some plant species is brought about chiefly by changes in specific leaf area, (i.e., the ratio of leaf area to leaf weight), whereas LWR leaf weight: entire plant weight) only plays a negligible part; in other plant species leaf weight ratio contributes to changes in LAR besides specific leaf area (BLACKMAN, 1956). We have shown that the onion plant belongs to the last group (Chapters IV and V).

Temperature also affects dry matter production in the onion plant. Before discussing this influence, it seems important to draw attention to the possibility that temperature effects are altered by a change in the prevailing environmental conditions, especially those connected with light. It has been repeatedly demonstrated that the optimum temperature for dry matter production shifts to higher values with increasing level of radiation. In our experiments, in the early stages of growth (up to 101 days after sowing), dry matter accumulation was slightly favoured by relatively low temperature while at later stages the position was changed, and the highest dry weight values were obtained at 20 to 25°C (after 186 days from sowing). The lowest dry weights was recorded at 30°C; 10 and 15°C being intermediate.

Moreover, we have shown that changes in dry weight at 10 and 15°C are mainly due to the total characteristic of photosynthesis, whereas the relative amount of leaves/plant (thus the type of plant) is more or less the same; at higher temperatures clearly there is a greater amount of leaves per unit weight present (fig. 77).

Associated with the increase in the rate of biochemical processes at increased temperatures is a shortening of the duration of the growth period. Plants grown at a temperature range of 20 to 30°C ended their life cycle after a growth period of 186 days; those grown at lower temperatures continued their growth up to 224 days. Maturity, however, was not attained, and the experiment was discontinued because no more plants were available. The dry matter production, found at 10°C at the end of the experiment (224 days), was more or less equal to that at 20 and 25°C at 186 days after sowing; that at 15°C by far exceeded those at all other temperatures. This implies that lengthening of the growth period may compensate or even more than compensate for decreased growth rate associated with lower temperature. This would seem profitable for onion bulb production, but plants may be induced to bolt at low temperature.

The present study has revealed some examples of morphogenetic effects of temperature upon growth and development of the onion plant. In the early stages of growth, leaf number increased with increase in temperature up to 30°C; later on, presumably owing to increased rate of leaf senescence, leaf number at 30°C was overtaken by that at 25 and 20°C.

It seems that high temperatures accelerate the rate of leaf initiation and emergence. In mangold, WATSON and BAPTISTE (1938) correlated the rate of leaf production with increased temperature. KHALIL (1956) also found the rate of leaf emergence in wheat to increase with temperature up to 30°C. Temperature also influenced leaf shape (length and diameter). However, differences in length were more pronounced than in leaf diameter. Similarly, in *Festuca arundinacea* TEMPLETON (1960) reported that length of leaf blades was affected more than width by temperature. Leaf length in onion increased with temperature up to 20°C; at 25°C no further increase was observed. Conversly, leaf length decreased again at 30°C (fig. 72b). MILTHORPE (1963) suggested that at high temperature the rate of leaf production is higher, and the plant is unable to maintain the supply of nutrients required by them; consequently each leaf does not grow as large. In the early stages of growth (SD), leaf diameter tended to be favoured by relatively low temperatures (15–20°C), whereas in the later stages of growth (LD), leaf diameter at 25°C was highest (fig. 72c). Whether this differential effect of temperature on growth in diameter is due to differences in daylength or to increase in daily total light energy (daylength was extended by high light intensity) is not certain. JONES (1955) concluded that there is a delicate balance between temperature and light in controlling leaf shape of certain water plants. It seems more likely that increase in leaf diameter at 25°C is due to increase in total daily light energy rather than to daylength extension, since results of other experiments we have described showed that long day increases leaf length and reduces leaf diameter (figs. 52a and 53a).

It is interesting to note that FRIEND, HELSON and FISHER (1962) found an increase in temperature to decrease the breadth of 'Marquis' wheat leaves.

According to ASHBY (1948), differences in leaf shape are determined by the shape of the primordium, the number and orientation of cell divisions, and the amount and distribution of cell enlargement. Up to now, we did not study these factors in the onion plant, but it appears likely that leaf diameter is chiefly controlled by cell division while leaf length is mainly determined by cell elongation. BORRILL (1961) found that differences in blade width of *Lolium temulentum* mainly reflect differences in cell number, but changes in blade and sheath length result mainly from differences in cell length, except with the flag leaf-sheath.

The ultimate total green leaf area per plant is the resultant of leaf initiation, emergence and longevity, which may be differently influenced by temperature. Data relating to the onion plant show that in the early stages of growth, leaf area increased with increasing temperature up to 25°C and then decreased with further increase in temperature. At the later stages of growth, leaf area decreased; the higher the temperature, the earlier this happened so that leaf area then became greater at lower temperatures (fig. 73a). This may be ascribed to an indirect effect of high temperatures on speeding up bulb development and to its predominance over new leaf emergence. However, this was clearer at 25 than at 30°C.

An important formative effect of temperature is that upon the relationship between total green leaf area and entire plant dry weight or leaf area ratio (LAR). We have shown that in the early stages of growth (up to 127 days), this ratio increased with increasing temperature from 15 to 25°C; within this range increase in LAR is brought about by increase in leaf weight ratio (LWR) and specific leaf area. At temperatures beyond the mentioned range, LAR was not greatly affected, and the small changes were similarly due to differences in LWR and in specific leaf area. In *H. annuus*, BLACKMAN (1956) found a positive effect of temperature on LAR. He showed that differences in LAR were chiefly due to changes in specific leaf area while leaf weight ratio (LWR) played a smaller part. The influence of temperature on LAR was most marked between 20 and 25°C.

The harmonious development of the plant body as a whole is a result of correlative influences, operating from organ to organ, e.g., of the leaves upon the root system and vice versa. Environmental factors, e.g., temperature, influence this relationship. WALKER (1921), with onion seedlings, found that roots and foliage had different optimal temperatures for growth. Our data point into the same direction; the top/root ratio, in general, increased with rise in temperature (fig. 76). One may perhaps suppose that depression of root growth at high temperature is due to shortage of oxygen, as the minimum oxygen requirement for root growth and function is not a fixed amount but that it varies directly with temperature. KHALIL (1956) induced better root growth of wheat plants at 30 °C with extra oxygen supply to the soil. The possibility, however, remains that the relation between top/root ratio and temperature is controlled by changes in the level of growth hormones within the plant. WENT (1951) found the production and the transport of auxin to be affected by temperature.

