A PHYSIOLOGICAL STUDY OF SHADING AND DENSITY EFFECTS ON THE GROWTH AND THE EFFICIENCY OF SOLAR ENERGY CONVERSION IN SOME FIELD CROPS

(met een samenvatting in het Nederlands)

by/door

M. S. KAMEL

Laboratory of Plant Physiological Research, Agricultural University, Wageningen, Netherlands, 192nd Communication, 71st Comm. on Photosynthesis

CONTENTS

1

INTRODUCTION

Sun is in fact the prime-mover of our civilization, up to now it has been the source of nearly all our energy, our material wealth, our power and our life. The sunlight which falls upon the earth represents a tremendous quantity of energy. Most of this energy is dissipated and only a small fraction is absorbed and utilized by the green plants through the process of photosynthesis. Till now the chlorophyllous plants still remain the only large scale converter of solar energy into potential energy.

In photosynthesis, nature has worked out a method of locking up radiant energy from the visible spectrum of sunlight between wavelengths of about 3500–7500 Å (about 40 to 50 per cent of the incident radiation), converting it into chemical energy. The compounds in which this chemical energy is stored in their turn supply the energy required for other plant activities, i.e. growth and development. It is evident that only the part of light which is absorbed can supply energy, but all of that absorbed even by chlorophyll is not necessarily effective in photosynthesis. It is well known that the maximum photosynthesis is reached at a certain light intensity (saturation intensity) so that a decrease in efficiency is found as the light intensity surpasses this saturation point. Under natural conditions, rates of photosynthesis rarely exceed two grams of carbohydrate per m^2 per hour, and one would expect the average for entire daylight periods and for entire leaf surface to be much below this. This average rate may be affected by external factors such as CO_2-concentration, temperature, and humidity, and internal changes responsible for permanent ageing and, probably, temporary rest of plants.

The natural overall process of photosynthesis is not very efficient, but it can serve as a most valuable guide to the development of a method of the utilization of solar energy.

Of great importance is the question how much the plant profits from the radiant energy that it receives, and what part is stored as potential energy of the accumulated organic compounds. Agriculture has been largely concerned only with the study of conditions of soil, climate, and cultivation for high crop production. Little consideration has been given to the vital process by which the plant manufactures its products and the efficiency of solar energy conversion that ultimately limits crop production.

Under natural conditions, it was found that during a growing season less than one to two per cent of the solar radiation usable in photosynthesis, is converted into organic matter by higher plants, while in experiments of brief duration under laboratory conditions the photosynthetic efficiency may reach 25–35 per cent, corresponding to 8–12 photons of red light per molecule of CO_2. The low energy conversion observed under field conditions appears to be due to various reasons, e.g. dissipation of energy absorbed by the photosynthetic apparatus in excess of its capacity.

SCOPE OF THE PRESENT STUDY

Because in most of the investigations carried out in the past there was a lack of detailed knowledge on the problem of solar energy conversion during the

growth cycle of crop plants (from sowing up to maturity), it is quite obvious that one of the most interesting and fundamental work in this field is to study, under natural conditions, the time or age trend, to follow the short period fluctuations, and to detect the stage at which maximum efficiency is reached.

Since the results of WASSINK and others on algae and some field crops favor the supposition that excessive solar radiation in summer may be one of the chief reasons for the low efficiency values under natural conditions, special attention has been given to the effect of reduced daylight intensity.

As variation in density gives another means for varying the solar radiation (although some factors other than light, especially water and nutrient factors may interfere), plant density has also been taken into consideration.

Besides this, an extensive study has been made of the formative effects of shading and density on plant growth and development, at the same time aiming to relate the efficiency of light energy conversion to growth and some of the morphological characters.

<center>CHAPTER II</center>

REVIEW OF LITERATURE

I. EFFICIENCY OF SOLAR ENERGY CONVERSION

Several investigations have attempted to determine the efficiency of plants in utilizing the light energy striking them. Some of these studies were of several hours duration (short-term experiments), the others were of several weeks or months duration (long-term experiments). In short-term experiments, BROWN and ESCOMBE (1905), made many determinations with detached leaves under different conditions and on several plants. The conversion yields were of the order of 0.4 to 1.7 per cent of the incident energy or an average of 2.5 per cent of the visible (or, rather, photosynthetically active) radiation absorbed by the plants. PURIEWITSCH (1914) calculated efficiency values from 0.6 to 7.7 per cent of the incident energy or an average of 7.5 per cent of the absorbed energy; BOSE (1924) arrived at considerably higher figures than those of PURIEWITSCH.

In long-term experiments, PÜTTER (1914) used figures of exceptionally high crops from agricultural yearbooks for the computation of the heat of combustion. He then added estimates of roots and stubbles and subtracted those of the seed. The required insolation data were taken from observations carried out in Kiel, over a period of several years, using the relation: one lux = 6.3 ergs/cm^2 sec., to calculate the corresponding energy flux. He neglected the energy above 1μ (it would be more reasonable to omit all radiation above 0.7μ since any radiation between 0.7 and 1μ probably is of very little effect in photosynthesis). The conversion yield for barley was found to be 3.2 per cent of the incident light and the estimations for the other crops used in his determinations varied from 1.8 to 4.6 per cent with an average of 3.2 per cent as referred to incident radiation below 1μ, or about 6 per cent of the absorbed radiation below 0.7μ. He attributed these high values to conditions that favor large-scale field experiments (particularly to the CO_2 supply from the soil). However, it seems more likely that these conversion yields were overestimated. According to RABINOWITCH (1951) at least two errors were made: 1. By the use of too low a factor for the

conversion of lux into energy units (in daylight, one lux corresponds to about 10 ergs/cm^{2}sec). 2. By the comparison of exceptionally high crops with average insolation data. TRANSEAU (1926) approached in a rather different way the problem of estimating the efficiency of plants in utilizing radiant energy. His calculations were based on actual yields of corn and meteorological data of the energy received from the sun at Madison, Wisconsin, during the period assumed as the growth period of corn (100 days). The calculations indicated that the plant utilized about 1.25 per cent of the incident energy, according to the various assumptions made by him. Since about 36 per cent of the total dry weight was deposited in the grain and thus available for mankind, the maximum effective transformation of incident light energy into food available for humans would be about 0.45 per cent. SPOEHR (1926) made calculations similar to those of PÜTTER, but took into consideration only the yield of grains in field crops and the utilizable timber in the forests. He obtained much lower values of energy conversion, 0.13 per cent of the total incident radiation for wheat and 0.35 per cent for a forest of fast-growing *Eucalyptus* trees. Similar figures were obtained by BOYSEN-JENSEN (1932) for forest trees. These calculations of SPOEHR and of BOYSEN-JENSEN were intended to estimate the practical efficiency of plants as converters of solar energy – so that stalks, husks, and roots of the wheat plants, and leaves and roots of the trees were neglected altogether, but the consideration of these terms could rarely more than double the calculated conversion yields – which could never approach the much higher figures of PÜTTER. NODDACK and KOMOR (1937) studied the efficiency of grass in converting solar radiation at two successive intervals of 20 days each. They used two plots of different areas, namely 9 m^2 and 74 m^2. The total solar radiation falling on these two plots was measured. The fraction of incident energy stored in the hay of the first plot was 0.67 and 0.80 per cent in the first and second periods, respectively; while it was 0.41 and 0.64 per cent for the second plot size during the first and second intervals, respectively. From these figures it can be concluded that the efficiency tended to increase with time and to decrease as the experimental area increased. In these determinations, the roots were not taken into account. The correction required for it is difficult to estimate, but it would bring the average up to one per cent of incident energy and close to 2.5 per cent of absorbed energy. MAXIMOV (1938) stated that the coefficient of radiant energy utilization by green plants in photosynthesis has a comparatively low value. Usually from 1 to 5 per cent, and only in exceptional cases as much as 10 per cent of the total energy absorbed, is used in photosynthesis. The remaining 90 to 99 per cent is transformed into heat and is utilized for the evaporation of water in transpiration. RILEY (1941) estimated the average utilization of solar energy falling on the surface of the sea to be from 0.6 to 0.8 per cent, similar to the average efficiency in fields and forests. RABINOWITCH (1945) estimated the average solar energy conversion of field crops and forests, during the summer vegetation period, under moderate climatic conditions to be 0.8 per cent of total incident solar radiation and about 2 per cent of the absorbed visible radiation. The average quantum yield of photosynthesis under these conditions is 0.01 (one molecule CO_2 reduced per 100 visible quanta absorbed). WASSINK (1948) computed the efficiency of some crops in converting solar energy. His calculations, based on optimal yields in the Netherlands including all parts of the plants, gave figures which ranged from 0.5 till 2.2 per cent. CURTIS and 'CLARK (1950) reported that if some factor such as carbon dioxide is limiting and light is in excess,

the efficiency would be lower than if light alone is limiting. But even with low light intensities the efficiency of solar energy conversion rarely exceeded 5 per cent of the absorbed visible radiation. RABINOWITCH (1951) estimated the average conversion yield of incident solar energy as 1.5 to 6.0 per cent (assuming 20 klux as the average intensity of illumination). KOK (1952), with *Chlorella* cultures under laboratory conditions in sodium light, reported efficiency values as high as 20–25 per cent under optimal conditions, thus confirming preliminary results obtained in this laboratory. GLAS and GAASTRA (1953) estimated the efficiency of beets under constant conditions and reported values of 12–19 per cent. WASSINK, KOK and VAN OORSCHOT (1953) found somewhat lower values of the order of 11–15 per cent. VAN OORSCHOT (1955), growing algae under natural conditions, obtained efficiency values ranging from 1–5 per cent of the visible solar radiation in full daylight. He found also that decreasing light intensity below full daylight resulted in higher efficiency values, *viz.*, 7.7 per cent in 25 % daylight and even higher values in mass cultures in artificial light. BERNARD (1956) estimated the photosynthetic efficiency for wood production under the shade of *Hevea* clones in Belgian Congo by taking, every 6 months, cuttings at 70 cm above the soil surface. He found that the average efficiency of solar energy conversion increased with shading. Values ranging from 0.88 to 11.50 per cent of the incident total radiation were obtained for light intensities from 21.8 to 1.39 per cent of full daylight, respectively. These values are very high and, moreover, the author stated that they were even underestimated owing to the neglection of the roots and because part of the shoot was left above the soil. He reported that this high values are due to the fact that under *Hevea* shade the radiation is rich in green light. He found also that the average photosynthetic efficiency increased with density as well as with fertilization and soil fertility. For maize crop the efficiency increased from 0.76 per cent in a normal planting of 20,000 plants/ha to 1.96 per cent of the incident radiation in a very thick planting of 160,000 plants/ha. If the very dense planting was well fertilized the efficiency increased from 1.96 per cent to 2.14 per cent of the incident radiation. For rice crop of 125,000 hills/ha, the efficiency was found to increase from 0.60 per cent in sandy soil to 0.98 per cent in loamy soil.

Comparing the results of the long-term experiments with those of short-time duration, one has to consider that some factors tend to reduce the long-time average value of energy conversion in a large amount of plants under natural conditions, as compared with that of a few isolated plants or leaves over a few hours while other factors may act in the opposite direction. Factors favouring high efficiency values are the lower average light intensity (sometimes light is limiting especially for the lower leaves), and possibly, partial retention of the respiratory gases in the dense foliage (sometimes a carbon dioxide-deficiency layer is formed around the plants and may limit the process and affect the saturation level). On the contrary, in a dense population a certain part may not be in a healthy state; furthermore, sometimes the temperature will be too low for maximum photosynthetic efficiency, sometimes it will be so high as to cause inhibition. Ordinarily, however, in natural vegetation where the plants completely occupy the soil, a total leaf area far greater than the surface of the soil is available for absorbing the incident light. As a result, a greater fraction of the photosynthetic tissues can absorb only the radiation that passes through some of the leaves or is reflected from their surface. Because of the fact that many leaves will be in the shade of others at least during part of the day, it is probable

that at any time even on the brightest days, light is limiting for some of the leaves, especially the lower ones. These unfavorable effects seem to predominate under natural habitats. 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. Furthermore, even when not shaded, many leaves are not at right angles to incident radiation, therefore, are not exposed to its maximum intensity.

TAKEDA and MARUTA (1956), on rice crop as affected by light intensity and spacing, pointed out that, in early stages of growth, light required for maximum photosynthesis was relatively low, then it increased gradually until at about the full tiller stage where practically all incident light was absorbed. This stage of maximal light absorption was reached first in the most dense planting. Thereafter, in normal planting the rate of photosynthesis was linear in relation to light intensity. With customary spacing (12 × 12 cm), the maximum rate extended from full tillering to the booting stage, then decreased. With wide spacing (24 × 24 cm or wider), maximum photosynthesis was found at the stage of active tillering, then decreased. WASSINK, RICHARDSON and PIETERS (1956) concluded that, in *Acer pseudoplatanus* grown at high light intensities, the saturating light intensity as well as the maximum rate of photosynthesis increase. The leaves formed are thicker. However, the efficiency in using low light intensities was found to decrease. RICHARDSON (1957) stated that, in general, maximum assimilation level and saturation light intensity increased with physiological age of plant material up to full leaf expansion and then fell off during senescence. IWAKI (1958) found the maximum assimilation of buckwheat leaves in densely planted stands to be lower than that in stands with lower densities.

II. SHADING AND GROWTH

Although much work has been done on the effect of shading on plant growth and development, evidence is rather conflicting. LUBIMENKO (1908) found that, in several plant species, dry matter production increased with increasing light intensity up to a certain maximum and then decreased. *Helianthus annuus* reached its maximum dry weight under full daylight, while plant height and leaf area attained their maximum development at lower light intensities. The dry matter percentage usually increased with increasing light intensity. In general, root growth increased and stem growth decreased with increasing light intensity within certain limits. COMBES (1910) found the optimum light intensity for the production of dry matter in several plant species to increase with the age of the plants. Maximum dry weight of fruit always occurred in full daylight intensity. ROSÉ (1913) on several plant species obtained maximum growth with full daylight intensity. SHANTZ (1913) found the fresh weight of potatoes, cotton, lettuce and radish to increase with decreasing light intensity from 50 to 15 per cent of full daylight. GARNER and ALLARD (1920) found reduction in seed production and in dry weight of tops of soybean plants grown under shade. GREGORY (1921) stated that the average leaf area of cucumber plants over a growth period of about 30 days was proportional to the total radiation received. MAXIMOV and LEBEDINCEV (1923) pointed out that, in bean, root and shoot dry weight, root/top ratio, and leaf area per plant increased with increasing light intensity. POP (1926) obtained the highest vigor of growth of soybeans in unshaded plants; on the other hand, shaded plants had longer stems. ZILLICH

(1926) on different plant species found a delay in the time of flowering and fruiting of plants grown under shade. The optimum intensity for fresh weight was 50 to 70 per cent daylight intensity for most of the plants he used. Weeds attained greater dry weight under reduced light intensities, while cultivated plants always had maximum dry weight when grown in the open. CLEMENTS et al. (1929) found, in wheat and sunflower plantations, that shoot length, shoot diameter, leaf number, size of the 2nd pair of leaves, shoot number, leaf area, and dry weight per plant increased as the light intensity increased. SHIRLEY (1929) pointed out that at low light intensity the dry matter produced by sunflower and other plants under investigation was almost directly proportional to the light intensity received, up to 20 per cent of full summer daylight. In the majority of cases maximum dry weight was produced by plants receiving the full normal daylight of the region in which they were grown. The dry matter percentage in the tops, the root/top ratio, the density of growth, the strength of stems, and the leaf thickness, all increased with increasing light intensity. Leaf area and height were found to be maximum at light intensities of about 20 per cent of full summer daylight. Time of maximum flowering and fruiting was considerably delayed by low light intensities. BOONSTRA (1929, 1937) gave quantitative characteristics about the change in leaf area of oats and sugar beet with time, increasing to a maximum and then decreasing. PORTER (1937) pointed out that the total mineral uptake was depressed by shading. MITCHELL and ROSENDAHL (1939) reported that, in white pine, root dry weight as well as shoot dry weight and root/top ratio decreased with shading. BLACKMAN and TEMPLEMAN (1940), on grasses and clover, concluded that the effect of light intensity on leaf production is, in part, dependent upon its effect on root development. At low light intensities leaves are produced at the expense of the roots since there is a transference of carbohydrates from the roots to the leaves when the plants are initially shaded. MILTHORPE (1945) found that shaded plants of flax as compared with plants grown in the open had a lower dry weight, leaf area and height, a higher water content, a lower net assimilation rate and fewer tillers. The reduction in leaf area per plant induced by shading was attributed to decrease in leaf number and leaf size. BLACKMAN and RUTTER (1948, 1950) reported that *Scilla non-scripta* and other plants grown in the open under shades, produced larger total leaf area than plants grown under full daylight illumination. The ratio of leaf area to total plant weight decreased linearly with increase in the logarithm of light intensity. In general, growth was reduced by shading, plant weight increased progressively with increasing light intensity, and maximum growth was in full daylight. MONSELISE (1951) showed that leaf area of citrus seedling increased by shading. Although most of the investigators concluded that growth in leaf area in open air conditions decreased by increasing light intensity, the results of GREGORY, MILTHORPE and others indicate that in some circumstances, possibly at high temperature, leaf area may increase with increase in illumination. BLACKMAN and WILSON (1951), on several plant species, pointed out that the leaf-area ratio under their experimental conditions was linearly related to log light intensity, and increased with decrease in intensity. They found also that the ratio decreased with age. WATSON (1952) concluded that the leaf area index increased with time, up to a maximum, and then decreased. MITCHELL (1953) found, in rye grass (*Lolium spp.*), that raising the light intensity increased the rate of tillering as well as the dry weight per unit leaf area. The length and width of the leaves followed a complex pattern of

8

response to light conditions and acted as independent variables. Conditions which influenced leaf length may or may not have influence on leaf width. VER-KERK (1955) found that less light resulted in less total dry weight, and thinner leaf blades in tomato. The leaf area was less reduced than leaf weight. KHALIL (1956) pointed out that increase of light intensity suppressed stem elongation of wheat, but both tillers and leaf number per plant were significantly increased. Under high light intensities the developmental growth of the reproductive organs was significantly faster. The root/top ratio as well as the leaf area increased with increasing light intensity, while on the contrary the leaf ratio decreased. BENSINK (1958) found that light has a morphogenetic effect on leaf growth of lettuce indicated by the length/breadth ratio. This ratio increased with decreasing light intensity.