It is of interest to note that low temperature exerts similar formative effects as high light intensity in that broad leaves, high root/top ratio and lower LAR are produced in both cases. Such correlation of low temperature (night temperature) and high light intensity was reported by BENSINK (1961) on lettuce.

B. EFFECTS OF LIGHT AND TEMPERATURE ON BULB DEVELOPMENT, ESPECIALLY IN THE ONION

Bulb development in the onion plant has two main morphological features: swelling of the base of the pseudostem (leaf sheaths), and the formation of scales from leaf initials produced at the stem apex. The rate of bulb development may be arbitrarily measured by the 'bulbing ratio' which is the ratio of the maximum diameter at the base to the minimum at the neck (CLARK and HEATH, 1962). HEATH and HOLLIES (1963) have introduced the 'leaf ratio', i.e., the ratio of blade to sheath length of small leaf initials as an assessment of bulb development. When bulb development starts, unlike in case of bulb absence, the sheath of a small initial begins to grow sooner than in foliage leaf formation while blade growth is suppressed, giving a leaf ratio less than unity which is a diagnostic of bulbing. In developing this method, the authors have shown that it indicates bulb development about one week earlier than the bulbing ratio. However, the bulbing ratio was adopted throughout our investigations for the sake of simplicity and also to avoid destruction of the samples. Moreover, HEATH and HOLLIES pointed out that 'leaf ratio' is a useful measure in the early stages of bulbing, but tends to a constant value in the late stages, when the outer scales have ceased to elongate.

The results obtained have demonstrated that the reduction of light intensity to 12% of full daylight, and to 10000 ergs/cm^2/sec in the phytotron, delayed bulb formation but did not prevent it (fig. 38b). As early as 1923, GARNER and ALLARD concluded from their experiment with the silverskin onion that bulb development is not due to excessive intensity of sunlight in summer as the plants grown under 3500 ft.c. ($^1/_3$ full light intensity) formed bulbs in the same way as those grown under full daylight. HEATH and HOLLIES (1963) found that reducing light intensity to as low as 15% of full daylight retarded bulb development, but did not prevent it. In their experiment, growth at 15% light intensity was so poor that none of the plants survived to give the last sample (10.5 weeks); in our case, indeed, growth was greatly reduced under 12% in the field and under 10000 ergs/cm²/sec in the phytotron but all plants survived and ultimately bulbed. This contradiction may be due either to differential response of cultivars to shading or to the fact that, in their experiment, the plants received comparatively low light intensity because of the season (autumn) and the structure of the green house, a fact which was referred to by the authors. The conclusion drawn by them that, as long as light intensity is sufficient for the survival of the plants, bulbing will eventually occur, though much delayed, thus is confirmed.

It is a well established fact that bulb development in the onion plant is only induced by exposure to long days, although cultivars may differ in their day-length requirements (GARNER and ALLARD, 1923; McCLELLAND, 1928; MAGRUDER and ALLARD, 1937; THOMPSON and SMITH, 1938; HEATH, 1943a, b; HEATH and HOLDSWORTH, 1948; CLARK and HEATH, 1962). Attempts, so far made, to induce bulbing under short day conditions, have failed.

Our results are an extension of these findings; no bulbing could be induced under SD conditions (8 or 12 hrs., figs. 45a, 62a). However, HEATH and HOLLIES (1963) found that apical buds excised from onion sets showed signs of bulbing under short day (8 hrs.) when a sterile culture was supplied with sugars; we will return to this later on.

Several other interesting features have emerged from our experiments. Of importance is the finding that bulb development is not only influenced by light duration but also by the quality of the light, so that bulb development was not induced in plants, grown under continuous light of a certain spectral composition (Photos 1–6). That light quality may strongly alter the photoperiodic response in both long and short day plants and that the optimal length of the photoperiod is determined to a significant degree by its spectral composition, has long been known. Used to extend a short photoperiod, red light proved in most cases to be ineffective, whereas for a brief night-break it may be most effective (BORTHWICK and co-workers, 1952). On the other hand, far-red as supplemetary light sometimes is more effective (WASSINK et al., 1951); STOLWIJK and ZEEVAART, 1955; DE LINT, 1958). In the onion plant, bulb development was neither induced by red nor by far-red alone, applied for 12 hrs. to extend a main photoperiod of 12 hrs. supplied by fluorescent tubes (TL/33 or TL/55; (photos 7–9). Incandescent light, either supplementary or admixed to fluorescent light in long day, appeared essential for bulb development. The superiority of incandescent to other light sources in flower induction of several plant species has been demonstrated by many investigators, e.g., BORTHWICK and PARKER (1952); DOWNS et al. (1959), and FRIEND, HELSON and FISHER (1961). Similarly, PALEG and ASPINALL (1964) found that supplementing a fluorescent light source in a long photoperiod with incandescent light, accelerated apical growth and floral differentiation in barley. The rate of apical development was linearly related to log incandescent light intensity over a wide range, but varying the intensity of the fluorescent source had only a minor effect. According to the authors, the promotive effect of incandescent light is due to an increased level of far-red radiation incident on the plants. Used as a supplementary light to extend a short photoperiod, VINCE et al. (1964) and VINCE (1965) with some LDP's found that the effectiveness of red light was considerably enhanced by the addition of far-red. The present and forthcoming results demonstrate the importance of maintaning red: far-red light energy in adequate proportion for a certain minimum photoperiod in order that the onion plant may receive a sufficient stimulus to form a bulb. One might argue that the failure of the plants to bulb under supplementary red or far-red light alone may be due to their low light intensity (5000 ergs/cm²/sec) but is should be remembered that incandescent light which contains a reasonable ratio of red: far-red, induced bulbing at lower light intensity (about 3000 ergs/cm²/sec, fig. 59a).

In most studies, carried out in the past, to investigate the effect of photoperiod on bulb development, incandescent light was used, and the response thus was obtained. The only exception, as far as we are aware, is the investigation of MANUEL et al. (1962) who could induce bulbing in the 'Granex' cultivar by supplementary fluorescent light. This may suggest either a differential response of cultivars to light quality, or the fluorescent light source they used may have contained a reasonable red: far-red ratio. Of special interest are the results of PARIBOK (1962), who found that in different onion cultivars, grown in Russia, incandescent light quickly induced bulbing, but under daylight type fluorescent tubes, formation of the bulbs was strongly retarded or did not occur at all.

That duration of exposure to a proper light quality is more important for bulb development than light energy level has been established in the present investigation. Eight hrs. of varying intensity of incandescent light supplemented to 12 hrs. fluorescent light stimulated bulb development, whereas 4 hrs. failed to do so, irrespective of the light intensity (figs. 59a, b). Furthermore, plants grown under long day conditions (16 hrs.) and reduced light intensity (12% in the field and 10000 ergs/cm²/sec in the phytotron) formed bulbs and reached maturity, while those grown under 12 hrs. of a mixture of fluorescent and incandescent light of high light intensity failed to do so. However, it should not be assumed that light intensity either in supplementary light or during the entire photoperiod is of no importance for bulb induction. The retardation of bulbing under the lowest light intensity in field and phytotron experiments needs no stress. Moreover, it seems that a certain minimum light energy should be reached, in order to bring about the photoperiodic stimulus. Bulb development was not homogeneous, i.e., some plants bulbed and others did not, e.g., under 8 hrs. of 720 ergs/cm²/sec incandescent light supplementation. We have also shown that the higher the light intensity of 8 hrs. supplementary light, the quicker bulb development tended to be (fig. 59a).

The quality of the light during the main photoperiod may also well play a role in bulb formation. This may be derived from the fact that a main photoperiod (12 hrs. of fluorescent light alone) supplemented by 4 hrs. (total 16 hrs.) incandescent light failed to cause bulbing; while 16 hrs. of a mixture of fluorescent and incandescent light produced mature bulbs. The question why bulb development could not be induced under 8 hrs. of natural day light extended by 8 hrs. of incandescent light remains not clear. This, however, may be due to the fact that the intensity of supplementary incandescent light was very low (750 ergs/cm^2/sec). This, however, does not seem the only explanation, since raising the light intensity in one part of the plot, also failed to cause bulbing (fig. 45b). It should be remembered that the experiment was continued only for about 4 weeks under these conditions, after which daylength was extended to 24 hrs. Thus, the possibility that, if plants were maintained growing for a longer time, they would have bulbed, is not excluded, especially if one considers the fact (as our results show) that old plants do not react to photoperiod to the same extent as those at intermediate ages.

Although daylength seems to play the dominant rôle in bulb development, temperature also plays an important part so that a certain critical daylength may not be defined without specifying the temperature (JONES et al., 1963). WILSON (1938), HEATH (1943); HEATH and HOLDSWORTH (1943) and CLARK and HEATH (1962) found that bulbing is speeded up by rise in temperature and greatly delayed or prevented by low temperature. Nevertheless, high temperature alone (not associated with LD) had no effect (WILSON, 1938). Our data confirm these findings. It was found that bulb development started earlier, as temperature increased up to 30°C. As the plants proceeded in age, however, bulb development at 25°C expressed in 'bulbing ratio' tended to exceed that at all other temperatures tested, and the final bulb weight was highest at 25°C, indicating that under our experimental conditions, 25°C was optimal for bulb growth and development. Low temperatures (10 and 15°C) do not seem to prevent bulbing, since plants grown at these temperatures, when maintained longer, ultimately showed some signs of bulbing, but then proceeded to bolting, thus spoiling the bulb from the economical point of view (fig. 75c). The relation between bulb and seedstalk development is a complex one. It is generally accepted that flower initiation is temperature sensitive, viz., low temperatures result in flower initiation, and high temperatures prevent it. High temperatures accompanied with long days speed up bulbing, while relatively low temperatures associated with long days favour seedstalk emergence. HEATH and HOLDSWORTH (1943) concluded that under long day conditions a race between the processes of scape elongation and bulb formation must often occur; if temperature is high, bulb formation dominates, while the reverse is true at low temperature.

The assumption put forward by HEATH and HOLDSWORTH (1943) that the of long days in action suppressing inflorescence emergence under conditions favourable to more rapid bulb formation is an indirect effect connected with the promotion of bulb development, does not seem justified. Evidence supporting our view may be derived from the fact that, in our experiments, plants which flowered (under a continuous mixture of fluorescent and incandescent light) were only those having bulbed before any sign of seedstalk emergence could be detected; those which did not bulb (grown under continuous fluorescent light alone at 15°C) also failed to develop a seedstalk. Furthermore, seedstalk emergence was first seen at 15 °C (15.5 hrs. of a mixture of fluorescent and incandescent light), although signs of bulbing also were observed earlier at 15 than at 10 °C.

Some plant species require a certain amount of growth to be fulfilled, or a certain physiological age to be attained, in order to respond to favourable environmental conditions for flowering (PURVIS, 1934; GREGORY and PURVIS 1936); PURVIS and GREGORY, 1937, and LANG and MELCHERS, 1943). The question arises as to whether this may be involved also in bulb formation by the stimulus of long days. Earlier work connected with this aspect in the onion plant is rather conflicting. MAGRUDER and ALLARD (1937) reported that the age of the plants has little influence on the date of maturity, so that seed sown at the same date on which plants 3 months old are set, produced mature bulbs within 5 days from the date at which the mentioned plants did. Similarly, under conditions that were very favourable to bulbing, 'Red Creole' cv. has been observed to bulb when it had developed only one leaf in addition to the cotyledon (JONES et al., 1963).

On the other hand, according to some investigators, e.g. HEATH and HOLDSWORTH (1943) and JONES and MANN (1963), the size and age of the onion plant influence bulbing and time of maturity. Dry onion sets, transplants and seed of the same cultivar, set on the same date, starts to bulb and mature in the order as named; even more, plants grown from large sets bulbs and mature earlier than those grown from small sets. Similarly, the present study on the 'Wijbo' cultivar demonstrates that the size and/or the physiological age play a not yet further defined role in triggering off the mechanism of bulbing. The results show that very young (below 74 days old) as well as very old plants (older than 158 days) are less sensitive to the photoperiodic treatment, as compared with those of intermediate ages (fig. 62a). Plants grown under long days (16 hrs.) from immediately after sowing do not show any signs of bulb development until after 53 days (fig. 62b); those transferred to long days at 45 days old failed to bulb during the first 4 weeks following long day exposure. As for the oldest group (158 days), bulb development was negligeable during the first 4 weeks of long day exposure, though bulbing markedly proceeded and plants yielded mature bulbs with further exposure (fig. 62a). In photoperiodically sensitive plants, it is generally agreed that the perception of the stimulus is in the leaves, then converted into a chemical message of unknwon nature which is transmitted to the apical meristem, where it initiates a different pattern of cell differentiation. It is a reasonable assumption, therefore, that the non-sensitivity of plants in the early stages of growth is due to the absence of a sufficient amount of leaf area. However, this does not seem the only explanation, since the oldest plants (158 days) were those having developed the greatest leaf area at the moment of transfer. This suggests that the meristemic age may also be involved. It is well known that recently matured leaf is most sensitive to photoperiod.