III. DENSITY AND GROWTH

It has long been established, that one of the major factors limiting the amount of growth per unit area, is the density of the stand. It is of great interest to study the nature of competition in field crops, and how the density of a plant community affects the growth of each individual plant. Although this problem has been studied for a long time, little attention has been paid to the critical relationship between density and the developmental changes taking place from sowing up to maturity. ENGLEDOW (1925) critically analysed the morphological complex contributing to seed production in *Triticum sativum*, and studied the changes induced in individual plants by varying the density. He found that the number of tillers and ears per plant is very sensitive to changes in plant density. They decreased in number with increasing density. The yield of cereal crops was positively correlated with plant number per unit area. CLEMENTS, WEAVER and HANSON (1929) with *Triticum sativum* and *Helianthus annuus*, reported that the average number of living tillers and leaves per plant, leaf length and leaf width, leaf area per plant, shoot diameter, ear length, ear number per plant, dry weight of tops, dry weight of roots, dry weight of entire plant, and weight of grain decreased with increasing density. Plant height and internode length, on the contrary, increased with increasing density. In some cases, plant height was found to decrease with increasing density, because competition had become sufficiently intense to compensate the effects of shade in producing elongation. The average weight, ear number, and yield of seeds per unit area increased with increasing density. SMITH (1937) pointed out that if a uniform distribution of plants in cereal crops was established at the higher densities found in a normally variable crop, competition would be more severe, and the yield of the crop would not necessarily be increased. KONOLD (1940), on *Vicia faba*, found that in general the production of seed per unit area increased with increasing density, but that on a plant basis the number of pods and the yield was inversely linked with density; SOPER (1952) confirmed these findings. In a previous paper (KAMEL, 1954) the author concluded from his studies on *Sesamum indicum* that plant height, branch number, flower number, fruit number and yield of seeds per plant increased in a highly significant way as the density decreased. HODGSON and BLACKMAN (1956), with decreasing density, demonstrated an increase in branching, in number of flowers which set, in number of pods reaching maturity, and in seed production per plant, in *Vicia faba*. With increasing density, the yield of seed per unit area rose to a maximum, after which there was no signi-

ficant change. There was some overall indication that at plant densities greater than the medium density, the yield may decrease. On *a priori* grounds, coupled with supporting observations, it was advanced that variations in the degree of mutual shading following increase in density was one of the principal factors involved. IWAKI (1958) showed that with increasing the density of a buckwheat population, a marked decrease in individual plant weight was observed. The differences induced by variations in density became more marked as the plants developed. The leaf area index increased as the density increased, especially at the early stages of growth. The C/F ratio, the ratio of the non-photosynthetic system (stems, roots, and reproductive organs) to the photosynthetic system (leaves) tended to become higher with increasing density in the earlier stages of growth, but in the later stages, no apparent correlation between C/F ratio and density was observed. WATSON (1958) found in kale, that thinning of the crop, *viz.*, decreasing the number of plants per unit area, caused a reduction in the leaf-area ratio.

<div align="center">CHAPTER III</div>

MATERIAL AND METHODS

A two-row variety of barley (*Hordeum distichum*, var. Heine 4804) and a local variety of mangold (*Beta vulgaris* var. Groeningia) were used in this study. These varieties were obtained from the.Plant Breeding Laboratory, University of Agriculture, Wageningen/Holland. The work was carried out in the open in the experimental garden of the Plant Physiological Research Laboratory, of the same University, during the growing seasons 1957 and 1958.

<div align="center">SHADING EXPERIMENTS</div>

For investigating the shading effect in barley, four treatments were applied in both seasons: 100 per cent (full daylight), 80 per cent, 50 per cent and 25 per cent. In order to reduce daylight intensity, a wooden frame with one or two metal gauze sheets of several widths was placed on the appropriate plot. For the second treatment, iron screens were employed with a transmission of 80 per cent daylight, while for the third and fourth ones, single and double copper gauze screens were used to reduce daylight to 50 and 25 per cent, respectively. Each screen was supported on wooden cornerposts some inches above the ground and extended over the whole plot.

Precautions were made to avoid any side illumination. In 1957, this has been realized, to some extent, by lowering the screens, as far as the plant height permitted, and placing side screens on the south and west, and by constructing complete cages, in 1958 (see Plate 1). Such screens or cages were fixed in a way that made it possible to be raised to a higher level as the plants increased in height. In 1957, screens were placed on plots immediately after planting while in 1958, the cages were fixed on May 13 after an initial period of 11 days from planting. Periodic measurements of light intensity under the screens with flat and spherical meters showed that the degree of shading differed very little at various times of the day.

10

1. *Barley:* For studying the density effect, in 1958, three densities were applied: dense planting of 500 plants/m² (which amounts to an area of about 4×5 cm²/plant), normal planting of 250 plants/m² (8×5 cm²/plant) and thin planting of 125 plants/m² (16×5 cm²/plant), while in 1957, only the first two densities were employed.

2. *Mangold:* This plant species was in two spacings taken up in the experiments in 1958 only: close spacing of 25 plants/m² (20×20 cm²/plant) and wide (normal) spacing of 8.3 plants/m² (40×30 cm²/plant).

GENERAL METHODS AND PREPARATIONS

Barley: Sandy soil had to be used for shading and density experiments. The field was prepared for planting and divided into plots. The plot size in the shading experiment had to be relatively small since otherwise the screens for shading would have been too heavy and difficult for periodic removal. Moreover, by keeping the screens rather small, indirect effects of shading especially raising of air temperature were minimized (measurements of air temperature under screens and in open showed that the temperatures deviated very little). The screens were 2×2 meters, plot size 4 m², surrounded by a belt of half a meter width. For uniformity, all plots in shading and density experiments were of the same size.

In the shading experiments, the seeding distances were 8 cm between rows and 5 cm within rows, giving an area of 40 cm²/plant as in the usual planting (2×20 cm²/plant) although the arrangement in both cases was different. In the density experiments, the plant distances varied according to the treatment. Seeds were planted by hand to secure uniformity and regularity in the field.

For circumstances beyond our control, the sowing date was retarded for more than two months from usual in 1957 (March is the proper time for planting in sandy soil), and sowing was on June 6. It was on April 17 in the density experiment and on May 2 in the shading one, in 1958. For the same reasons and for limitation of land, insufficient space prevented replication of treatments in 1957 and permitted only the use of two replications in a random block arrangement in 1958. After sowing, the field was immediately irrigated artificially and the plants were watered during the season when necessary. The field was manured with farmyard manure and complete artificial fertilizer. As the plants under 50 and 25 per cent daylight showed severe lodging in 1957, precautions were made in the next season and plants were supported by stretched wire. Plots were in reach of full daylight most of the day (except those under screens which differed according to treatment).

Periodic harvests were taken during the entire growing season. On sampling days, top photographs were taken up to the 3rd harvest to determine the surface covered by plants. In subsequent harvests this was no more necessary, since the cultivated area was completely covered. In 1957, up to the 3rd harvest, a sample of 625 cm² was uprooted randomly, thereafter sampling was made on plant basis, and a sample of 15 or 30 plants from a closed area within each treatment was selected randomly at each harvest. In 1958, the latter technique was applied for each harvest. At the end, an area of 0.5 m² from the center of each plot was used for determination of the average efficiency of solar energy conversion during the entire growing season.

Preliminary measurements of reflexions, relative light intensity penetrating to ground level, and relative light received from the apex to the base at vertical intervals, were made.

Mangold: Soil type and land preparation were the same as in the barley experiments. Plot size was 15 m² (5 × 3 m); two replicates were used. The seeding distances differed according to the treatment. Each hill received five seeds, and the plants were later thinned to secure one plant per hill. For the same reasons mentioned previously, planting was late, *viz.*, on May 9. Plants were well manured and watered when necessary. To determine the area covered by plants, top photographs were taken till the cultivated area was completely covered. Periodic harvests were made from June 18 till the end of the season. A sample of 16 plants from a closed area, within each treatment, was randomly selected at each harvest.

GENERAL OBSERVATIONS AND DETERMINATIONS

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

1. Shoot length (main axis), internode length, and shoot diameter (average of the first two or three internodes of the main axis).

2. Shoot number and leaf number (green and dead) per plant and per unit area (cm²).

3. Leaf dimension (length and breadth), leaf ratio (length/breadth) and leaf area (length × breadth), recorded for the second well developed leaf from the top.

4. Time of awn emergence of main shoot, ear length of the main axis from the collar to the tip of the apical spikelet (excluding awns), percentage of completely emerged ears, ear number and seed number per plant and per unit area.

5. Fresh and dry weight per sample, recorded separately for roots, stems and sheaths, leaf blades, ears, and seeds in barley, and for roots, leaf blades, and petioles in mangold. Drying was carried out for two days at 90°C followed by half an hour at 105°C in a large electric oven with ventilation.

6. Leaf area, determined at early stages of growth by drawing an outline of a sample of leaf blades and measuring its area by planimeter. At later stages it was estimated by punching 100 discs of 6 mm and 16 mm diameter for barley and mangold, respectively. The dry weight of these measured leaf blades or discs was determined. In this way an estimate of the leaf area/leaf dry weight ratio for each sample was obtained which, multiplied by the dry weight of the green blades per plant or per unit area, gave the total green leaf area per plant or per unit area (leaf area index).

7. Percentage of the surface covered by plants, estimated by taking top photographs and measuring the leaf area by planimeter.

8. Leaf thickness (on dry weight basis) determined by punching 100 discs of 6 and 16 mm diameter for barley and mangold, respectively, and drying and weighing them.

9. Spike development, studied by micro-dissection of the growing points on July 10 in 1957, and on June 13 in the shading experiment, and on June 6 in the density experiment, in 1958.

10. Time of maturing, or length of the growing season.

Calculations were made also for the percentages of ear number/shoot number, number of ears producing seeds/total ear number, dry weight/fresh weight, ear dry weight/stem and leaf dry weight, seed dry weight/ear dry weight, and for root and top growth expressed as a percentage of the total dry weight of the plant, root/top ratio (on dry weight basis), C/F ratio (the ratio of non-photosynthetic tissues/photosynthetic tissues, on dry weight basis), dry weight increase per plant or per unit area per day (daily growth rate), leaf-area ratio (total green leaf area per plant/entire plant dry weight), and other growth characteristics.

LIGHT ENERGY CONVERSION ESTIMATION

The required meteorological data for the daily total radiation (cal/cm^2) was obtained from the Laboratory of Meteorology and Physics of the same University in the neighbourhood. The visible photosynthetic radiation was calculated by multiplying the total radiation by 0.45. The dry weight increase for calculating the efficiency per period was based on the area really covered by plants, while it was based on the cultivated area (including covered and uncovered surface) for calculating the average efficiency from the time of planting up to the final harvest. From the meteorological data together with the total dry weight increase of crop per unit area, assuming its composition to be CH_2O (3.7 kcal/g), the efficiency of solar energy conversion in per cent is given by:

$$\frac{\text{Chemical energy of dry weight production}}{\text{Photosynthesizable radiation energy}} \times 100$$

Note: For simplicity and to save space, most of the Tables as well as all those of the statistical analysis (analysis of variance) are not given here. In this publication the author intends to discuss in detail his results obtained in 1957 and 1958 on barley, and those on the efficiency of solar energy conversion in mangold as affected by density of planting. Data on growth characteristics of mangold together with other results of a shading experiment will be left to a forthcoming publication.

CHAPTER IV

RESULTS AND DISCUSSION – SHADING EFFECTS

I. SHADING AND GROWTH

A. Growth in shape, size, and number

1. *Shoot length and thickness*

The results presented in fig. 1a indicate that in 1957 up to June 27 (21 days after planting) the shoot length increased with decreasing light intensity down to 50 per cent daylight. Further reduction in light intensity had the reverse effect. As the plants advanced in growth up to 35 days, the shade became still more unfavorable. Thus, the shoot length decreased with any reduction below 80 per cent of full daylight. By that time, the plants under 50 and 25 per cent of full daylight suffered greatly from lodging. From July 11 (35 days after sowing) up to the end of the season, shoot length increased with increasing light intensity up to full daylight. It seems that the dwarfing effect of higher light intensity (growth inhibiting influence) may be masked by indirect effects; obviously, the more excessive supply of energy in full daylight is responsible for the better growth of the plants.

FIG. 1. Shading effect on shoot length (main axis) in cm, in barley, at successive harvests in 1957 (a) and in 1958 (b).

△————————△ :•Full daylight   ▲—·—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼·········▼ : 25 per cent

Fig. 1b shows that in 1958 up to 25 days, the shoot length followed closely the general rule, and increased with decreasing light intensity down to 25 per cent. From the second harvest up to June 23 (52 days after planting), plant length increased with reducing daylight down to 50 per cent, with still further reduction it decreased. This indicates that the detrimental effects induced by heavy shading increased with age and masked the shading effect on stem elongation. In the period from 52 days up to the end of the season, due to long exposure to shade, the plants at 50 per cent daylight failed to exceed in length those at 80 and 100 per cent of full daylight.

In both seasons, the differences induced by shading increased with age, and were maximal at the later stages of growth. Statistical analysis at the last harvest showed that the differences were highly significant. The plant length in cm at the final harvest was:

	Full daylight	80%	50%	25%
1957	106	105	70	66
1958	122	126	118	87

LUBIMENKO (1908), POP (1926), SHIRLEY (1929) and KHALIL (1956) found that plant height attained maximum development at relatively low light intensities. CLEMENTS et al. (1929) showed that reducing the light intensity from 50 to 10 per

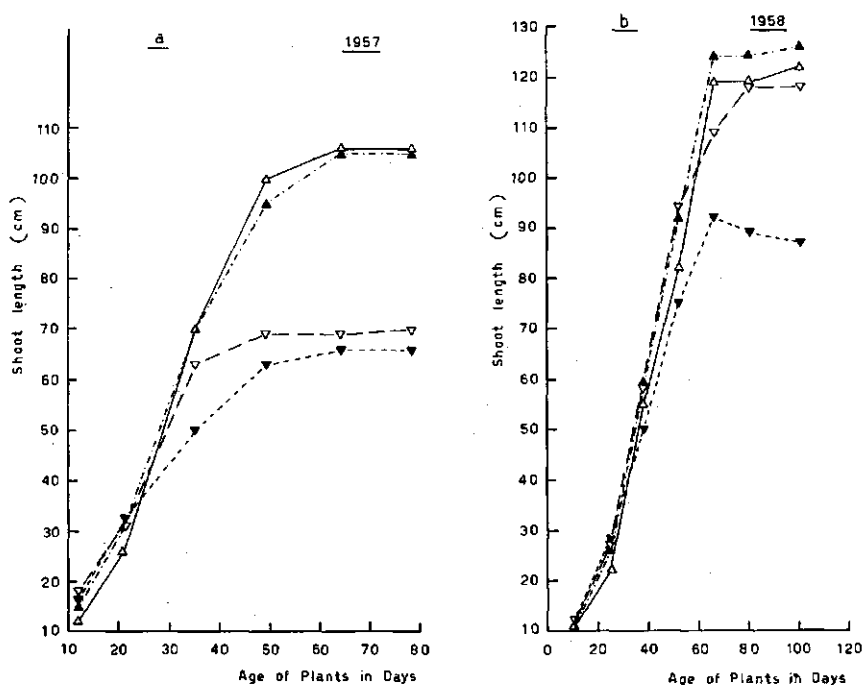14

FIG. 2. Shading effect on internode length (main axis) in cm, in barley, at successive harvests, in 1957 (a) and in 1958 (b).

☐ : Full daylight   ▨ : 80 per cent
▦ : 50 per cent   ■ : 25 per cent
a) A: 35 days after planting   B: 49 days after planting   C: 64 days after planting
b) D: 38 days after planting   E: 52 days after planting   F: 66 days after planting

cent of full daylight resulted at first in an increase in the length of wheat and sunflower plants, but later on the position was reversed. Starch tests of the leaves showed that starch was abundant at 50 per cent daylight and scarce at 10 per cent daylight, indicating that the reduction in assimilation rate is responsible herefor. MILTHORPE (1945) pointed out that flax plants grown in full daylight had longer stems as compared with those under shade.

In general, these observations appear to be in good agreement with our results.

In both seasons, the plants were found to increase rapidly in length in the early stages of their development, then less rapidly till they practically came to a standstill. At all light intensities, the growth curves were close to the S-shape.

It has for long been established that shading within certain limits increases internode extension. Fig. 2a shows that, in 1957, at all harvests under investigation, the internodes, with few exceptions, increased in length with decreasing light intensity only down to 80 per cent daylight, and fell off rapidly upon any further reduction in the intensity. Fig. 2b indicates that in 1958, at all harvests, the first internode followed closely the general rule, and increased with decreasing light intensity down to 25 per cent. From the second internode up to the fifth one, it was found, to some extent, that the maximum internode length was

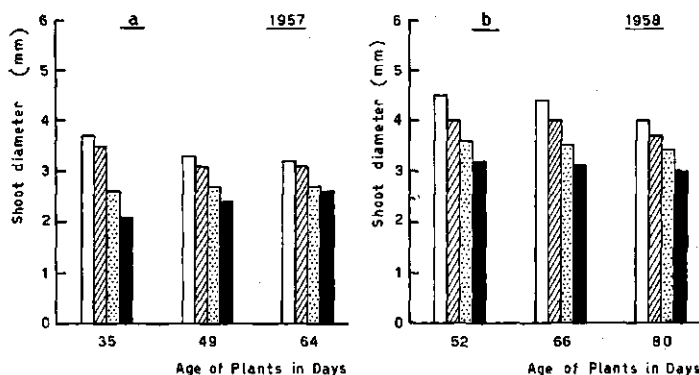FIG. 3. Shading effect on shoot diameter in mm (average of the first two or three internodes of the main axis), in barley, at successive harvests, in 1957 (a) and in 1958 (b).

☐ : Full daylight   ▨ : 80 per cent
▨ : 50 per cent   ■ : 25 per cent

attained at higher intensities, i.e. 50 or 80 per cent of full daylight. For the last internode, the maximum length was reached at 80 per cent daylight.

The internodes increased progressively in length and in number as the plants advanced in growth.

Fig. 3 shows that the shoot diameter at all harvests increased with increasing light intensity up to full daylight. In general, the greatest differences were found in the period from July 11 to 25 (35–49 days after planting) in 1957, and from June 23 to July 6 (52–66 days after sowing) in 1958. By that time, the shoot diameter, in 1957, varied from 3.7 to 3.3 mm for full daylight and from 2.1 to 2.6 mm for the 25 per cent daylight. In 1958, it differed from 4.5 to 4.4 mm for the plants in the open, and from 3.2 to 3.1 mm for the plants under the heaviest shade. The differences due to shading were statistically analysed at the last harvest, and were found to be highly significant.

It is evident that the stems of the plants grown under heavy shade were rather weak, often too weak to support the plant, owing to lack of sufficient woody material.

Similar results were obtained by CLEMENTS et al. (1929) and many other investigators.

2. Tillering

Table 1a and fig. 4a show that in 1957 at the first harvest the number of living shoots per plant was not yet affected by shading, but at more advanced age it increased with increasing light intensity, up to full daylight. In 1958 (Table 1b and fig. 4b), up to 66 days the shoot number per plant increased with increasing light intensity up to full daylight (see also Plate 2a). By the 6th harvest the position was changed and the plants at 50 per cent of full daylight prevailed over those at 80 per cent. This can be explained, in part, by the fact that, although shading retarded growth, yet growth cessation and dying off of the small shoots connected with early maturity were more pronounced at the higher light intensities. But with any further retardation in growth, the plants at the 25 per cent of daylight were still unable to exceed those at higher intensities. Later on, due
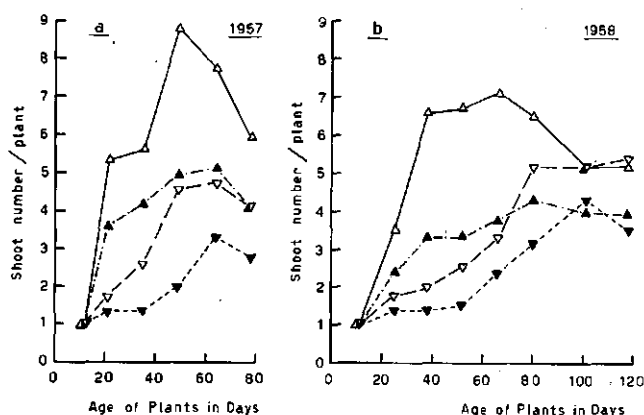
16

FIG. 4. Shading effect on shoot number per plant, in barley, at successive harvests, in 1957 (a) and in 1958 (b).

△————△ : Full daylight   ▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼········▼ : 25 per cent

to cessation of new shoot production and to more senescence at the higher light intensities, and at the same time to the formation of more shoots owing to extension of the vegetative period in the heavily shaded plots, the 50 per cent dominated over full daylight and the 25 per cent over 80 per cent daylight. Such case was not observed in 1957 and may be attributed to the unfavorable effect of severe lodging in the heavily shaded plots or to placing the screens immediately after planting. During further development, the plants at the 25 per cent daylight owing to the detrimental effect of heavy shading and to increased dying off of small shoots again possessed the lowest shoot number per plant.

TABLE 1. Shading effect on mean shoot number per plant, in barley, at successive harvests.

Shading treatment (% daylight)	1957 (a)					1958 (b)						
	Age of plants in days					Age of plants in days						
	21	35	49	64	78	25	38	52	66	80	101	118
100	5.3	5.6	8.8	7.7	5.9	3.5	6.6	6.7	7.1	6.5	5.2	5.2
80	3.6	4.2	4.9	5.1	4.1	2.4	3.3	3.3	3.8	4.3	4.0	3.9
50	1.7	2.6	4.5	4.7	4.1	1.8	2.0	2.5	3.3	5.2	5.2	5.4
25	1.3	1.3	2.0	3.3	2.8	1.4	1.4	1.5	2.4	3.2	4.3	3.5

In both seasons, the differences induced by shading increased with age up to a maximum and then decreased towards the end of the season. The differences were statistically analysed at the last harvest and were found to be still highly significant. CLEMENTS et al. (1929), in sunflower and wheat, and MILTHORPE (1945), in flax, found that the shaded plants as compared with those in the open had less tillers per plant. MITCHELL (1953) pointed out that, in ryegrass, raising the light intensity increased the rate of tillering. KHALIL (1956), on wheat, found the shoot number per plant to increase with increasing light intensity.

At all light intensities, the shoot number per plant increased with age to a

maximum, and then decreased. At the early stages of growth, the number of shoots produced per plant increased more rapidly at the higher light intensities. Later on, this was no more true. The maximum shoot number per plant was delayed by shading due to retardation of growth and prolongation of the vegetation period. In 1957, it was reached by July 25 (49 days after seeding) at the highest intensity and on August 9 (about two weeks later) at the lowest intensity. In 1958, it was attained on July 7 (66 days after planting) at full daylight and on August 11 (5 weeks later) at the heaviest shading. The maximum shoot number per plant ranged from 8.8 for full daylight to 3.3 for 25 per cent daylight in 1957, and from 7.1 for the former to 4.3 for the latter in 1958.

For explaining the nature of the shading effect on shoot formation, it is reasonable to mention here some of the hypotheses given for the mechanism of the inhibition of the lateral buds. THIMANN (1937) suggested that auxin acts directly by diffusion down from the centers of production in sufficient quantities to inhibit the lateral buds below. WENT (1939) supposed that auxin acts indirectly by diverting "food factors" required for growth to its centres of production, and away from lateral buds. SKOOG and TSUI (1951) suggested that both organ formation and subsequent development are brought about by quantitative changes in amount and interaction between nutrients and growth factors, so that development is determined by the relative supply through synthesis, transport and accumulation of these materials at particular loci. Probably arising from this, suggestions have been put forward that variations in amount of tillering in grasses (LEOPOLD, 1949) are associated with equivalent variations in rate of auxin production or sensitivity of the plant tissue to auxin. If such view is applied to the barley plants, it follows that auxin production, or sensitivity to auxin, is increased by a reduction in light intensity. MITCHELL (1953) supposed that there is a balance between the rate of increase in amount of active meristematic tissue in the zone of growth and the ability of the plant to supply energy containing substrates to it. It may safely be assumed that this balance is changed by varying the light intensity.

3. *Leaf production*
a. Leaf number

The variations with time in leaf number per plant (green and dead) and in the percentage of dead leaves to total leaf number, in barley, as affected by shading are represented in fig. 5 for the 1958 experiment. Up to the age of 52 days (June 23) the number of green leaves per plant (fig. 5a) increased regularly, and the more so inasmuch as the light intensity was higher. Thus, the greatest differences between the highest and lowest intensities were found after 52 days. During further development, the green leaf number per plant decreased with increasing light intensity, owing to earlier onset of senescence at the higher light intensities as compared with the lower, at which shoot and leaf production were still in progress. It can be concluded that, in general, changes in green leaf number per plant induced by differences in light intensity followed closely the changes in shoot number (cf. figs. 4b and 5a). Thus, the increase in green leaf number per plant observed at the early stages in the higher light intensities is due primarily to an increase in shoot number per plant and not to an increase in leaf number per shoot. In later stages, owing to increased dying off of the lower leaves in connection with senescence at the higher light intensities the leaf number per shoot decreases. Therefore, the higher green leaf number per plant at the lower
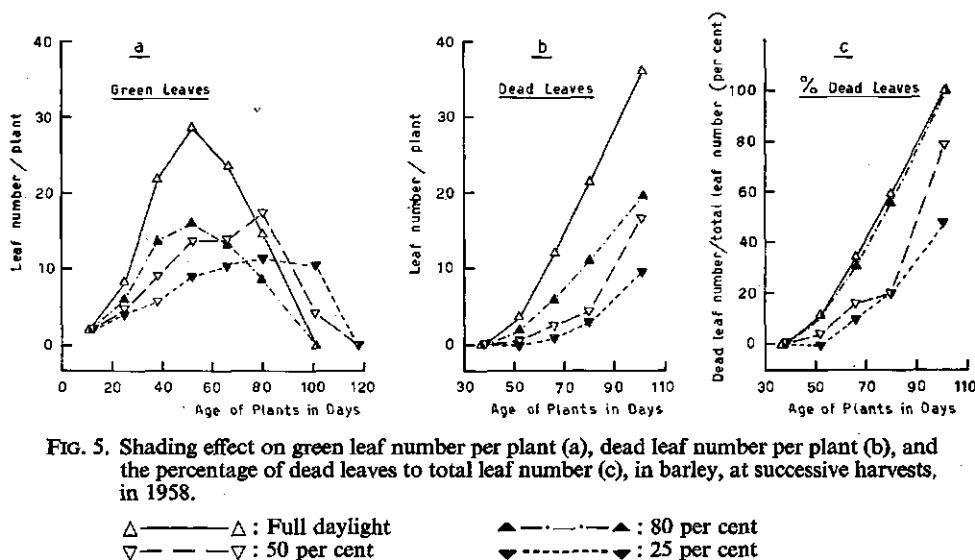
18

Fig. 5. Shading effect on green leaf number per plant (a), dead leaf number per plant (b), and the percentage of dead leaves to total leaf number (c), in barley, at successive harvests, in 1958.

△————————△ : Full daylight   ▲—·—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼·········▼ : 25 per cent

intensities is obviously to be attributed to higher green leaf number per shoot.

The maximum green leaf number reached on June 23 (52 days after planting) was 28.6 in full daylight and 16.1 in 80 per cent daylight. It was attained at July 21 (4 weeks later) in the 50 and 25 per cent daylight and was 17.3 for the former and 11.4 for the latter.

The onset of senescence as shown by the appearance of dead leaves was delayed two weeks at the lowest light intensity. The number of dead leaves per plant as well as the percentage of dead leaves to total leaf number (fig. 5b and c) increased more sharply with increasing light intensity, indicating earlier maturity at the higher intensities. By August 11 (101 days after sowing) the plants in full and 80 per cent daylight intensities no more had any green leaves, while those under heavy shade reached this stage on August 28 (17 days later), another indication of the effect of shading on extending the vegetation period.

Similar results were obtained in 1957 with the only exception that the green leaf number per plant in the plants under shade never exceeded that at the higher light intensities, following closely the shoot number trend (cf. fig. 4a). Similarly, MILTHORPE (1945) on flax and KHALIL (1956) on wheat found leaf number per plant to increase with increasing light intensity.

b. Leaf dimensions

It has been demonstrated long ago that reducing light intensity, within proper limits, increased leaf length and decreased leaf breadth. From fig. 6 it is evident that the leaf length, in general, increased with decreasing light intensity at least down to 50 % of full daylight. On the contrary, leaf breadth, except in the late stages, tended to decrease with decreasing light intensity.

At all light intensities, both leaf length and leaf breadth increased with age up to a maximum, and then tended to decrease. The greatest leaf length was obtained on June 9 (38 days after planting) in full daylight, and on July 21 (6 weeks later) in 25 per cent daylight. The greatest leaf breadth was reached on July 7 (66 days after seeding) at the highest light intensity and two weeks later
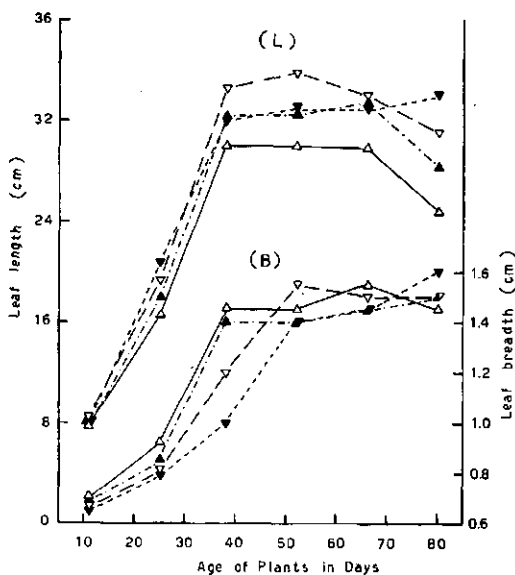
FIG. 6. Shading effect on leaf length (L) and leaf breadth (B), in cm, of the 2nd leaf from top, in barley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼········▼ : 25 per cent

at the lowest. The reduction, clearly observed in leaf length after the maximum, can be explained by the fact that, when an inflorescence develops at a growing point, production of leaves ceased, and in addition, the presence of the growing inflorescence has an inhibitory effect on the expansion of the young leaves immediately below it.

Fig. 7a shows that the leaf ratio (length/breadth) decreased with increasing light intensity up to full daylight. These results are in general agreement with those obtained by KHALIL (1956) on wheat and by BENSINK (1958) on lettuce.

At all light intensities, the leaf ratio was found to increase with time to a maximum on June 9 (38 days after planting). and the greatest differences between the highest and lowest intensities were found at that time. After this maximum, the ratio decreased towards a minimum at the last harvest still including green leaves (80 days after planting).

It is a familiar fact requiring no documentation that leaf size, in common with other size attributes, is greatly affected by shading. Fig. 7b shows that although there was a tendency for the leaf area (length × breadth) to increase with decreasing light intensity within limits, yet the differences were not so marked, especially not in the early stages of growth. Strongly marked differences were obtained by July 21 (80 days after sowing) where the leaf area increased with decreasing light intensity down to 25 per cent daylight.

At all light intensities, the leaf area increased progressively with time till a maximum was reached, and thereafter decreased. At the lowest light intensity, a maximum was not yet reached during the experimental period.

CLEMENTS et al. (1929) on wheat and sunflower found the size of the 2nd pair of leaves to increase with increasing light intensity. MILTHORPE (1945) on flax reported that leaf size decreased with shading. KHALIL (1956) found, in wheat, that the multiplied leaf ratio (length × breadth) increased with increasing light intensity.

4. *Ear production*

It has been established for long that while weak light promotes development of vegetative structures, intense light favors development of flowers, fruits and

20

FIG. 7.

Shading effect on leaf ratio [length/breadth] (a) and on leaf area [length × breadth] (b), in cm, of the 2nd leaf from top, in barley, at successive harvests, in 1958.

△————△: Full daylight
▲—·—·—▲: 80 per cent
▽— — —▽: 50 per cent
▼·········▼: 25 per cent

seeds, e.g. GARNER and ALLARD (1920) found reduction in seed production of soybean plants grown under shade.

Awn emergence had already started, in 1958, on June 19 (48 days after planting) in full daylight, on June 21 (50 days after sowing) in 80 per cent daylight, on June 28 (57 days after seeding) in 50 per cent and on July 9 (68 days after planting) in 25 per cent daylight. ZILLICH (1926), on several plant species, found a delay in the time of flowering and fruiting of plants grown under shade. SHIRLEY (1929) showed that, in sunflower and other plants, the time of maximum flowering and fruiting was considerably delayed by low light intensities.

Micro-dissection studies of the growing points on June 13, in 1958, showed that increase in light intensity up to full daylight induced earlier development of the spike and, accordingly, earlier awn emergence. Similar results were obtained in 1957. These findings are in accordance with those of KHALIL (1956) on wheat, under laboratory conditions.

Table 2 shows that at 49 and 66 days from planting in 1957 and in 1958, respectively, the percentage of completely emerged ears increased with light intensity up to full daylight. By that time, no ears were emerged at either 50 or 25 per cent of full daylight in 1957, and at 25 per cent of full daylight in 1958.

The ratio of the number of partly emerged ears to the total ear number, on the contrary, increased with decreasing light intensity.

TABLE 2. Shading effect on mean number of completely and partly emerged ears per plant, and on percentage of completely emerged ears/total ear number, in barley, after 49 days from planting in 1957 and after 66 days in 1958.

Shading treatment (% daylight)	1957				1958			
	Ear number per plant			Compl. emerged Total %	Ear number per plant			Compl. emerged Total %
	Completely emerged	Partly emerged	Total		Completely emerged	Partly emerged	Total	
100	1.0	2.9	3.9	25.6	4.1	0.1	4.2	97.6
80	0.6	2.5	3.1	19.4	2.6	0.2	2.8	92.9
50	0.0	0.0	0.0	0.0	1.0	0.8	1.9	52.6
25	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0

FIG. 8. Shading effect on ear number per plant, in barley, at successive harvests in 1957 (a) and in 1958 (b).

△————————△ : Full daylight   ▲—·——·—▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼ ....▼ : 25 per cent

In both seasons, the ear number per plant in general increased with increasing light intensity up to full daylight (Table 3 and fig. 8). During the last two harvests, the ear number per plant at 50 per cent daylight exceeded that at 80 per cent. It has been for a long time demonstrated that one of the major factors determining ear number per plant in cereals is the shoot number. And since by that time, the plants at the 50 per cent daylight exhibited the higher number of tillers per plant as compared with those under 80 per cent, it is not surprising that they consequently formed the higher number of ears per plant, regardless of the fact that shading retarded ear emergence. In 1957, the plants under the lowest light intensity failed to produce any ears. Examination of the growing points showed that the spike was in fact initiated, but owing to insufficient energy it developed very poorly and failed to emerge. This may be attributed to severe lodging or to applying the screens immediately after sowing, so that the plants have not received full daylight prior to placing the screens, as in 1958, and, therefore, respond more strongly to shade, especially at the lowest light intensity.