A clear positive correlation has been established between plant size at the time at which bulbing is induced by long days, and the final bulb size and weight (fig. 66a). Therefore, the importance for bulb production to grow the onion plant under short day conditions in the early stages of growth in order to develop a considerable leaf area before bulb induction, needs no further emphasis.

There is now sufficient evidence that tuberization in its widest sence is largely controlled by environmental conditions, particularly photoperiod and temperature. However, the role of photoperiod and temperature on triggering off the mechanism of bulbing is not quite clear; and this is a matter of controversy among plant physiologists. Two theories have been developed in this respect.

Some investigators believe that the concentration of metabolities arising from photosynthesis, especially carbohydrates, is the causal factor for bulb development under long day conditions. They provide evidence supporting this view. For instance the delay of bulb development under conditions leading to reduction of the carbohydrate level within the plant such as ample nitrogen supply (WILSON, 1934, and SCULLY et al., 1945); defoliation (COCKSHULL and HEATH, 1962), and reduction of light intensity (HEATH and HOLLIES, 1963). Moreover, by culture of onion buds in vitro, HEATH and HOLLIES (1963) showed that sugars (sucrose and glucose) fed to the plants induced bulbing under short days (8 hrs.) and that swelling was proportional to the sugar content of the culture medium. As pointed out by CLARK and HEATH (1962), attempts made to induce bulbing under short day conditions by spraying or injecting auxin solutions into the leaf cavities yielded negative results. Analogous to bulbing, tuberization in the potato, being favoured by short days, has been suggested to be caused by increased level of carbohydrates or C/N ratio (MOLLIARD, 1915, 1920; WELLENSIEK, 1929; WERNER, 1934; BORAH and MILTHORPE, 1959, and MILTHORPE, 1962).

In contrast to the aforementioned group of investigators are those who suggest that more specific substances formed under long photoperiod and high temperature are the factors responsible for bulb development. It was HEATH and HOLDSWORTH (1948) who formulated a hypothesis in terms of a bulbing factor which they thought, was hormonal in nature. The latter should result in mobilization of carbohydrates in the bases of the onion leaves, in cessation of growth of the apical meristem and roots, in cessation of cell division in general and in a lateral swelling type of growth by the young leaves. By colorimetric determination and by a new bio-assay, CLARK and HEATH (1962) found an increase in the IAA content to a very high level during the first week following bulb induction. Furthermore, in interpreting their results, HEATH and HOLLIES (1963) did not exclude the possibility of the bulbing hormone being stored in the sets which induced bulb development under short day conditions when sugar was fed to plants.

The results of the present study showed that bulb development is accompanied by carbohydrate accumulation in various plant organs and that reducing light intensity diminished carbohydrate content as a result of which bulb development was delayed (figs. 39a, b, c, d). However, carbohydrate by itself does not seem to be a causal factor in triggering off the mechanism of bulbing. The action of long days does not directly result in an increased carbohydrate level, but photoperiod may exert its effect through a regulation of the internal processes, so that carbohydrate is directed to be stored in the form of a bulb, instead of being used in new leaf or root production. It should be remembered that under very low light intensities, plants developed bulbs although carbohydrate concentration under such conditions was lower than at higher light intensity. HEATH and HOLLIES (1963) also concluded that under long day conditions, bulbs will be formed as long as light intensity is sufficient for the survival of the plants. Also, the failure of the plants to form bulbs under continuous light of certain wavelengths (fluorescent light) may indicate that bulbing is a formative process initiated by induction. Furthermore, the great delay in bulb development at 15 °C, as compared with higher temperature, in spite of the fact that the carbohydrate level in the different plant organs was highest at 15 °C throughout the growth period (up to 186 days) proves in any case that sugars are not the primary cause of bulbing.

Perhaps, the aforementioned two hypothesises may be regarded as complementary rather than incompatible if one differentiates between bulb induction and the subsequent enlargement of the bulb. The first phenomenon requires the presence of a substance or substances, perhaps of a hormonal nature, which are synthesized under certain environmental conditions (long day and high temperature) by the leaves. The enlargement of the bulb which requires filling of the elongated cells, presupposes a continuous current of carbohydrates. Bulb enlargement continues as long as induction is sustained, that is to say as long as the hormone is present at an adequate concentration which, moreover, may remain active in the plant for a certain time under non-inductive conditions. Plants exposed to inductive cycles for about one month and then transferred back to short days, continued bulb growth for one month under these conditions and thereafter lost their ability to bulb with still longer exposure to short days. Summarizing, it thus is not surprising, that aside of hormonal effects, the factors acting on carbohydrate supply have effects on the manifestation of bulb formation.

SUMMARY

Growth, morphogenesis and carbohydrate content of the onion plant (*Allium cepa* L., cv. 'Wijbo' as influenced by light and temperature, during the entire growth cycle, were studied under field conditions and controlled conditions (phytotron).

A. LIGHT INTENSITY EFFECTS

Plants were grown at various light intensities in the field and in the phytotron.

1. Fresh and dry weight of the entire plant and its various organs, i.e., root, blade, neck, and bulb increased with increasing light intensity. The time trend shows a rise in entire plant fresh and dry weight up to a maximum at the end of the growing season. Bulb weight progressively increased with time to a maximum at the end of the growth period, whereas root, neck, and leaf weight usually increased with time up to a certain moment and then decreased or flattened off; however, in some cases, leaf and neck continued to increase up to the end of experiment.
2. The average daily growth rate over the entire season (dry weight gain per plant per day) increased with increasing light intensity; the increase was exponential in 1964, linear in 1965 and curvilinear in the phytotron experiment. The average NAR over 126 and 135 days after sowing in the 1964 and 1965 field experiments respectively was linearly related to relative light intensity, while in the phytotron a curvilinear relationship was found. Although NAR at the highest light intensity in the phytotron only was about one-half of that in the field experiments, the daily growth rate in the phytotron was about two times that in the field experiments, owing to more vigorous growth in leaf area under controlled conditions.
3. Leaf number per plant was positively correlated with light intensity; at all light intensities, leaf number increased with time to a maximum, and thereafter decreased. Leaf thickness and diameter decreased with reduction of light intensity; this also holds true for leaf length in the early stages of growth, while later on leaf length at 37% in the 1965 field experiment and at 35% in the phytotron experiments, surpassed that at all other light intensities. Leaf length/diameter ratio increased with reduction of light intensity.
4. In the early stages of growth, total green leaf area per plant in all experiments increased with increasing light intensity; later on total green leaf area at 35% light intensity in the phytotron experiment exceeded that in all other treatments. In all cases, total green leaf area increased with time to a maximum, and then decreased.
5. There was a positive effect of light intensity on neck diameter; it increased with time to a maximum, and then fell off in most cases. In the 1965 field experiment and in the phytotron experiment, neck length in the 37 and 35% treatments at a certain moment surpassed that at all light intensities.

6. Leaf area ratio, top/bulb ratio and top/root ratio were negatively correlated with light intensity. With the exceptional rise between the first and the second harvest, leaf area ratio decreased with time to a minimum at the end of the experiment.
7. The reduction of light intensity to as low as 12% in the field experiments and to 11% = 10000 ergs/cm^2/sec in the phytotron experiment delayed bulb development, but did not prevent it.
8. With reduction in light intensity, the total soluble sugar content in various plant organs decreased. The sugar level in different plant parts increased with time to a maximum and then, in some cases, tended to decline especially in leaf and neck.

In general, growth of the onion plant was reduced by the reduction of light intensity and, moreover, distribution of dry weight over the various organs changed with change in light intensity in such a way that with reduction of light intensity, leaves accumulated relatively more weight, roots and bulbs relatively less. Along with energetic effects, light intensity also induced some morphogenetic changes, e.g., relative increase in length and decrease in diameter of leaves with the reduction in light intensity. As long as the light intensity is sufficient for the survival of the plants, bulb development will ultimately occur.

B. DAYLENGTH, INTENSITY AND QUALITY OF SUPPLEMENTARY LIGHT EFFECTS

1. Under short day conditions (8hrs. in the field, or 12 hrs. of a mixture of fluorescent and incandescent light in the phytotron), the plants failed to develop bulbs. This also holds true when fluorescent light of 120 W/33 or 40 W/55 Philips tubes was used to extend a short photoperiod or even under continuous fluorescent light alone (24 hrs.).
2. In the early stages of growth (up to 120 days after sowing), total plant fresh and dry weight was little affected by the quality of the supplementary light (fluorescent or incandescent); being somewhat higher under supplementary incandescent light than under short day (8 hrs.) or short day with supplementary fluorescent light. Later on, the position was reversed. Similarly, root, neck and swollen neck base early in the season tended to have slightly higher weights under incandescent light supplementation than under short day or short day with fluorescent light extension. At later stages the reverse was true, however, bulb weight under incandescent supplementary light exceeded that of swollen neck base under short day or short day extended by fluorescent supplementary light. Leaf fresh and dry weight and total green leaf area per plant were more or less the same in all treatments from the date of sowing up to 120 days old; at more advanced age, leaf fresh and dry weight and total green leaf area were lower in plants grown under long day with incandescent light supplementation.
3. In general, longer leaves were produced under long day conditions, and particularly with incandescent light supplementation. Leaf diameter under

short day and long day with supplementary incandescent light, while close together, exceeded that under long day with supplementary fluorescent light. Specific leaf weight (weight per unit area) under long day with supplementary incandescent light was lower than under short day and under long day with supplementary fluorescent light.

4. Neck length was greater under long day conditions, especially with incandescent light extension. Up to 120 days after sowing, neck length, while equal under short day and long day with supplementary incandescent light, surpassed that under long day with supplementary fluorescent light. At more advanced age, neck diameter under long day with supplementary incandescent light lagged behind those at the other treatments.
5. Whether admixed to fluorescent light in a long photoperiod or used to extend a short photoperiod, incandescent light proved essential to bring about the photoperiodic reactions. The superiority of incandescent light over other light sources is due to the ratio of red: far-red it contains; neither red nor far-red alone induced bulbing.
6. The daily duration of light appears more important than the intensity of supplementary light. Eight hours of incandescent supplementary light, used to extend a main photoperiod of 12 hrs. supplied by fluorescent light tubes induced bulbing, whereas 4 hrs. failed to do so within the range of intensities of the supplementary light used. However, under 720 ergs/cm^2/sec supplementary incandescent light for 8 hrs., bulb development was not homogeneous; increasing the intensity of supplementary light supplied for 8 hrs. tended to speed up bulb development.
7. Young (up to 45 days old) as well as very old plants (189 days) are less sensitive to photoperiodic treatments than those of intermediate ages. In 45 days old plants, total green leaf area per plant continued to increase during 8 weeks in long day; in plants ranging from 74 to 130 days old it increased during the first 4 weeks in long day only; in still older plants total green leaf area did not show any increase following transfer to inductive cycles.
8. A positive correlation was observed between the size of the plant at the time of exposure to long day, and the final bulb weight.

Generally speaking, bulb development begins only under long day conditions provided the light is of the proper light quality. Incandescent light which contains a reasonable ratio of red: far-red energy proved essential in this respect. Increase of the intensity of supplementary light speeds up bulb development, the daily duration of light, however, is more important than the intensity of supplementary light. The quality of supplementary light induces some formative changes aside of induction of bulbing, e.g., in leaf shape. The plants do not respond to the photoperiodic treatment until after they had attained a certain physiological age.