TABLE 3. Shading effect on mean number of completely emerged ears per plant, in barley, at successive harvests.

| Shading treatment (% daylight) | 1957 | | | 1958 | | | |
| | Age of plants in days | | | Age of plants in days | | | |
	49	64	78	66	80	101	118
100	1.0	5.3	5.8	4.1	5.9	5.2	5.2
80	0.6	3.9	4.1	2.6	3.4	3.5	3.5
50	0.0	0.4	2.0	1.0	3.0	4.4	4.3
25	0.0	0.0	0.0	0.0	0.8	1.3	1.7

The ear number per plant increased with time to a maximum, after which there was no obvious decrease. In 1958 the maximum was attained on July 21 (80 days after planting) in full daylight, on August 11 (three weeks later) at the

22

medium light intensities, and on August 28 (17 days later) at the lowest intensity. In 1957, a similar tendency was observed. In this case, a reduction in ear number per plant after the maximum was observed at full and 50 per cent daylight, and probably may be due to sampling variation. The ear number per plant at the last sampling ranged from 5.8 to 0.0 in 1957 and from 5.2 to 1.7 in 1958 between the highest and the lowest light intensities. The differences due to shading were statistically analysed at the last harvest and were found to be highly significant.

Fig. 9 shows that, in 1958, ear length of the main axis increased with increasing light intensity up to full daylight (see also Plate 2b). The ear length at the higher light intensities was the same until the end of the season, while at the lower intensities it increased progressively with time. This means that the ear of the main shoot under the higher intensities developed more rapidly in the boot stage as well as immediately after emergence. The maximum ear length was attained already on July 7 (66 days after planting) at the higher light intensities, and on August 11 (5 weeks later) at the lower intensities. It differed from 10.1 cm in full daylight to 5.6 cm in 25 per cent daylight.

FIG. 9. Shading effect on ear length, in cm, of the main axis, in barley, at successive harvests in 1958.

△————△: Full daylight
▲—·—·—▲: 80 per cent
▽— — —▽: 50 per cent
▼········▼: 25 per cent

5. Seed production

The results presented in Table 4 and graphically illustrated in fig. 10a show that seed number per plant increased with increasing light intensity up to full daylight. In the graphs and in the discussions "seed number" refers to mature seeds only. The differences increased with time to a maximum in the period from August 11 to 28 (101–118 days after planting), in 1958. Statistical analyses at the final harvest showed that these differences, induced by shading, were highly significant. GARNER and ALLARD (1920) found reduction in seed production of soybeen plants grown under shade.

Comparison of figs. 8 and 10a shows that although in 1958 the plants at 50 per cent daylight exceeded those at 80 per cent in their ear number per plant, during the late stages of development, they did not prevail in seed production. This probably is due to the smaller number of seeds per ear, and the failure of the ears, emerged later, to form seeds.

The number of seeds per plant increased progressively with time, owing to formation of seeds in ears produced after the main ear. The figures for the

FIG. 10. Shading effect on seed number per plant (a) and per ear (b), in barley, at successive harvests, in 1958.

△————△ : Full daylight   ▲ —·—·— ▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼ ·········▼ : 25 per cent

TABLE 4. Shading effect on seed number per ear and per plant, in barley, at successive harvests.

Shading treatment (% daylight)	1957		1958					
	Age of plants in days		Age of plants in days					
	78		80		101		118	
	Ear	Plant	Ear	Plant	Ear	Plant	Ear	Plant
100	18.6	108.0	15.2	89.8	21.5	111.7	21.0	100.2
80	18.2	75.0	16.3	55.5	18.2	63.8	19.1	66.8
50	2.0	4.0	7.8	23.5	10.4	45.9	10.3	43.3
25	0.0	0.0	0.0	0.0	0.5	0.7	1.4	2.4

heaviest shading always remained lowest, and practically no seeds were formed at 25 per cent of full daylight under our conditions. In 1958, while after 80 days from planting no seeds were yet formed at the lowest intensity, 89.8 seeds were produced per plant in full daylight. Three weeks later, 0.7 seeds were formed per plant at the former and 111.7 seeds per plant at the latter. The final seed number per plant varied from 0.0 to 108.0 in 1957 and from 2.4 to 100.2 in 1958 for the lowest and highest light intensities, respectively. As has been mentioned earlier, the slight drop in ear number per plant in 1958 at very advanced stages of development in full daylight and in 50 per cent daylight, being

also reflected in the seed number per plant, may be attributed to sampling variations. Also failure of some seeds to reach maturity, and loss of seeds owing to ripening may have occurred.

Fig. 10b indicates that, in general, the number of seeds per ear increased with light intensity. The prevalence of the 80 per cent daylight over full daylight at the beginning (80 days after sowing) may be due to increase in relative number of ears forming seeds by that time in the former. In addition, in the 80 per cent daylight, there was a smaller number of shoots per plant, a more uniform growth, and also a smaller number of ears per plant. The competition for nutrients and other substrates was, therefore, less pronounced, so that ears formed by each individual plant in the 80 per cent daylight varied little in their seed number. In the average this turned out to be higher than in the full daylight plot where more ears of strongly variable size were present at the same moment so that the high light intensity effect on producing higher number of seeds per ear was masked at this early stage of seed development by the competitive effect of several ears. Later on, the number of undeveloped ears in full daylight was greatly reduced due to completion of development of the firstly emerged ears and consequently to less competition between the remainder. Thus, seed formation was in progress and the highest number of seeds per ear was obtained in full daylight. By that time, up to the end of the season, shading effects became more marked so that at reduced light intensities seed number per ear was greatly depressed. The differences due to shading were statistically analysed at the last harvest and were found to be highly significant.

It is worth noting here that the low number of seeds per ear associated with low light intensity may be due to either the direct effect of shading on seed formation or to its effect on ear length, or to both. Reducing the light intensity to 25 per cent seems to have also a detrimental effect on flower fertility since most or even all flowers failed to form seeds. This failure may be due also to limited photosynthesis from the beginning, and consequently to a lower degree of growth and development.

At all intensities, the number of seeds per ear increased progressively with age. The small decrease in seed number per ear at the end of the season in full daylight may be due to production of more ears with lower numbers of seeds, or to sampling variations.

6. *Efficiency of shoots in producing ears, and of ears in forming seeds*

Of great importance is the question how much the efficiency of shoots in producing ears (ear number/shoot number in per cent) is affected by shading. It has been demonstrated previously that shoot number as well as ear number per plant were greatly influenced by varying light intensity. For more critical examination, it seems more reasonable to follow the variations in the percentage of ears to shoots, as induced by shading. Fig. 11a shows that, in general, the percentage increased with increasing light intensity up to full daylight, so that the number of shoots developing ears decreased with shading. The differences increased with time and were maximal after 101 days from planting, especially between the highest and lowest intensities. By that time, the percentage varied from 100.0 for the highest intensity to 30.2 for the lowest light intensity, while at the final harvest it differed from 100.0 to 48.6 per cent for the former and latter, respectively.

FIG. 11. Shading effect on the efficiency of shoots in producing ears [ear number to shoot number, in per cent] (a) and on the efficiency of ears in forming seeds [number of ears forming seeds to total ear number, in per cent] (b), in barley, at successive harvests, in 1958.

△————△ : Full daylight   ▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent   ▼---------▼ : 25 per cent

Shoot efficiency in producing ears increased consistently with time, owing to emergence of more ears, as well as to decay of small shoots. Practically, the maximum efficiency was reached after 101 days from planting at the first three light intensities, and later at the lowest intensity.

A further interesting feature is that, although the 50 per cent daylight plants exceeded those at 80 per cent in their shoot number and ear number per plant, they predominate no more as far as the percentage of ears to shoots was taken into consideration. Relatively, a higher number of shoots per plant at 50 per cent daylight were unable to develop ears.

No doubt that one of the most important factors determining yield of cereal crops is the percentage of the ears forming seeds. Since shading depressed ear and seed production per plant, it is reasonable, as the next step, to follow the variations in the percentage of ears forming seeds to total ear number, as induced by shading. Fig. 11b indicates that the percentage decreased with shading.

At the first stages, over a period of three weeks (80–101 days after sowing) the percentage increased rapidly, especially in full daylight. At more advanced age, the increase of the efficiency of ears came to a standstill at full daylight while it was still in progress at the lower light intensities, and more rapidly so at the lowest intensity. This may be due to the retarding effect of shading on growth and ear emergence, leading to the extension of the vegetative and the vegetation period. At the final harvest, the percentage of the ears forming seeds ranged from 100.0 per cent for the highest intensity to 64.7 per cent for the lowest one.

B. Growth in weight

It has been demonstrated in a previous paper (KAMEL, 1958) that the entire

26   *Meded. Landbouwhogeschool, Wageningen 59 (5), 1–101 (1959)*

plant fresh weight as well as dry weight and dry weight percentage were greatly affected by shading during the growth period. There is still the question how several plant parts respond to shading and to age. Since the plant is composed of roots, leaves, stems and reproductive organs, the differences in entire plant weight induced by shading during the season are the result of changes in these constituents.

Table 5 and the next figures represent the effect of shading on the weight of each of the individual plant organs and on other growth characteristics.

1. *Roots*

Since roots can make none of their own carbohydrates, but are dependent on tops for this material, and since shading suppressed top growth (see later), one would expect that root growth will be influenced by shading.

a. Fresh weight

Fig. 12a shows that with increasing light intensity up to full daylight, the fresh weight of roots per plant increased. The differences increased with time to a maximum at June 23 (52 days after planning).

At all light intensities, the fresh weight of roots decreased after the maximum at 52 days from planting, and more gradually so at the lower light intensities. Due to the extension of the growth period by heavy shading, fresh weight of roots at low light intensities tended to change very little during the late stages of growth, from July 7 to August 28 (66 to 118 days after planting). The maximum fresh weight of roots per plant differed from 0.42 g for the highest light intensity to 0.10 g for the lowest one.

Similar results were obtained in 1957.

b. Dry weight

Fig. 12b indicates that also the dry weight of roots was greatly depressed by reduced light intensities. The differences became more marked as the plants developed and were maximal after 80 days from planting. The same trend was observed in 1957. These results confirm those of LUBIMENKO (1908), MAXIMOV and LEBEDINCEV (1923), and MITCHELL and ROSENDAHL (1939).

The dry matter in roots increased progressively with age – and more rapidly so at the higher light intensities – till the maximum, and then decreased more gradually at the lower light intensities. This reduction may be due to maturing and dying off of most of the absorbing roots, connected with top senescence. The decrease in dry weight started after 80 days from planting (on July 21) at the higher light intensities, and was practically absent at the lower light intensities. The latter is connected with the extension of the vegetative period under heavy shading. The dry weight of roots per plant on July 21 (80 days after sowing) varied from 0.21 g in full daylight to 0.01 g in 25 per cent daylight, while at the final harvest it ranged from 0.17 g to 0.01 g for the highest and lowest light intensities, respectively.

c. Dry weight percentage

Fig. 12c shows that during the first stages of growth the dry matter percentage of roots increased with decreasing light intensity. This may be due to differences in water uptake, since it has been demonstrated long ago that shading decreased uptake of water and minerals by roots. PORTER (1937) and others found that the total uptake of minerals was depressed by shading.

Later on, the position was changed and the dry matter percentage increased

Shading treatment (% daylight)	Date	Age of plants (days)	Entire plant			Roots		
			Fresh	Dry	%	Fresh	Dry	'
100			0.157	0.021	13.4	0.009	0.005	5:
80	13 V	11	0.158	0.021	13.3	0.009	0.005	5:
50			0.169	0.021	12.4	0.008	0.004	5(
25			0.155	0.020	12.9	0.007	0.004	5'
100			1.580	0.171	10.8	0.074	0.015	2(
80	27 V	25	1.292	0.126	9.8	0.027	0.009	3:
50			0.894	0.082	9.2	0.013	0.005	4(
25			0.785	0.066	8.4	0.010	0.004	4(
100			12.712	1.463	11.5	0.328	0.100	3(
80	9 VI	38	8.209	0.790	9.6	0.102	0.037	3(
50			4.586	0.400	8.7	0.060	0.015	2:
25			2.689	0.213	7.9	0.033	0.008	2<
100			26.157	4.162	15.9	0.409	0.173	4:
80	23 VI	52	16.107	2.133	13.2	0.176	0.067	3(
50			14.343	1.413	9.9	0.131	0.041	31
25			6.502	0.483	7.4	0.087	0.012	1:
100			30.027	7.204	24.0	0.311	0.205	6:
80	7 VII	66	18.922	3.983	21.0	0.132	0.080	6(
50			15.296	2.069	13.5	0.081	0.040	4:
25			8.200	0.829	10.1	0.031	0.011	3:
100			20.956	7.850	37.5	0.305	0.210	6:
80	21 VII	80	14.823	5.000	33.7	0.133	0.083	6:
50			17.056	2.982	17.5	0.077	0.040	51
25			8.675	1.044	12.0	0.030	0.012	4(
100			14.909	8.492	57.0	0.244	0.175	71
80	11 VIII	101	13.168	5.458	41.4	0.116	0.075	6:
50			14.491	3.883	26.8	0.076	0.044	5:
25			8.954	1.326	14.8	0.032	0.014	4:
100			11.570	8.479	73.3	0.233	0.173	74
80	28 VIII	118	8.645	5.484	63.4	0.113	0.075	6(
50			11.268	4.078	36.2	0.070	0.041	5:
25			6.953	1.419	20.4	0.027	0.012	44

28

	Tops (*continued overleaf*)									
	Stems + Leaves									
	Leaves (Blades)					Stems + Sheaths			Total		
	Green		Total								
sh	Dry	%	Fresh	Dry	%	Fresh	Dry	%	Fresh	Dry	%
86	0.010	11.6	0.086	0.010	11.6	0.062	0.006	9.7	0.148	0.016	10.8
87	0.010	11.5	0.087	0.010	11.5	0.062	0.006	9.7	0.149	0.016	10.7
92	0.011	12.0	0.092	0.011	12.0	0.069	0.006	8.7	0.161	0.017	10.6
86	0.010	11.6	0.086	0.010	11.6	0.062	0.006	9.7	0.148	0.016	10.8
40	0.109	11.2	0.940	0.109	11.2	0.566	0.047	8.3	1.506	0.156	10.4
84	0.081	11.1	0.784	0.081	11.1	0.481	0.036	7.5	1.265	0.117	9.2
51	0.053	9.6	0.551	0.053	9.6	0.330	0.024	7.3	0.881	0.077	8.7
07	0.044	8.6	0.507	0.044	8.6	0.268	0.018	6.7	0.775	0.062	8.0
73	0.729	13.3	5.473	0.729	13.3	6.911	0.634	9.2	12.384	1.363	11.0
48	0.423	11.3	3.748	0.423	11.3	4.359	0.330	7.6	8.107	0.753	9.3
60	0.226	10.5	2.160	0.226	10.5	2.366	0.159	6.7	4.526	0.385	8.5
34	0.126	8.8	1.434	0.126	8.8	1.222	0.079	6.5	2.656	0.205	7.7
45	1.114	15.2	7.614	1.158	15.2	18.134	2.831	15.6	25.748	3.989	15.5
02	0.683	13.4	5.220	0.700	13.4	10.711	1.366	12.8	15.931	2.066	13.0
25	0.585	11.6	5.047	0.588	11.6	9.165	0.784	8.6	14.212	1.372	9.7
08	0.250	8.9	2.808	0.250	8.9	3.607	0.221	6.1	6.415	0.471	7.3
67	1.109	21.5	5.512	1.311	23.8	20.817	4.550	21.9	26.329	5.861	22.3
74	0.696	18.0	4.016	0.779	19.4	12.934	2.507	19.3	16.950	3.286	19.4
99	0.558	14.3	3.950	0.580	14.7	10.457	1.243	11.9	14.407	1.823	12.7
65	0.359	12.1	3.016	0.371	12.3	5.040	0.430	8.5	8.056	0.801	9.9
86	0.476	40.1	1.829	0.984	53.8	11.940	3.482	29.2	13.769	4.466	32.4
69	0.304	35.0	1.266	0.609	48.1	9.377	2.522	26.9	10.643	3.131	29.4
18	0.570	17.2	3.538	0.638	18.0	11.404	1.667	14.6	14.942	2.305	15.4
81	0.332	13.9	2.666	0.416	15.6	5.704	0.557	9.8	8.370	0.973	11.6
00	0.000	00.0	0.706	0.620	87.8	8.210	3.360	40.9	8.916	3.980	44.6
00	0.000	00.0	0.608	0.502	82.5	8.154	2.280	28.0	8.762	2.782	31.8
87	0.130	33.3	0.911	0.513	56.3	10.290	1.780	17.3	11.201	2.293	20.5
72	0.243	17.7	1.766	0.460	26.0	6.744	0.737	10.9	8.510	1.197	14.1
00	0.000	0.0	0.533	0.487	91.4	5.843	3.430	58.8	6.376	3.917	61.4
00	0.000	0.0	0.377	0.337	89.4	4.940	2.324	47.0	5.317	2.661	50.0
00	0.000	0.0	0.420	0.357	85.0	8.334	1.980	23.8	8.754	2.337	26.7
00	0.000	0.0	0.632	0.382	60.4	6.004	0.871	14.5	6.636	1.253	18.9