C. TEMPERATURE EFFECTS (EXPERIMENTS UNDER CONTROLLED CONDITIONS)

1. In the early stages of growth (up to 73 days after sowing), differences in entire plant fresh and dry weight were not marked at a temperature range of 15 to 25 °C, though there was a tendency to be slightly higher at 15 and 20 °C than at 25 °C; with temperatures beyond this range, total plant fresh and dry weight markedly decreased. The decrease, however, was more pronounced at 10 than at 30 °C. At all temperatures, the entire plant fresh and dry weight increased with time till a maximum was obtained at the end of the experiment; the highest values recorded by then (186 days after sowing) were those at 20 and 25 °C. Growth in weight of various plant organs was differently affected by temperature; leaf and bulb weight in contrast to root weight was favoured by relatively high temperature. The time trend shows an increase in root, leaf and neck weight up to a certain moment which varied with temperature, thereafter, usually decreased or levelled off. The higher the temperature, the earlier this tended to be. By contrast, bulb fresh and dry weight progressively increased with time, up to the end of the growth period; the highest bulb weight was found at 25 °C.
2. Early in the growth cycle, leaf number per plant increased with rise in temperature up to 30 °C; however, in the range from 20 to 30 °C, differences in leaf number were not appreciable. Later on, leaf number at 25 °C exceeded those at all other temperatures. At all temperatures, leaf number increased with time to a maximum, and then decreased. The predominance of bulbing on new leaf emergence was clearer at 25 than at 30 °C.
3. Temperature influences leaf shape. Increase in temperature up to 25 °C resulted in longer leaves; higher temperature (30 °C) reduced leaf length. Leaf diameter was less influenced by temperature. Up to 127 days old, growth in leaf diameter tended to be favoured by relatively low temperature (15–20 °C); leaf diameter at 10 and 30 °C, while close together, lagged behind those at the other temperatures.
4. The largest total green leaf area per plant was found at 20 or 25 °C; higher or lower temperatures reduced green leaf area per plant. At all temperatures, green leaf area increased with time up to a certain moment, different according to treatment, and then declined.
5. Leaf area ratio and top/root ratio increased with temperature up to 25 °C and then slightly decreased with further increase in temperature; these ratio's, however, at 30 °C were still higher than in the temperature range from 10 to 20 °C. In general, leaf area ratio at all temperatures decreased with time.
6. Under long day conditions (15.5 hrs.) high temperatures speeded up bulb development; low temperatures (10 and 15 °C) markedly delayed it and all plants bolted. Under the experimental conditions applied, 25 °C appeared optimal for bulb growth.
7. Throughout the growth cycle, the total soluble sugar content in various plant organs was highest at 15 °C, except in the latest stage where the con-

centration at 10°C, generally, exceeded those at other temperatures. The time trend shows an increase in sugar level till a maximum was reached at a certain moment which differed according to treatment.

On the whole, temperature influences growth and development of the onion plant, induces some morphogenetic changes, alters the duration of the growth cycle, affects dry weight distribution over the various plant parts and leads to changes in the total soluble sugar content of the different plant organs.

Carbohydrate by itself does not appear to be a causal factor for bulb development.

It should be observed that the reported temperature effects are found under the values for the other experimental conditions as applied. It is likely that the effect of temperature on various growth and development phenomena differs, e.g., in different light intensity, as far as magnitude or optimal temperatures for the various effects are concerned.

It might be remarked that the same may hold for, e.g., light intensity effects with respect to temperature, but this is not the same, as light intensity as the main source of energy strongly predominates other effects under not specifically extreme conditions.

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SAMENVATTING

Bij de ui, *Allium cepa* L. (cv. Wijbo), werd gedurende de gehele groeicyclus de invloed van licht en temperatuur op de groei, de morphogenese en het koolhydraat gehalte nagegaan, zowel onder veld- als onder phytotronomstandigheden.

A. INVLOED VAN DE LICHTINTENSITEIT

De planten werden bij verschillende lichtintensiteiten in het veld en in het phytotron opgekweekt.

1. Vers- en drooggewicht van de gehele plant en zijn verschillende organen, d.w.z. wortel, bladschijf, hals[1] en knol namen toe met toenemende lichtintensiteit. Vers- en drooggewicht van de gehele plant verlopen in de tijd met een stijging tot een maximum aan het einde van het teeltseizoen. Het bolgewicht nam in de tijd versneld toe tot een maximum aan het einde van de groeiperiode, terwijl wortel, hals en bladgewicht gewoonlijk tot een zeker moment toenamen en vervolgens afnamen, of een vlakker verloop vertoonden; in sommige gevallen echter bleven blad en hals toenemen tot aan het einde van de proef.
2. De gemiddelde snelheid van de dagelijkse groei over het gehele seizoen (toename drooggewicht per plant per dag) nam toe met toenemende lichtintensiteit; de toename was exponentieel in 1964, rechtlijnig in 1965 en kromlijnig in het phytotronexperiment. De gemiddelde N.A.R.[2] over 126 en 135 dagen vanaf zaaien vertoonde in de veldproeven van resp. 1964 en 1965 een lineair verband met de relatieve lichtintensiteit, terwijl in het phytotron een kromlijnig verband werd gevonden.

   Hoewel de N.A.R. bij de hoogste lichtintensiteit in het phytotron slechts ongeveer de helft bedroeg van die in veldproeven, was de snelheid van de dagelijkse groei in het phytotron ongeveer tweemaal zo groot als in veldproeven, dankzij de krachtiger groei wat betreft het bladoppervlak onder beheerste omstandigheden.
3. Het aantal bladeren per plant was positief gecorreleerd met de lichtintensiteit; bij alle lichtintensiteiten nam het aantal bladeren in de tijd toe tot een maximum; daarna nam het af. De bladdikte en -diameter namen af met verlaging van de lichtintensiteit; hetzelfde geldt voor de bladlengte in de vroege groeistadia, terwijl later de bladlengte bij 37% licht in de veldproef van 1965 en bij 35% licht in de phytotronproeven die bij alle andere lichtintensiteiten overtroffen. De verhouding bladlengte/bladdiameter nam toe met verlaging van de lichtintensiteit.
4. In de vroege groeistadia nam het totale oppervlak aan groen blad per plant in alle proeven toe met toenemende lichtintensiteit; in de phytotronproef overtrof later het totale oppervlak aan groen blad bij 35% lichtintensiteit dat

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[1] hals, in de Engelse tekst 'neck': de tot een pseudo-stengel gebundelde bladscheden.

[2] 'net assimilation rate.

van alle andere behandelingen. In alle gevallen nam het totale oppervlak aan groen blad toe met de tijd; vervolgens nam het af.

5. De lichtintensiteit had een positief effect op de halsdiameter; deze nam met de tijd toe tot een maximum en daalde vervolgens in de meeste gevallen. In de veldproef van 1965 en in de phytotronproef overtrof de halslengte op een zeker moment die bij alle andere lichtintensiteiten.