Shading treatment (% daylight)	Date	Age of plants (days)	Ears					To
			Seeds			Total		
			Fresh	Dry	%	Fresh	Dry	
100			0.000	0.000	0.0	0.000	0.000	
80	13 V	11	0.000	0.000	0.0	0.000	0.000	
50			0.000	0.000	0.0	0.000	0.000	
25			0.000	0.000	0.0	0.000	0.000	
100			0.000	0.000	0.0	0.000	0.000	
80	27 V	25	0.000	0.000	0.0	0.000	0.000	
50			0.000	0.000	0.0	0.000	0.000	
25			0.000	0.000	0.0	0.000	0.000	
100			0.000	0.000	0.0	0.000	0.000	
80	9 VI	38	0.000	0.000	0.0	0.000	0.000	
50			0.000	0.000	0.0	0.000	0.000	
25			0.000	0.000	0.0	0.000	0.000	
100			0.000	0.000	0.0	0.000	0.000	
80	23 VI	52	0.000	0.000	0.0	0.000	0.000	
50			0.000	0.000	0.0	0.000	0.000	
25			0.000	0.000	0.0	0.000	0.000	
100			0.000	0.000	0.0	3.387	1.138	3:
80	7 VII	66	0.000	0.000	0.0	1.840	0.617	3:
50			0.000	0.000	0.0	0.808	0.206	2:
25			0.000	0.000	0.0	0.113	0.017	1:
100			5.245	2.390	45.6	6.882	3.174	4(
80	21 VII	80	3.167	1.384	43.7	4.047	1.786	4:
50			1.061	0.352	33.2	2.037	0.637	3:
25			0.000	0.000	0.0	0.275	0.059	2
100			4.854	3.630	74.8	5.749	4.337	7:
80	11 VIII	101	3.550	2.167	61.0	4.290	2.601	6(
50			2.461	1.174	47.7	3.214	1.546	4!
25			0.036	0.015	41.7	0.412	0.115	2!
100			4.254	3.755	88.3	4.961	4.389	8!
80	28 VIII	118	2.680	2.314	86.3	3.215	2.748	8:
50			1.907	1.357	71.2	2.444	1.700	6!
25			0.071	0.046	64.8	0.290	0.154	5:

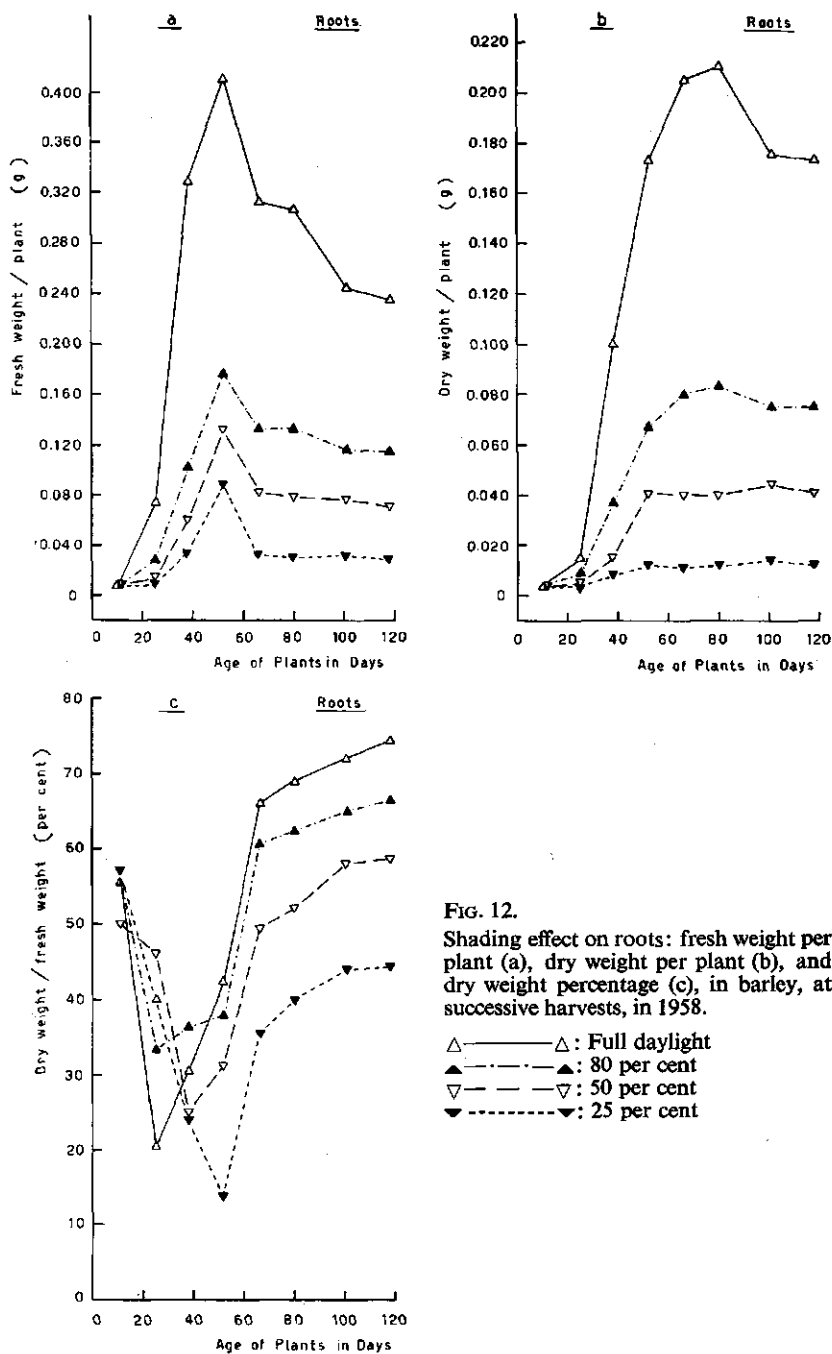| Total			Root/Top Ratio	% Ears/Stems + leaves	% Seeds/Ears
Fresh	Dry	%			
0.148	0.016	10.8	0.3125	0.0	0.0
0.149	0.016	10.7	0.3125	0.0	0.0
0.161	0.017	10.6	0.2353	0.0	0.0
0.148	0.016	10.8	0.2500	0.0	0.0
1.506	0.156	10.4	0.0962	0.0	0.0
1.265	0.117	9.2	0.0769	0.0	0.0
0.881	0.077	8.7	0.0649	0.0	0.0
0.775	0.062	8.0	0.0645	0.0	0.0
2.384	1.363	11.0	0.0734	0.0	0.0
8.107	0.753	9.3	0.0491	0.0	0.0
4.526	0.385	8.5	0.0390	0.0	0.0
2.656	0.205	7.7	0.0390	0.0	0.0
5.748	3.989	15.5	0.0434	0.0	0.0
5.931	2.066	13.0	0.0324	0.0	0.0
4.212	1.372	9.7	0.0299	0.0	0.0
6.415	0.471	7.3	0.0255	0.0	0.0
9.716	6.999	23.6	0.0293	19.4	0.0
8.790	3.903	20.8	0.0205	19.1	0.0
5.215	2.029	13.3	0.0197	11.3	0.0
8.169	0.818	10.1	0.0134	2.1	0.0
0.651	7.640	37.0	0.0275	71.7	75.3
4.690	4.917	33.5	0.0169	57.0	77.5
6.979	2.942	17.3	0.0136	27.6	55.3
8.645	1.032	11.9	0.0116	6.1	0.0
4.665	8.317	56.7	0.0214	109.0	83.7
3.052	5.383	41.2	0.0139	93.5	83.3
4.415	3.839	26.6	0.0115	67.4	75.9
8.922	1.312	14.7	0.0107	9.6	13.0
1.337	8.306	73.3	0.0208	112.1	85.6
8.532	5.409	63.4	0.0139	103.3	84.2
1.198	4.037	36.1	0.0101	72.7	79.8
6.926	1.407	20.3	0.0085	12.3	29.9

FIG. 12.
Shading effect on roots: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼········▼ : 25 per cent

with light intensity, connected with earlier maturity at the higher light intensities. The differences increased with time and were maximal at the end of the season. The reduction in dry matter percentage of roots associated with lower light intensities is to be qualified as a formative effect and is not simply due to higher water absorbing capacity of the roots. MILTHORPE (1945) found that shaded plants of flax as compared with plants grown in the open had a higher water content.

During the early stages, the dry matter percentage of roots decreased up to 25 days in full daylight and 52 days at the 25 per cent daylight, and then increased progressively with time. At the final harvest the dry weight percentage of roots differed from 74 to 44 for full and 25 per cent daylight intensities, respectively.

2. Leaves

a. Fresh weight

Fig. 13a shows that up to July 7 (66 days after planting) the fresh weight of the total leaves (blades) increased with increasing light intensity, due of course to production of more leaves per plant at the higher intensities. In the first period, the differences increased with time and were maximal between the highest and lowest intensities on June 23 (52 days after planting). Later on, the situation was changed in favor of the lower light intensities, owing to extension of the growth period and consequently to production of more new leaves per plant, so that plants at 25 per cent daylight prevailed over those at 50 per cent 101 days after planting.

The maximum fresh weight of the leaves was reached on July 7 (66 days after planting) at the lowest light intensities and two weeks earlier at light intensities above 25 per cent daylight. Especially at the higher light intensities it decreased sharply after the maximum due to earlier ripening. After 101 days from planting the fresh weight of green leaves was still 1.4 g at the lowest intensity while it was zero in full daylight. The zero-value was reached 17 days later at the lowest light intensity which again reflects the effect of shading in prolonging the vegetation period. In this connection, full ripening was reached after 124 days in full daylight and after 140 days at 25 per cent of full daylight.

b. Dry weight

It is evident from fig. 13b that, in general, the higher the light intensity, the higher the total leaf dry weight was. The differences became more pronounced as the plants advanced in growth and were maximal in the period from June 23 to July 21 (52–80 days after sowing). It can be seen that in the period from July 21 (80 days after planting) to August 28, the plants at 50 per cent of full daylight exceeded those at 80 per cent in their total leaf dry weight. The plants at 25 per cent of full daylight always had the lowest values, but at the last harvest succeeded to prevail over the two medium intensities, remaining, however, below those in full daylight.

The total leaf dry weight increased rapidly with age, especially in the unshaded plot. The maximum was attained on July 7 (66 days after sowing) in 100 and 80 per cent of full daylight, on July 21 (two weeks later) in 50 per cent, and on August 11 (5 weeks later) in 25 per cent of full daylight.

Owing to more rapid senescence, absence of photosynthesis in the lower part of the plant, and because a larger fraction of the products of photosynthesis in the leaves passed into the grain after ear emergence especially at higher light
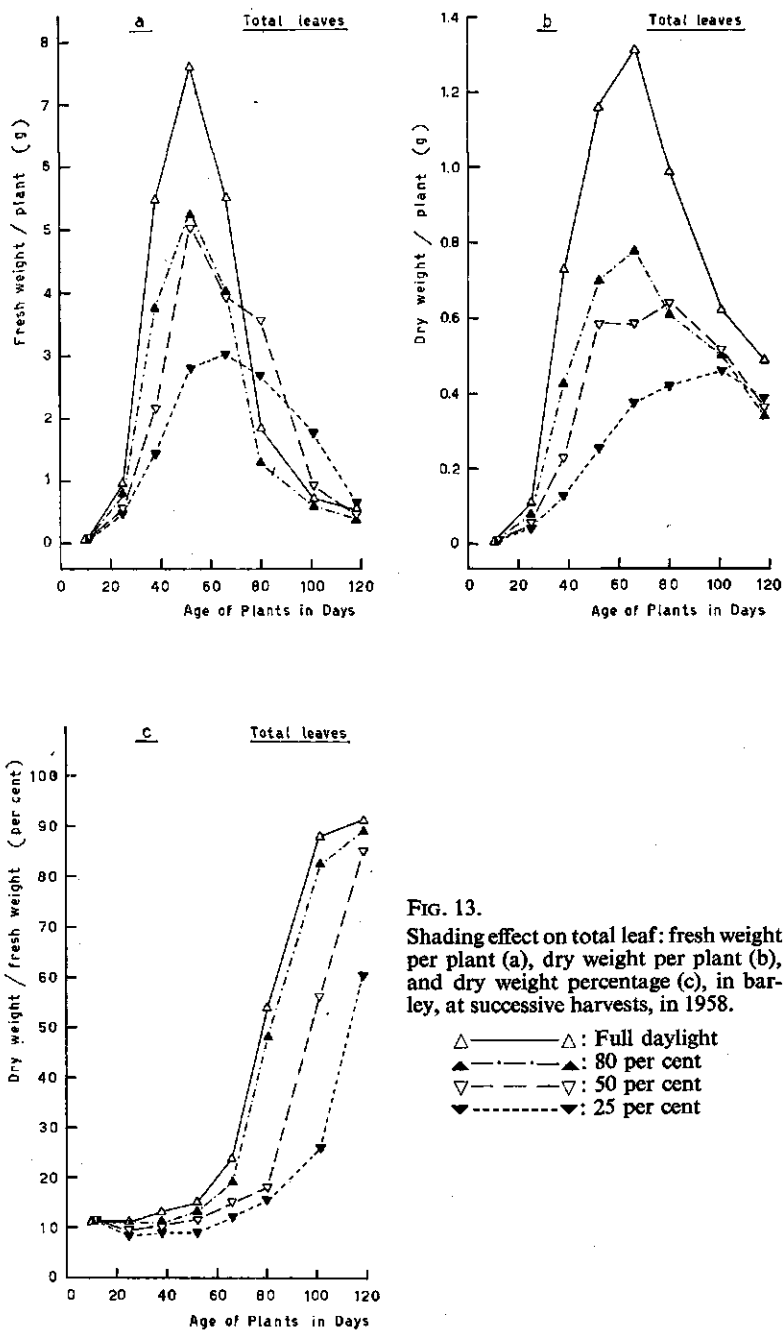
FIG. 13.
Shading effect on total leaf: fresh weight
per plant (a), dry weight per plant (b),
and dry weight percentage (c), in bar-
ley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
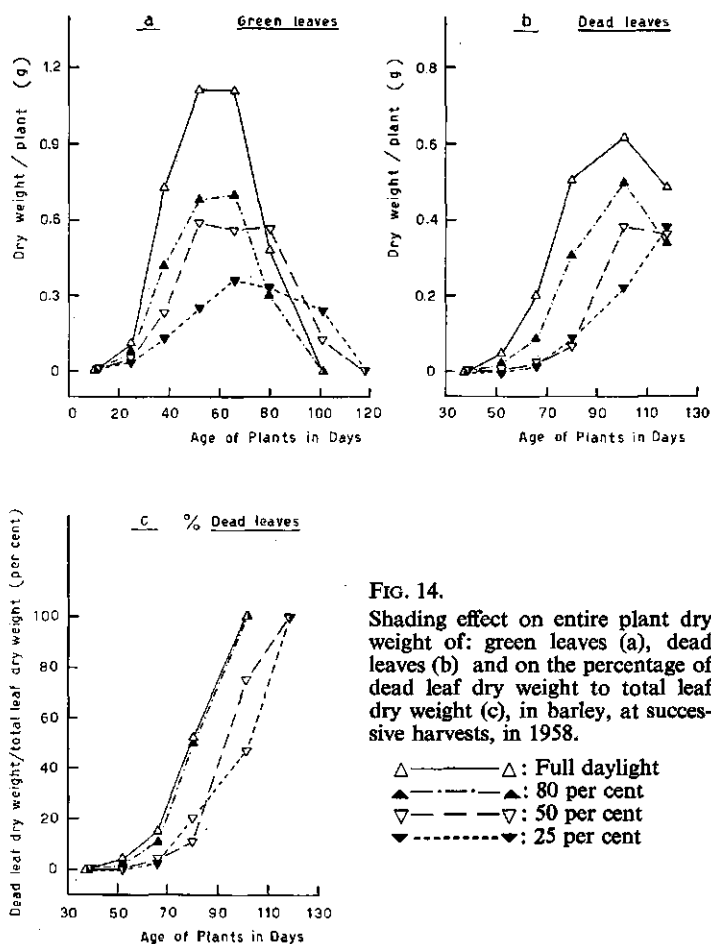▼········▼ : 25 per cent

34

FIG. 14.

Shading effect on entire plant dry weight of: green leaves (a), dead leaves (b) and on the percentage of dead leaf dry weight to total leaf dry weight (c), in barley, at successive harvests, in 1958.

△————————△ : Full daylight
▲—·—·—·—▲ : 80 per cent
▽— — — —▽ : 50 per cent
▼·········▼ : 25 per cent

intensities, the dry weight of leaves, in contrast to the entire plant dry weight, decreased strongly after the maximum. Part of this reduction may be attributed to losses through over-ripening of the leaves.

In this connection, it is of great interest to follow the variations induced by age and by shading in the dry weight of green leaves as well as dead leaves, and in the percentage of dead leaves. Fig. 14a indicates that up to 66 days, the dry weight of green leaves decreased with shading, and the greatest differences were found in the period from June 23 to July 7 (52–66 days after sowing). Later on, owing to extension of the vegetative period in the lower light intensities, the position was changed and, to some extent, the reverse was true. In general, the age trend was similar to that of total leaves. After 101 days from planting the dry weight of green leaves differed from zero in full daylight to 0.243 g in 25 per cent daylight, again indicating earlier maturity at the higher intensities.

Fig. 14b shows that, in general, the dry weight of dead leaves increased with light intensity. The differences increased with time and were maximal in the

period from July 21 to August 11 (80–101 days after sowing). It must be mentioned here that the onset of senescence was greatly affected by shading. It started somewhere in the period from June 9 to June 23 (38–52 days after planting) in full daylight and between June 23 and July 7 (52–66 days after sowing) in 25 per cent daylight.

The dry weight of dead leaves per plant increased progressively with time till a maximum was reached after 101 days in full, 80 and 50 per cent daylight and after 118 days in 25 per cent daylight. During further development, it decreased owing to losses through over-ripening. This was not yet observed at the lowest intensity.

Fig. 14c indicates that the percentage of dead leaves in total leaf dry weight increased with increasing light intensity up to full daylight and also with time, indicating earlier maturity at higher light intensities.

Before proceeding to shading effect on leaf dry weight percentage, a few words may be said here about its effect on leaf thickness. According to our results, with increasing light intensity leaf thickness (on dry weight basis) increased. The differences became more pronounced with time and were maximal at the last harvest still including green leaves. Similar results were obtained by SHIRLEY (1929), MITCHEL (1953) and VERKERK (1955). Leaf thickness was found also to increase progressively with time. At the last harvest under investigation (80 days after planting), the dry weight/28.3 cm² varied from 0.117 g for the highest light intensity to 0.074 g for the lowest one.

c. Dry weight percentage

Fig. 13c shows that the dry weight percentage of total leaves increased with increasing light intensity up to full daylight, the highest differences were obtained after 101 days from planting.

At early stages of growth, the dry matter percentage of the total leaves decreased owing to extension growth, and more sharply so at the lower light intensities. After this reduction the dry matter percentage increased progressively with age. The maximum dry weight percentage of leaves varied from 91.5 in full daylight to 60.5 in 25 per cent intensity, the former leaves then are, in majority, dead. The same trend was observed when the percentage was based on green leaves only. The dry weight percentage of leaves may be considered as another indication of the high light intensity effect on inducing earlier maturity.

3. *Stems and sheaths*

a. Fresh weight

Fig. 15a shows that up to July 7 (66 days after sowing) the fresh weight of stems + sheaths increased with increasing light intensity, and the greatest differences between the highest and lowest light intensities were found by that time. At more advanced age (80 days after seeding), the plants at 50 per cent daylight exceeded those at 80 per cent in their fresh weight of stems + sheaths, but still were below those in the open. Till that time, the plants under 25 per cent daylight always had the lowest values. During further development, the plants at 50 per cent daylight prevailed even over those in full daylight, followed by those at 25 per cent. The failure of the plants at 25 per cent daylight to predominate over those at 50 per cent may be due to the fact that the retarding effect induced by heavy shading was so intense that it masked the benefits of prolonging the vegetation period so that at this harvest the mentioned plants were not yet quite ripe.

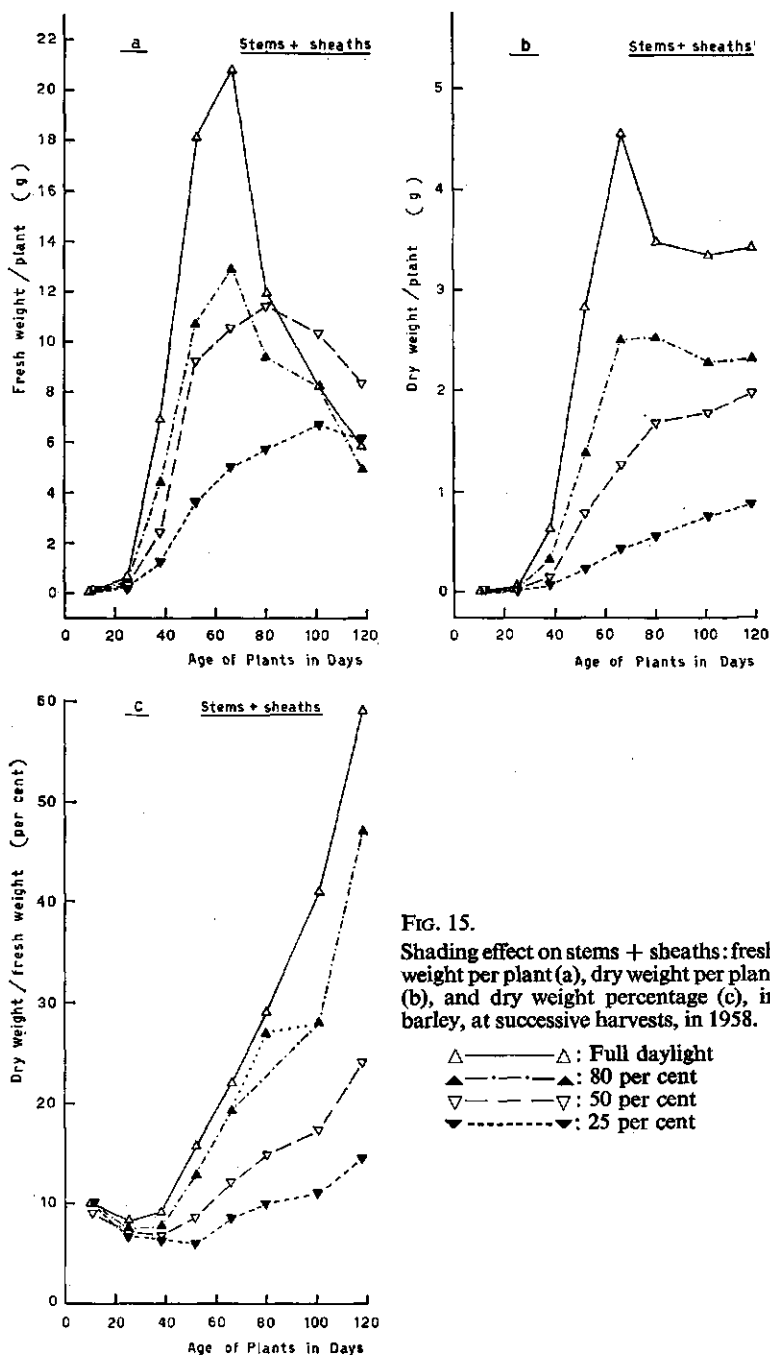36   *Meded. Landbouwhogeschool, Wageningen 59 (5), 1–101 (1959)*

Fig. 15.
Shading effect on stems + sheaths: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼········▼ : 25 per cent

At all light intensities, the fresh weight of stems and sheaths per plant increased rapidly with age – especially at the higher light intensities – till the maximum, and then decreased, and more gradually so at the lower light intensities owing to later ripening. The maximum was reached after 66 days from planting in full daylight and five weeks later in 25 per cent daylight, owing to growth retardation and extension of the vegetative or the vegetation period induced by shading. The maximum fresh weight of stems and sheaths per plant ranged from 21 g in full daylight to 7 g in the lowest light intensity.

b. Dry weight

Fig. 15b indicates that the dry weight of stems + sheaths was greatly depressed by shading. The differences were less marked at the first stages of growth at which obviously the harmful effect of reduced light intensity was not yet very pronounced. Later on, the plants respond greatly to shading and the differences increased to a maximum after 66 days from planting.

At the beginning the plants increased very slowly in their dry weight of stems + sheaths, then increased more rapidly – especially in the unshaded plot – till a maximum. The maximum was reached on July 7 (66 days after planting) in full daylight, and not even seven weeks later in 25 per cent daylight. After this maximum the dry weight of the shoots at the higher light intensities decreased somewhat and rather sharply in full daylight. This is because of earlier maturity and transfer to the ears of all the assimilates produced in the shoots during this period. If any was retained in the stems it was not sufficient to compensate losses by respiration or export of dry matter produced previously. In part, the observed reduction may be due also to sampling variation. The maximum dry weight of stems + sheaths per plant in full daylight was five times that at 25 per cent of daylight, being 4.5 g and 0.9 g, respectively.

c. Dry weight percentage

Fig. 15c shows that the dry weight percentage of stems + sheaths increased with increasing light intensity up to full daylight. The differences increased with time and were maximal at the end of the season.

During the initial phase of development, the dry matter percentage of stems + sheaths decreased owing to extension growth, and more sharply so, and for a longer period, at the lower light intensities. After this fall, it increased progressively as the plants advanced in growth; the values for the highest light intensity always were highest. The maximum dry weight percentage of stems and sheaths in full daylight was about four times that at the lowest light intensity, namely 60 and 15 per cent, respectively.

The data on characteristics of stems and sheaths discussed furnish another indication of the effect of shading on prolonging the vegetative period as well as the vegetation season. In addition, variations induced by shading were more pronounced in stems than in leaves, indicating that reducing light intensity favors production of leaves at the expense of stems. It is evident from our results that plants grown under shade tended to be leafy and watery as compared with those grown at an open habitat.

4. *Leaves and stems*

If stems and leaves were taken into account together, there was a tendency for their fresh weight as well as dry weight and dry weight percentage to follow closely those of stems in their responses to shade and to age. This is not sur-

prising since stems during most of the season represent the greatest fraction of the plant. The same trend was observed in 1957, with the only difference that shading depressed the fresh weight of stems and leaves during the entire season.

5. *Ears*

a. Fresh weight
Fig. 16a shows that the fresh weight of ears increased with increasing light intensity up to full daylight, and the greatest differences were found after 80 days from planting.

At all light intensities, the fresh weight of ears increased rapidly as the plants developed till a maximum was reached on July 21 (80 days after sowing) in full daylight and three weeks later in the other light intensities. The values for the open plots always were the highest. The maximum fresh weight of ears per plant ranged from 6.9 g in full daylight to 0.4 g (1/17 of the highest intensity) in the lowest light intensity. This indicates that reduced light intensities are unfavorable for ear production.

b. Dry weight
From fig. 16b it is evident that decreased light intensities suppressed dry weight of ears. The differences increased progressively with time and were maximal at the end of the season, indicating that the harmful effect of reduced light intensity became very marked by that time. COMBES (1910) on several plant species obtained maximum dry weight of fruit in full daylight.

At all light intensities, dry weight of ears increased rapidly with age – especially at the higher light intensities – till the maximum was reached at the end of the season. The maximum dry weight of ears varied from 4.4 g in full daylight to 0.2 g in 25 per cent of daylight. This confirms that heavy shading is unfavorable for ear production.

c. Dry weight percentage
Fig. 16c indicates that the dry weight percentage of ears increased with increasing light intensity up to full daylight. The differences increased with time and were maximal in the period from August 11 to 28 (101–118 days after sowing).

In contrast to roots, leaves, and stems the dry matter percentage of ears increased progressively with time, without any drop at the beginning. Due to earlier maturity, the dry weight percentage of ears at the higher light intensities increased more rapidly. At all light intensities, the maximum was reached at the end of the season, and ranged from 89 to 53 per cent for the highest and lowest light intensities, respectively.

The same trend for the fresh weight as well as for the dry weight and for the dry weight percentage of ears was found in 1957.

6. *Seeds*

If seeds only were taken into consideration, the same trend was observed (fig. 16d, e and f). The fresh weight of seeds increased with increasing light intensity, the differences changed only little with time. Statistical analyses at the last harvest showed that the differences induced by shading were highly significant. Similar results were obtained by GARNER and ALLARD (1920) on soybean plants.
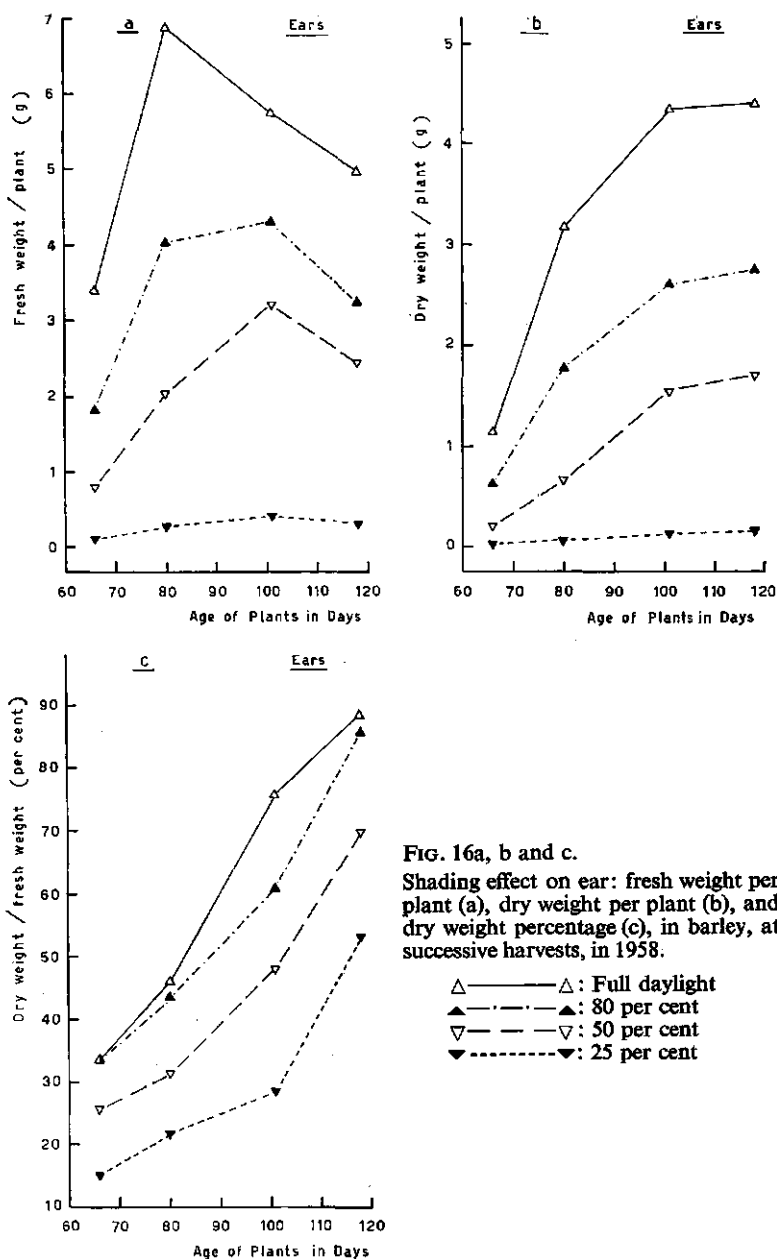
FIG. 16a, b and c.

Shading effect on ear: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.
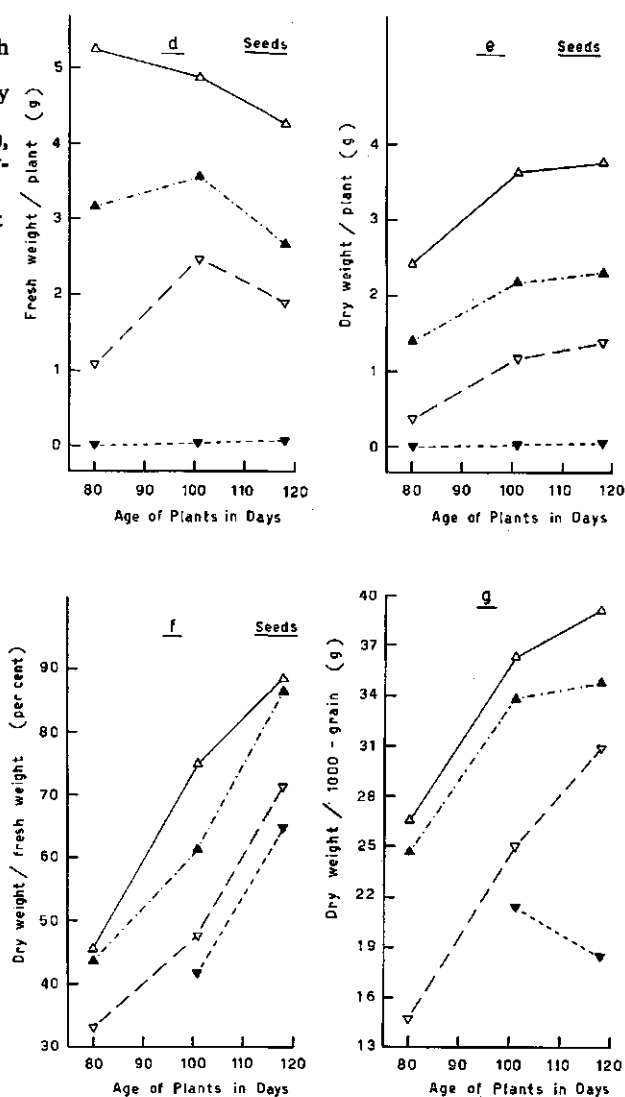
△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼········▼ : 25 per cent

FIG. 16d, e, f and g.

Shading effect on seed: fresh weight per plant (d), dry weight per plant (e), and dry weight percentage (f); and on 1000-grain dry weight (g), in barley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼·········▼ : 25 per cent

The time trend was not the same at all light intensities. At full daylight, the fresh weight of seeds already decreased from the first harvest at which there was any detectable number of mature seeds (80 days after planting), indicating earlier ripening. At the medium light intensities, it increased rapidly with time – especially at 50 per cent daylight (as a result of ear emergence retardation and of formation of more new seeds with higher water content) – till a maximum was attained on August 11 (101 days after planting). After the maximum, the fresh weight of the seeds decreased more sharply at 80 per cent daylight due to earlier maturity. At the lowest intensity, it increased very slowly with time and the maximum was reached at the last harvest under investigation, indicating

extension of the growing season and retarded maturity. Values ranged from 4.3 g per plant for full daylight to 0.1 g per plant for 25 per cent daylight as obtained at the end of the season, in 1958.

Dry weight as well as dry weight percentage of seeds were found to follow closely the general rule; increase with increasing light intensity and with time. The differences in seed dry weight induced by shading were statistically analysed at the last harvest and were found to be highly significant. Dry weight values ranging from zero for the lowest light intensity to 2.4 g per plant for the highest light intensity and from 0.05 g for the former to 3.80 g per plant for the latter were obtained in 1958 after 80 days and after 118 days from planting, respectively. The dry matter percentage varied from 42 for the lowest light intensity to 75 for the highest one, and from 65 for the former to 88 for the latter after 101 days and after 118 days from planting, respectively.

These results are in general accordance with those obtained in 1957 and confirm earlier suppositions and conclusions that heavy shading is unfavorable for seed or ear production.

1000-grain dry weight

With light intensity reduced below full daylight, the 1000-grain dry weight was greatly depressed (fig. 16g). It has been established that, in general, shading brings about reduction in level and in translocation of assimilates out of the leaves and stems. Thus, it appears that the depression in the 1000-grain dry weight associated with lower light intensities may be attributed, in part, to less photosynthesis in leaves and consequently to less accumulation of assimilates in seeds. Moreover, it may be due to less photosynthesis in ears, since ear length was greatly depressed by shading. In this connection, ARCHBOLD (1938), WATSON and NORMAN (1939) and others reported that some of the dry matter in barley grain was formed by photosynthesis in the ears themselves and some in the parts of leaves and stems that still remain green. In general, the differences induced by shading increased with age and were maximal at the end of the season.

At all light intensities above 25 per cent daylight, the 1000-grain dry weight increased progressively as the plants advanced towards maturity owing to more accumulation of assimilates in seeds. On the contrary, the 1000-grain dry weight at the lowest intensity decreased with time at the harvests taken. This may be due to the fact that the dry matter accumulated through photosynthesis was insufficient for seed development and consequently smaller seeds were formed as the plants advanced in growth and produced more seeds. By that time, the detrimental effect of shading became more pronounced. At the last harvest, the 1000-grain dry weight varied from 39.1 g for the highest light intensity to 18.4 g for the lowest one.