6. De verhoudingen $\frac{\text{oppervlak groen blad}}{\text{drooggewicht totale plant}}$ [1]), spruit/bol en spruit/wortel waren negatief gecorreleerd met de lichtintensiteit. Met uitzondering van een stijging tussen de eerste en de tweede oogst nam de verhouding $\frac{\text{oppervlak groen blad}}{\text{drooggewicht totale plant}}$ [1]) met de tijd af tot een minimum aan het einde van proef.

7. Verlaging van de lichtintensiteit tot slechts 12% in de veldproeven en tot 11% = 10000 ergs/cm^2/sec in de phytotronproef vertraagde de bolontwikkeling, maar verhinderde deze niet.

8. Met de verlaging van de lichtintensiteit nam het totaal gehalte aan oplosbare suiker in de diverse planteorganen af. Het suikerniveau in verschillende plantedelen nam met de tijd toe tot een maximum en vertoonde vervolgens in sommige gevallen neiging af te nemen, in het bizonder in blad en hals.

Over het algemeen werd de groei van de ui verminderd door verlaging van de lichtintensiteit; bovendien veranderde met de verandering in de lichtintensiteit de verdeling van het drooggewicht over de verschillende organen zodanig dat bij verlaging van de lichtintensiteit de bladeren relatief meer gewicht ophoopten, wortels en bollen evenwel relatief minder. Naast energetische effecten werden door de lichtintensiteit ook enige morphogenetische veranderingen geïnduceerd, bijv. bij bladeren een relatieve toename in lengte en afname in diameter bij verlaging van de lichtintensiteit. Zolang de lichtintensiteit voldoende is om de planten te doen overleven, zal uiteindelijk bolontwikkeling plaats vinden.

B. INVLOED VAN DE DAGLENGTE, DE INTENSITEIT EN DE KWALITEIT VAN AANVULLEND LICHT

1. Onder korte-dag omstandigheden (8 uur in het veld of 12 uur gemengd licht van fluorescentiebuizen en gloeilampen in het phytotron) ontwikkelden de planten geen bollen. Dit gebeurde evenmin wanneer fluorescentielicht van Philips 120 W/33 of 40 W/55 TL-buizen werden gebruikt om een korte licht periode te verlengen, of onder continu fluorescentielicht alleen.

2. In de vroege groeistadia (tot 120 dagen vanaf zaaien) werd het totale vers- en drooggewicht van de plant weinig beïnvloed door de kwaliteit van het aanvullende licht (fluorescentie- of gloeilampen), hoewel het onder aanvullend

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[1] d.i. 'leaf area ratio'.

licht van gloeilampen wat hoger was dan onder korte dag (8 uur) of onder korte dag met aanvullend fluorescentielicht. Later was de situatie omgekeerd. Evenzo vertoonde vroeg in het seizoen wortel, hals en gezwollen hals basis de tendens tot een iets hoger gewicht onder aanvullend gloeilampenlicht dan onder korte dag of bij korte dag met dagverlenging met fluorescentielicht. In latere stadia was het omgekeerde het geval, doch het gewicht van de bol overtrof onder aanvullend gloeilampenlicht dat van de gezwollen hals basis onder korte dag of onder korte dag, verlengd door aanvullend fluorescentielicht.

Het vers- en drooggewicht en het totale oppervlak aan groen blad per plant waren min of meer gelijk bij alle behandelingen vanaf de zaaidatum tot 120 oud; bij meer gevorderde leeftijd waren vers- en drooggewicht en totaal oppervlak aan groen blad lager bij planten opgekweekt onder lange dag met aanvulling door gloeilampenlicht.

3. In het algemeen werden onder lange dag langere bladeren geproduceerd, in het bijzonder bij aanvulling door gloeilampenlicht. De bladdiameter, onder korte dag en onder lange dag met aanvullend gloeilampenlicht weinig verschillend, overtrof die onder lange dag met aanvullend fluorescentielicht. Het specifieke bladgewicht (gewicht per eenheid van oppervlak) was onder lange dag met aanvullend gloeilampenlicht lager dan onder korte dag en onder lange dag met aanvullend fluorescentielicht.
4. De halslengte was groter onder lange-dag omstandigheden, in het bijzonder bij dagverlenging met gloeilampenlicht. Tot 120 dagen vanaf zaaien overtrof de halslengte – gelijk bij korte dag en lange dag met aanvullend gloeilampenlicht – die, verkregen onder lange dag met aanvullend fluorescentielicht. Bij meer gevorderde leeftijd bleef de halslengte onder lange dag met aanvullend gloeilampenlicht achter bij die verkregen bij de andere behandelingen.
5. Hetzij gemengd met fluorescentielicht bij een lange fotoperiode, hetzij gebruikt om een korte fotoperiode te verlengen, gloeilampenlicht bleek noodzakelijk om fotoperiodiciteitsreacties teweeg te brengen. De superioriteit van gloeilampenlicht ten opzichte van licht uit andere bronnen is te danken aan de verhouding rood/nabij-infrarood die het bevat; rood noch nabij-infrarood alléén induceerden bolvorming.
6. De dagelijkse duur van de belichting blijkt belangrijker dan de intensiteit van het aanvullende licht. Aanvullend gloeilampenlicht van 8 uur, aangewend om een 12-urige basisbelichting, geleverd door fluorescentiebuizen, te verlengen induceerden bolvorming, terwijl 4 uur, binnen het traject van intensiteiten gebruikt voor het aanvullend licht, daarin te kort schoten. Bij aanvullend gloeilampenlicht van 720 erg/cm^2 sec gedurende 8 uur was de bolontwikkeling echter niet gelijkmatig; verhoging van de intensiteit van het aanvullend licht, gedurende 8 uur gegeven, leidde tot versnelling van de bolontwikkeling.
7. Jonge planten (tot 45 dagen oud) zowel als zeer oude (van 189 dagen) zijn minder gevoelig voor daglengte-behandeling dan die van daartussen gelegen leeftijden. Bij planten van 45 dagen oud bleef het totale oppervlak aan groen blad per plant onder lange dag gedurende 8 weken toenemen; bij planten tussen 74 en 130 dagen oud nam dit alleen gedurende de eerste 4 weken in lange dag toe;

bij nog oudere planten vertoonde het totale oppervlak groen blad geen enkele toename na het overbrengen in inducerende cycli.