7. *Tops*

Since growth in weight of leaves as well as of stems and of ears was greatly affected by shading, one would expect the same trend in tops which are composed of leaves, stems and ears.

a. Fresh weight

Fig. 17a shows that, in general, fresh weight of tops decreased with reduced light intensity. The differences increased with age and were maximal after 66 days from planting. Statistical analyses at the final harvest showed that the

42

differences were highly significant. ROSÉ (1913) and POP (1926) also, on several plant species, obtained maximum vigour of growth in full daylight.

During the first stages of growth, fresh weight of tops increased slowly, especially under heavy shading. At more advanced age, it increased rapidly – especially at the higher light intensities – till the maximum, and then decreased sharply owing to maturity. Maximum fresh weight of tops was reached later by shading, indicating extension of the vegetation period. It was attained on July 7 (66 days after planting) in full and 80 per cent daylight intensities and five weeks later in 25 per cent daylight. The maximum fresh weight of tops per plant varied from 30.0 g for the highest light intensity to 8.5 g for the lowest one.

Similar results were obtained in 1957.

b. Dry weight

Fig. 17b shows that dry weight of tops increased with increasing light intensity up to full daylight. The differences increased with time and were maximal at late stages of growth at which the harmful effect of shading was very marked. These differences were statistically analysed at the last harvest and were found to be highly significant.

The same trend was observed in 1957. These results confirm those obtained by GARNER and ALLARD (1920), MAXIMOV and LEBEDINCEV (1923), POP (1926), ZILLICH (1926), CLEMENTS et al. (1929), SHIRLEY (1929), MITCHELL and ROSENDAHL (1939), MILTHORPE (1945), and BLACKMAN and RUTTER (1948, 1950).

As in the entire plant, top dry weight similarly increased slowly at the beginning, then increased more rapidly, especially in the unshaded plot. The increase in dry weight came to a standstill at a moment which differed according to the treatment, viz., after 101 days from planting in full and 80 per cent daylight intensities, and only at the end of the growing season in 50 and 25 per cent daylight. At the last harvest, the dry weight of tops per plant differed from 8.1 g at the highest light intensity to 1.4 g at the lowest one.

c. Dry weight percentage

Fig. 17c shows that the dry weight percentage of tops was greatly depressed by shading, and the greatest differences were obtained towards the end of the season.

Similar results were obtained in 1957. These results are in general agreement with those of LUBIMENKO (1908), SHIRLEY (1929), and MILTHORPE (1945).

At early stages of growth, dry matter percentage of tops decreased, owing to extension growth, and more sharply so, and for a longer period, at low light intensities (a difference of 5 weeks between the extremes was observed). After this fall, the percentage increased progressively with time – and more rapidly so at the higher light intensities – till a maximum was attained at the end of the season. The maximum dry weight percentage of tops ranged from 20 in the lowest light intensity to 73 in the highest one.

C. Relative root and top growth

In comparing different studies on growth of individual plant organs, the data on the effect of various factors on growth expressed as absolute weights often seem to contradict each other. However, in several cases this contradiction disappears if growth of each of the plant organs is expressed as a percentage of the entire plant weight or as a ratio (root/top ratio). This expression is of more than
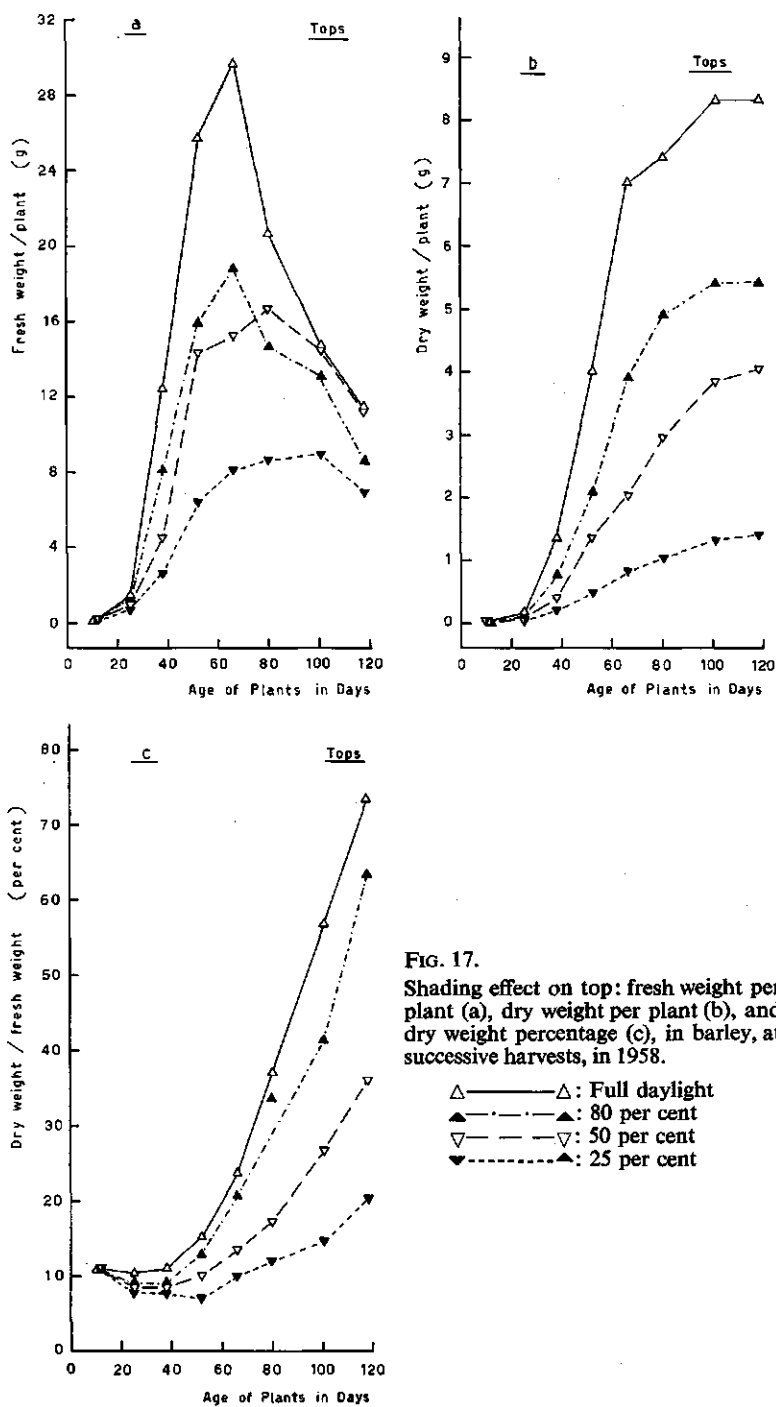
FIG. 17.
Shading effect on top: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼·········▲ : 25 per cent

merely theoretical interest and may be of considerable practical importance to any one interested in growing plants.

Table 6 and fig. 18 represent shading effects on growth of roots, leaves, stems and ears expressed as percentages of the total dry weight of the plant, at successive harvests in 1958. During all harvests, the percentage of roots, in accordance with the absolute weights, increased with increasing light intensity up to full daylight, while on the contrary, the percentage of tops – in contrast to the actual weights – increased with shading, indicating that reducing light intensity favors relative shoot growth at the expense of root growth. The percentage of leaves, in contrast to the absolute values, increased with shading. On the other

TABEL 6. Shading effect on root and top growth expressed as a percentage of the total dry weight of the plant, in barley, at successive harvests, in 1958.

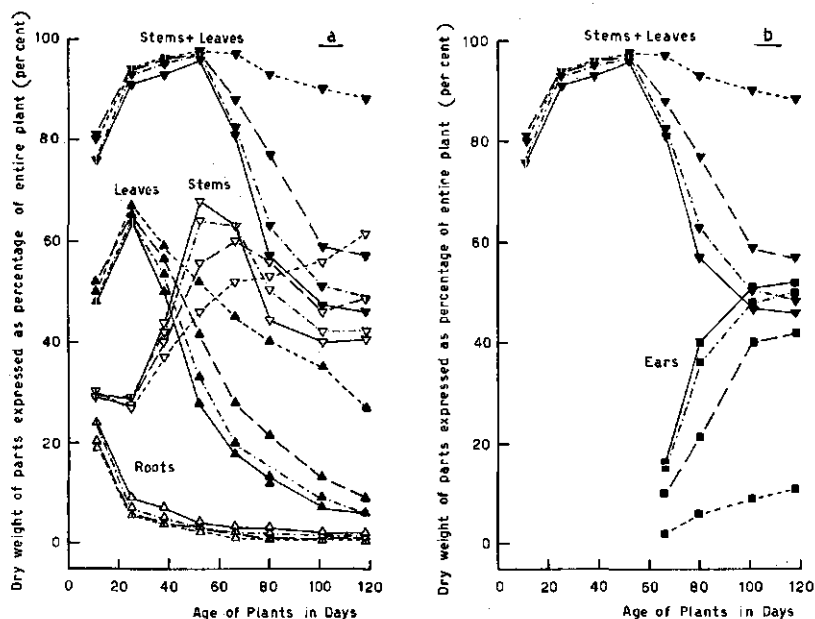| Shading treatment (% daylight)	Age of plants in days	Roots	Tops							
			Stems + Leaves				Ears			Total
			Leaves (Blades)		Stems + Sheaths	Total	Seeds	Total		
			Green	Total						
100	11	23.8	47.6	47.6	28.6	76.2	0.0	0.0		76.2
80		23.8	47.6	47.6	28.6	76.2	0.0	0.0		76.2
50		19.0	52.4	52.4	28.6	81.0	0.0	0.0		81.0
25		20.0	50.0	50.0	30.0	80.0	0.0	0.0		80.0
100	25	8.8	63.7	63.7	27.5	91.2	0.0	0.0		91.2
80		7.1	64.3	64.3	28.6	92.9	0.0	0.0		92.9
50		6.1	64.6	64.6	29.3	93.9	0.0	0.0		93.9
25		6.1	66.7	66.7	27.2	93.9	0.0	0.0		93.9
100	38	6.8	49.8	49.8	43.4	93.2	.00	0.0		93.2
80		4.7	53.5	53.5	41.8	95.3	0.0	0.0		95.3
50		3.8	56.5	56.5	39.7	96.2	0.0	0.0		96.2
25		3.8	59.1	59.1	37.1	96.2	0.0	0.0		96.2
100	52	4.2	26.7	27.8	68.0	95.8	0.0	0.0		95.8
80		3.2	32.0	32.8	64.0	96.8	0.0	0.0		96.8
50		2.9	41.4	41.6	55.5	97.1	0.0	0.0		97.1
25		2.5	51.8	51.8	45.7	97.5	0.0	0.0		97.5
100	66	2.8	15.4	18.2	63.2	81.4	0.0	15.8		97.2
80		2.0	17.5	19.6	62.9	82.5	0.0	15.5		98.0
50		1.9	27.0	28.1	60.0	88.1	0.0	10.0		98.1
25		1.3	43.3	44.7	51.9	96.6	0.0	2.1		98.7
100	80	2.7	6.1	12.6	44.4	57.0	30.3	40.3		97.3
80		1.7	6.1	12.2	50.4	62.6	27.7	35.7		98.3
50		1.3	19.1	21.4	55.9	77.3	11.8	21.4		98.7
25		1.1	31.8	39.8	53.4	93.2	0.0	5.7		98.9
100	101	2.1	0.0	7.3	39.6	46.9	42.7	51.0		97.9
80		1.4	0.0	9.2	41.8	51.0	39.7	47.6		98.6
50		1.2	3.3	13.2	45.8	59.0	30.2	39.8		98.8
25		1.1	18.3	34.7	55.6	90.3	1.1	8.6		98.9
100	118	2.0	0.0	5.7	40.5	46.2	44.3	51.8		98.0
80		1.4	0.0	6.1	42.4	48.5	42.2	50.1		98.6
50		1.1	0.0	8.8	48.5	57.3	33.2	41.6		98.9
25		0.8	0.0	26.9	61.5	88.4	3.2	10.8		99.2

Fig. 18. Shading effect on root, leaf, stem and ear growth expressed as a percentage of the total dry weight of the plant, in barley, at successive harvests, in 1958.

——————: Full daylight   —·—·—: 80 per cent
— — —: 50 per cent   ---------: 25 per cent

△: roots   ▲: leaves   ▽: stems   ▼: stems and leaves   ■: ears

hand, the percentage of stems, during first stages of growth up to 66 days after planting increased with increasing light intensity, but at more advanced age the position was changed and the lower the light intensity, the higher the percentage of stems was (actual dry weight of stems always decreased with shading). This may be due, in part, to extension of either the vegetative or the vegetation period under shade and to production of more ears at the higher light intensities by that time. The percentage of stems and leaves together increased with shading during the entire growing season. The percentage of ears as well as that of seeds, in general agreement with the absolute values, followed the roots in their responses to shading. Also, the percentage of seeds to total ear dry weight was found to increase with light intensity and with time (fig. 19c), indicating that at higher light intensities ears are more efficient in producing seeds. Values ranging from 87.5 per cent in full daylight to 30.0 per cent in 25 per cent daylight were obtained at the last harvest in 1958.

The previous findings confirm that reducing light intensity favors top growth, and ear and seed production contrary to root growth.

Another interesting feature is the shift in the percentage of the different organs with time. For roots, the percentage, being maximal at the beginning, decreased consistently with time. The values for full daylight intensity were always highest. On the contrary, the percentage of tops increased progressively with time, and the values for full daylight were always lowest. For leaves, the percentage increased with age to a maximum after 25 days from sowing, there-

46

after decreased to a minimum towards the end of the season. The values for the lowest intensity were always highest. This reduction in the percentage of leaves after the maximum is due primarily to stem development at the early stages and to ear production at more advanced age. For stems, the percentage nearly remained constant in the period from May 13 to 26 (11–25 days after planting) at which time the percentage of leaves was maximal. The plants, obviously, at first builds its food factory (leaves) while later on the products of this factory are converted to a large degree into other useful structures (stems and ears). As the plants developed, the percentage of stems increased with time up to a maximum and then decreased (except at the lowest light intensity) mainly owing to the development of ears. The maximum percentage of stems was reached after 52 days from planting in full daylight and not even after 118 days from sowing in 25 per cent daylight. For stems and leaves together, the percentage increased to a maximum after 52 days from sowing, then decreased, and more gradually so under shade. A difference of 42.2 per cent was found, at the last harvest, between the highest and lowest intensities in favor of the latter. The percentage of ears as well as that of seeds increased progressively with time, and was maximal at the end of the season. At the last harvest, the percentage of ears varied from 51.8 per cent for the highest light intensity to 10.8 per cent for the lowest one, while that of seeds differed from 44.3 per cent in full daylight to 3.2 per cent in 25 per cent daylight.

Similar results were obtained in 1957.

Fig. 19a indicates that the root-top ratio decreased with shading and with time, indicating that plants exposed to conditions of high light intensity almost invariably have relatively larger roots (in relation to entire plant weight), and commonly have actually larger root systems also, than similar plants grown under low light intensities.

The same trend was observed in 1957. These results confirm those of LUBI-MENKO (1908), MAXIMOV and LEBEDINCEV (1923), SHIRLEY (1929), MITCHELL and ROSENDAHL (1939) and KHALIL (1956).

A point of special interest is the efficiency of stems and leaves in producing ears (ear dry weight/stem and leaf dry weight in per cent) as affected by shading. Fig. 19b shows that the percentage of ears/stems and leaves was greatly depressed by shading, indicating that the lower light intensities are unfavorable for ear production. The differences increased with time and were maximal in the period from August 11 to 28 (101–118 days after planting). At the last harvest the percentage varied from 112 in full daylight to only 12 in 25 per cent daylight.

The efficiency of the shoots in producing ears increased rapidly with age – especially at the higher light intensities – till the maximum was reached at the end of the season.

Similar results were obtained in 1957.

D. C/F ratio

The C/F ratio, the ratio of non-photosynthetic system (roots, stems, reproductive organs and dead leaves) to photosynthetic one (green leaf blades), may be used to determine the extent of the dry matter losses through respiration which seems to play an important rôle.

Table 7 gives the C/F ratio (on dry weight basis) as affected by shading, in successive harvests, in 1958. The ratio increased with light intensity, so that one
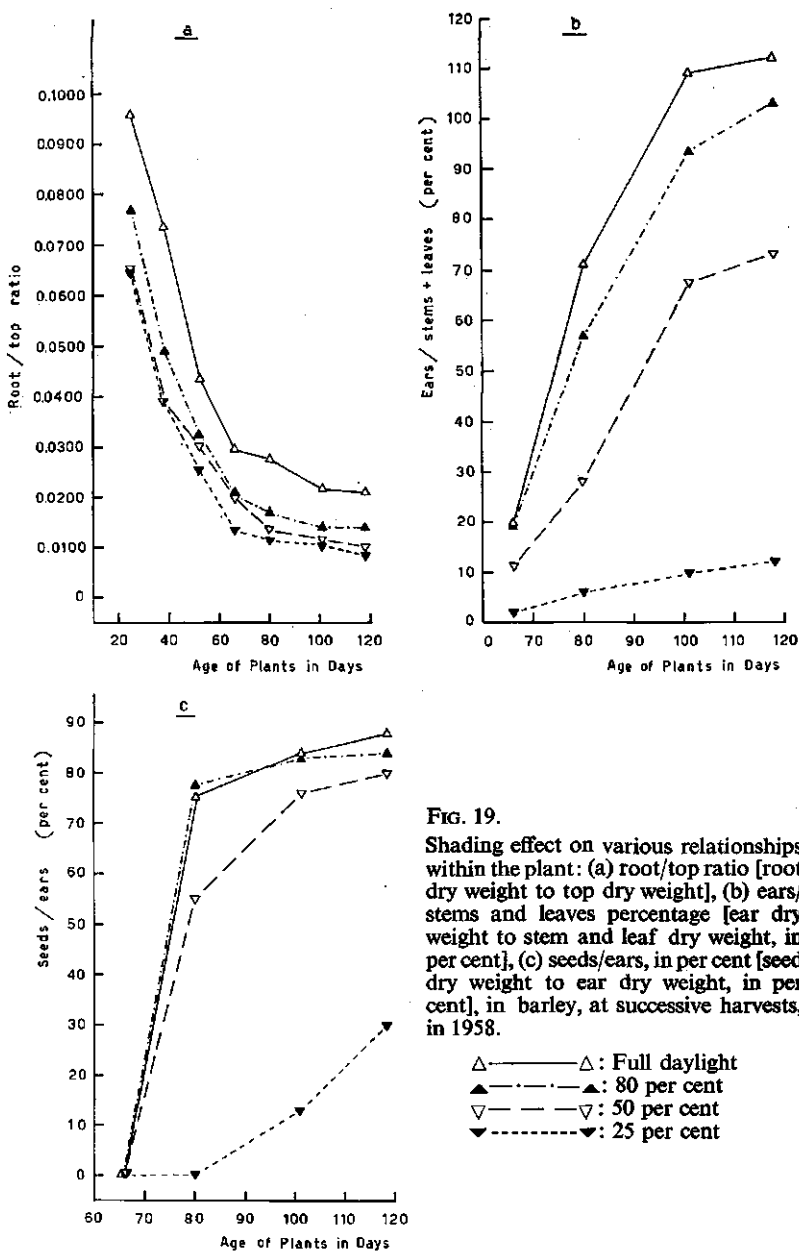
FIG. 19.
Shading effect on various relationships within the plant: (a) root/top ratio [root dry weight to top dry weight], (b) ears/stems and leaves percentage [ear dry weight to stem and leaf dry weight, in per cent], (c) seeds/ears, in per cent [seed dry weight to ear dry weight, in per cent], in barley, at successive harvests, in 1958.