8. Er werd een positieve correlatie waargenomen tussen de grootte van de plant op het tijdstip van blootstellen aan lange dag en het uiteindelijke bolgewicht.

Over het algemeen gesproken, begint de bolontwikkeling alleen onder lange dag omstandigheden, mits het licht van de juiste kwaliteit is. Gloeilampenlicht, dat een redelijke verhouding rode/nabij-infrarode energie bevat bleek in dit opzicht noodzakelijk. Toename van de intensiteit van aanvullend licht versnelt de bolontwikkeling, de dagelijkse duur van de belichting is echter belangrijker dan de intensiteit van het aanvullend licht. De kwaliteit van het aanvullende licht induceert naast de inductie van bolvorming, enkele formatieve veranderingen, bijv. in de bladvorm. De planten reageren niet op de daglengte-behandeling totdat ze een zekere physiologische leeftijd bereikt hadden.

C. TEMPERATUUREFFECTEN (PROEVEN ONDER BEHEERSTE OMSTANDIGHEDEN)

1. In de vroege groeistadia (tot 73 dagen vanaf zaaien), waren de verschillen in het versgewicht en in het drooggewicht van de gehele plant over een temperatuurtraject van 15 tot 25° niet opvallend, ofschoon de tendens bestond dat deze grootheden bij 15 en 20°C wat hoger waren dan bij 25°C; bij temperaturen buiten dit traject namen het totale vers- en drooggewicht duidelijk af. De afname was echter meer uitgesproken bij 10 dan bij 30°C. Bij alle temperaturen namen vers- en drooggewicht van de gehele plant met de tijd toe, tot een maximum werd bereikt aan het einde van de proef; de hoogste waarden werden dan (186 dagen vanaf zaaien) bij 20 en 25°C genoteerd. De toename in gewicht van de diverse plantenorganen werd verschillend beinvloed door de temperatuur; het blad- en het bolgewicht werden in tegenstelling tot het wortelgewicht begunstigd door betrekkelijk hoge temperatuur. Het verloop in de tijd vertoont een toename in wortel-, blad- en halsgewicht tot op een zeker moment, dat wisselt met de temperatuur; daarna vertoonde het gewoonlijk een daling of een afvlakking. Hoe hoger de temperatuur, hoe eerder dit optrad. In tegenstelling hiermee namen vers- en drooggewicht van de bol in versnelde mate toe met de tijd tot aan het einde van de groeiperiode; het hoogste bolgewicht werd bij 25°C gevonden.
2. Vroeg in de groeicyclus nam het aantal bladeren per plant toe bij stijging van de temperatuur tot 30°C; in het traject van 20 tot 30°C waren de verschillen in aantal bladeren evenwel gering. Later overtrof het aantal bladeren bij 25°C dat bij alle andere temperaturen. Bij alle temperaturen nam het aantal bladeren in de tijd toe tot een maximum en nam dan af. De voorkeur voor bolvorming boven vorming van nieuw blad was duidelijker bij 25 dan bij 30°C.
3. De temperatuur beinvloedt de bladvorm. Een temperatuurverhoging tot 25°C leidde tot langere bladeren; een hogere temperatuur (30°C) verkleinde de bladlengte. De bladdiameter stond minder onder invloed van de temperatuur.

Tot 127 dagen vertoonde de toename in bladdiameter een gunstige invloed van betrekkelijk lage temperaturen (15–20 °C); de bladdiameter verschilde bij 10 en 30 °C niet veel, en bleef beneden die bij andere temperaturen.

4. Het grootste totale oppervlak aan groen blad per plant werd bij 20 of 25 °C gevonden; hogere of lagere temperaturen verkleinden het oppervlak aan groen blad per plant. Bij alle temperaturen nam het oppervlak aan groen blad met de tijd toe tot een zeker moment, verschillend al naar de behandeling, en nam dan af.

5. De verhouding $\frac{\text{oppervlak groen blad}}{\text{drooggewicht totale plant}}$ spruit/wortel verhouding namen toe met de temperatuur tot 25°; vervolgens namen ze langzaam af bij verdere stijging van de temperatuur; bij 30 °C evenwel waren deze verhoudingen nog hoger dan in het temperatuur traject van 10 tot 20 °C. Over 't algemeen nam de verhouding $\frac{\text{oppervlak groen blad}}{\text{drooggewicht totale plant}}$ bij alle temperaturen af met de tijd.

6. Onder lange-dag omstandigheden ($15^{1}/_{2}$ uur) versnelden hoge temperaturen de bolontwikkeling; lage temperaturen (10 en 15 °C) vertraagden deze duidelijk, en alle planten gingen schieten. Onder de toegepaste proefomstandigheden bleek 25 °C optimaal voor de groei van de bol.

7. Over de gehele groeicyclus was het totaal gehalte aan oplosbare suiker in de diverse plantenorganen het hoogste bij 15 °C, behalve in het laatste stadium, waar de concentratie bij 10 °C over het algemeen die bij de andere temperaturen overtrof. Het verloop in de tijd vertoont een toename in het suikerniveau tot op een zeker tijdstip, dat wisselde al naar de behandeling, een maximum werd bereikt.

Over het geheel genomen beïnvloedt de temperatuur de groei en de ontwikkeling van de ui: hij induceert enkele morphogenetische veranderingen, verandert de duur van de groeicyclus, beïnvloedt de verdeling van drooggewicht over de verschillende delen van de plant en leidt tot veranderingen in het totaal gehalte aan oplosbare suiker van de verschillende plantenorganen.

Koolhydraat als zodanig blijkt geen causale factor te zijn voor de ontwikkeling van de bol.

Er zij op gewezen dat de beschreven temperatuurinvloeden gevonden worden onder de gegevens voor de andere proefomstandigheden zoals die toegepast werden. Het is waarschijnlijk dat de invloed van de temperatuur op de diverse groei- en ontwikkelingsverschijnselen verschilt bijv. bij verschillende lichtintensiteit, voor zover het de omvang of de optimale temperaturen voor de diverse invloeden betreft.

Er zou opgemerkt kunnen worden dat hetzelfde kan gelden voor bijv. invloeden van de lichtintensiteit ten aanzien van de temperatuur, doch dit is niet hetzelfde, aangezien onder niet-specifiek extreme omstandigheden de lichtintensiteit als de voornaamste energiebron sterk de andere invloeden overheerst.

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