△————————△ : Full daylight
▲—·—·—·—▲ : 80 per cent
▽— — — —▽ : 50 per cent
▼·········▼ : 25 per cent

may expect that the losses of dry matter by respiration will increase in the same way. But this does not mean that the balance between photosynthesis and respiration is less favourable at the higher light intensities. The differences induced by shading increased with time and were maximal at late stages of growth.

At all light intensities, the C/F ratio increased progressively with age, and

TABLE 7. Shading effect on the C/F ratio, the ratio of non-photosynthetic system (roots, stems, dead leaves, and reproductive organs) to the photosynthetic system (leaves), in barley, at successive harvests, in 1958.

Shading treatment (% daylight)	Age of plants in days				
	25	38	52	66	80
100	0.57	1.01	2.74	5.50	15.50
80	0.56	0.87	2.12	4.72	15.45
50	0.55	0.77	1.42	2.71	4.23
25	0.50	0.69	0.93	1.31	2.14

more rapidly so at the higher light intensities till the maximum was reached at the last harvest. C/F values ranging from 15.50 in full daylight to 2.14 in 25 per cent daylight were obtained after 80 days, in 1958.

E. Daily growth rate

Table 8 and fig. 20 indicate that up to the period from June 23 to July 6 (52–66 days after planting), the daily growth rate increased with increasing light intensity, and the greatest differences between the highest and lowest intensities were found by that time. In the period from July 7 to 20 (66–80 days after sowing) the daily growth rate in full daylight, owing to earlier maturity, fell off rapidly below that at 80 and 50 per cent daylight, while that at 25 per cent, because of more retardation of growth, still remained the lowest. At more advanced age, in the period from July 21 to August 10 (80–101 days after sowing), the highest daily growth rate was obtained under 50 per cent daylight, while the lowest rate was still at 25 per cent daylight. In the last period under investigation, the plants at 25 per cent daylight exceeded those at full and 80 per cent daylight. The plants in full daylight showed a decrease not only in their gain in dry matter but also in their total dry weight, indicating partial decay, associated with ripening.

The daily growth rate increased progressively with age till a maximum was reached in the period from June 23 to July 6 (52 to 66 days after seeding) at 100, 80, and 25 per cent daylight, and in that from June 9 to July 20 (38 to 80 days after sowing) at 50 per cent daylight, then decreased to a minimum towards the end of the season. The maximum dry weight increase varied from

TABLE 8. Shading effect on mean daily growth rate (dry matter increase in mg/plant/day), in barley, at successive intervals, in 1958.

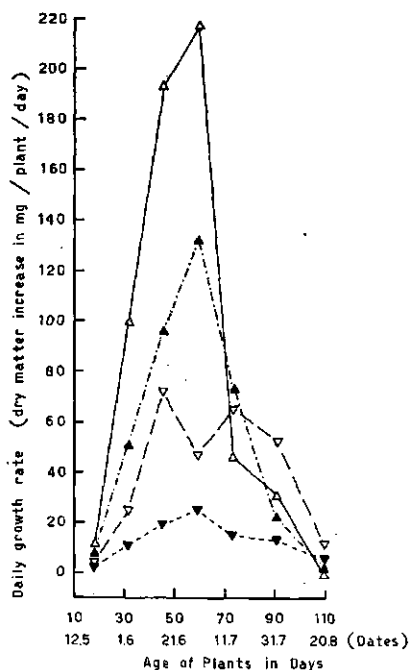| Growing period	Shading treatment (% daylight)			
	100	80	50	25
May 13–May 26	10.7	7.5	4.4	3.3
May 27–June 8	99.4	51.1	24.5	11.3
June 9–June 22	192.8	95.9	72.4	19.3
June 23–July 6	217.3	132.1	46.9	24.7
July 7–July 20	46.1	72.6	65.2	15.4
July 21–Aug 10	30.6	21.6	52.4	13.4
Aug. 11–Aug 27	-0.8	1.5	11.5	5.5

FIG. 20. Shading effect on the daily growth rate (dry matter increase in mg per plant per day), in barley, at successive intervals, in 1958.

△————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼········▼ : 25 per cent

217.3 to 24.7 mg/plant/day for the highest and lowest light intensities, respectively. The daily growth rate curves in relation to time tended to be more flattened at reduced light intensities, so that the change with age was less pronounced at the lower light intensities. This is another indication of the shading effect in retarding growth and prolonging the vegetation period.

With few exceptions, the same trend was observed in 1957.

F. Growth in leaf area

Fig. 21 indicates that up to July 7 (66 days after planting), the green leaf area per plant increased with increasing light intensity, and the greatest differences between the highest and the lowest intensities were found at that time. The maximum leaf area, reached after 66 days from planting was 280 cm²/plant in full daylight, and 146 cm²/plant at 25 per cent daylight. It was attained by June 23 (two weeks earlier) at the medium intensities. These results are in accordance with those of GREGORY (1921), CLEMENTS et al. (1929), MILTHORPE (1945) and VERKERK (1955). From the 6th harvest up to the end of the season the position was converted and, due to later maturity induced by shading, the green leaf area increased as the light intensity decreased. These findings are in general agreement with those of SHIRLEY (1929), BLACKMAN and RUTTER (1948, 1950), and MONSELISE (1951).

The leaf area increased to a maximum more rapidly at the higher light intensities, and when dropping, it decreased more gradually at the lower light intensities. This may be considered as another indication of the shading effect on the extension of the vegetation period. BOONSTRA (1929, 1937) and WATSON (1952) stated that leaf area per plant or per unit area (leaf area index) increased with time, up to a maximum, and then decreased.

G. Leaf-area ratio

Fig. 22 shows that, in general, the leaf-area ratio increased with decreasing light intensity. With the exceptional rise observed in the second harvest, the leaf-area ratio in all cases decreased with age. Thus, the ratio increased from 208 in the first harvest to 273 in the second one under full daylight intensity, and from 233 to 502 in the heaviest shading. For unexplicable reasons, the tendency of the leaf-area ratio to decrease with age was masked at the early stages.
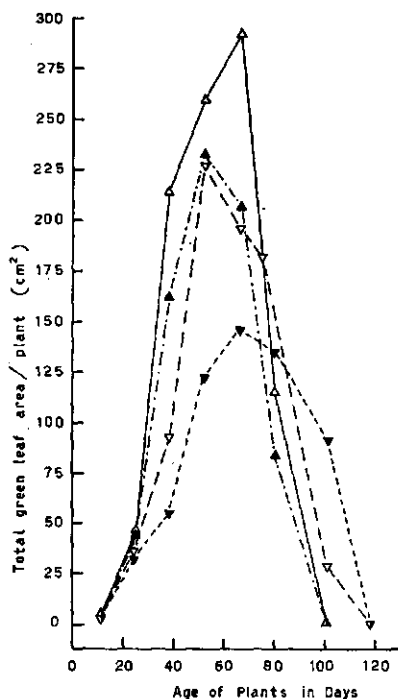
FIG. 21.

Shading effect on total green leaf area per plant, in barley, at successive harvests, in 1958.

△————————△ : Full daylight
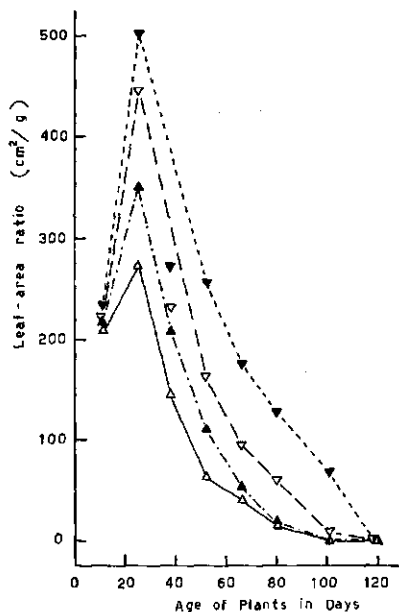▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼·········▼ : 25 per cent

FIG. 22.

Shading effect on leaf-area ratio (total green leaf area/entire plant dry weight), in barley, at successive harvests, in 1958.

△————————△ : Full daylight
▲—·—·—▲ : 80 per cent
▽— — —▽ : 50 per cent
▼·········▼ : 25 per cent

BLACKMAN and WILSON (1951) pointed out that this may be due to the fact that the plants, having received full daylight prior to placing the screens, were not yet completely adapted to shading since at lower light intensities the ratios invariably increased between the 1st and 2nd periods. It appears that this explanation is not the only one since the ratio increased also in full daylight. BLACKMAN and WILSON (1951) emphasized that nutrient deficiency may have been a factor in slowing down the rate of adaptation, or in other words, is responsible for such increase in the ratio (regardless the intensity).

Whatever may be from these detailed considerations, we would like to point out that the leaf-area ratio curve primarily only expresses the relations between leaf area and dry weight formed at each harvest. The curve thus shows that between the first and second period the plant mainly produces leaves, it converts most of its acquired dry matter into leaves. During this phase the plant seems to prepare itself for the big rise in dry weight starting after the 2nd period. After the second harvest, the amount of leaves still strongly increases (cf. fig. 21), together with a still more pronounced increase in dry weight. Fig. 22 expresses the

relation between both, indicating that, gradually, the amount of other tissues becomes prevailing. Only after about 80 days the amount of leaves actually decreases.

II. SHADING AND EFFICIENCY OF SOLAR ENERGY CONVERSION

The effect of shading on the efficiency of solar energy conversion, in barley, measured during the growing season 1958, at successive intervals, is given in fig. 23. It is evident that the efficiency, in general, tended to be low at the early stages of growth where the plants were still small and the photosynthetic apparatus was not yet well developed. As the plants advanced in growth the efficiency increased rapidly. During a period of about 6 weeks, from May 27 to July 6 (25 to 65 days after sowing), the plants in the open showed the highest efficiency of solar energy conversion. It attained a maximum of 13.6 per cent in full daylight in the period from June 23 to July 6 (52 days to 65 days after planting). After this maximum, the efficiency dropped and reached a minimum at the end of the growing season. The figures tended to be more flattened at lower light intensities, indicating growth cycle prolongation. This time trend was also observed in 1957.

In certain periods, the efficiency increased with decreasing light intensity. This was observed only in the first period (11–24 days after seeding) and at late stages of growth, from 66 days up to maturity of the plants. Conversely, the efficiency per unit area really covered by plants during the period from May 27 to July 6 (25–65 days after sowing) increased with increasing light intensity. It appears, to some extent, that daylight was in great excess of plant requirements during the early stages of growth and at the late ones. At the early stages, the plants, being still very young, form small and thin leaves with a low absorbing capacity (transmission is more than absorption [SAUBERER, 1937]) and have produced only one or two layers of leaves. Consequently, all the leaves are exposed to full daylight intensity, and fail to trap most of the incident light and thus profit very little. At this stage, decreased light intensity resulted in increased efficiency of solar energy conversion.

As the plants develop, more tillers and thick leaves are formed, securing a well developed apparatus with many leaf layers (due to growth in height). Thus, the plants grown under full daylight conditions, possessing a greater photosynthetic system than the shade plants, may utilize the energy more efficiently. It seems that during this period the plants under open-air conditions reached a certain degree of self-shading, more favorable for the balance between photosynthesis and respiration, and for maximum efficiency. Lowering the light intensity may cause a reduction in the efficiency of solar energy conversion because reduced light intensity, increased plant height or leaf area, results in an increase in the fraction of the surface that receives light of very low intensity, near to or below the compensation point.

Besides this, COMBES (1910) found that the optimum light intensity for the production of dry matter in plants increased with the age of the plants. In addition, TAKEDA and MARUTA (1956) pointed out that, in early stages of growth, light required for maximum photosynthesis was relatively low, then increased gradually until full tiller stage, when practically all incident light was absorbed. RICHARDSON (1957) stated that, in general, maximum assimilation level and
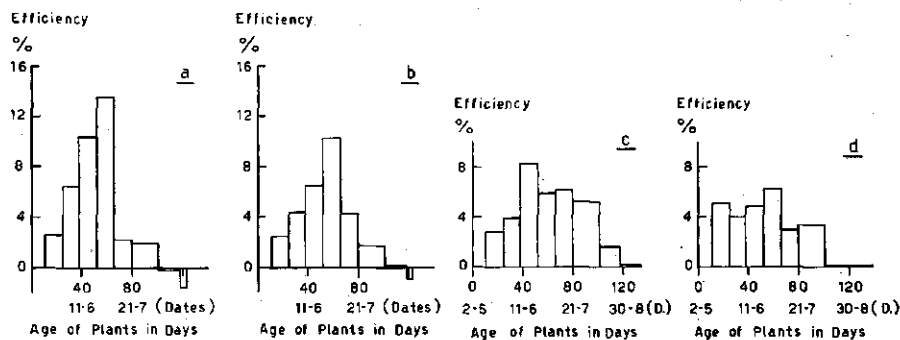
FIG. 23. Shading effect on the efficiency of solar energy conversion during growth (in per cent), in barley, at successive intervals, in 1958.

a: Full daylight   b: 80 per cent   c: 50 per cent   d: 25 per cent

saturation light intensity increased with physiological age of plant material up to full leaf expansion, and then fell off during senescence.

At late stages of growth, the plants grown under full daylight profit little from the light, owing to senescence, while those under shade, owing to growth cycle prolongation, then exhibited the highest efficiency values. Thus, at a light intensity of 50 per cent, the efficiency increased. But, at only 25 per cent it decreased again, maybe due to a detrimental effect of heavy shading which increased with time. Also the excess (photosynthesis–respiration) is smaller at low light intensity (cf. p. 54). The maximum efficiency was found to be 13.6, 10.3, 8.3 and 6.2 per cent for 100, 80, 50 and 25 per cent of daylight intensity. With the exception of the 50 per cent series, the maximum was reached when the plants were 52 to 65 days old.

The average efficiency during the entire growing season increased with increasing light intensity up to full daylight. Statistical analysis showed that the differences induced by shading in the average efficiency as well as in the final yield per cm² of entire plant dry weight were highly significant. The efficiency values ranged from 2.9 per cent for full daylight to 1.4 per cent for the 25 per cent daylight. And since seeds represent 44.3 per cent of the entire plant dry weight in full daylight and only 3.2 per cent in the 25 per cent daylight intensity, the practical efficiency of plants as converters of solar energy ranged from 1.27 per cent for the former to 0.04 per cent for the latter. The same trend was observed in 1957. BERNARD (1956), on the contrary, found the average photosynthetic efficiency (over a period of six months) for wood production under the shade of *Hevea* clones to increase with decreasing light intensity. His figures seem to be very high, but he attributed these high values to richness in green light under *Hevea* shade. It is worth noting here that he only studied the effect of very low light intensities (the highest value, *viz.*, 21.8 per cent, is still below the lowest light intensity we used in our experiments). He also worked on shade plants (well adapted to shade) which probably use low light intensities more efficiently.

The decrease in efficiency associated with decreased light intensity may be attributed to a detrimental effect of shading on growth of open habitat plants. This effect, usually, increased with time and with decreasing light intensity.

Thus, the photosynthetic apparatus formed by the heavily shaded plants is very small, owing to limited photosynthesis from the beginning. As a result, growth is greatly depressed as compared with that under full daylight. Under field conditions, the rate of growth depends on the excess of assimilatory products made during the day over the respiratory losses by the entire plant during the night. Therefore, with reducing daylight intensity the changes in growth will not only be correlated with effects on assimilation but also with those on respiration. BLACKMAN and TEMPLEMAN (1940) reported that, in grasses and clover, shading has very considerably increased the protein level of leaves and may therefore have also increased the respiration rate since it has been pointed out by GREGORY and SEN (1937) and RICHARDS (1938) that respiration of barley leaves is largely correlated with their protein content.

It seems that the lower degree of growth and development of shaded plants is not only the result of the lower assimilation rate, but apart from this, several kinds of morphogenetic effects appear. Besides a possible effect of reduced light intensity on leaf thickness (light absorbing power of leaves), we have the modification in leaf structure, stomatal number, etc., while, moreover, shading affects the formation of mechanical and conductive tissues and root growth. This may influence the uptake of nutrients and water, as well as translocation. In this connection, PORTER (1937) found that the total mineral uptake was depressed by shading.

From our data, it is evident that the depression in growth owing to shading is more effective than one might suppose from the mere reduction in light intensity. It appears that many internal and metabolic factors as well as external factors may directly or indirectly influence synthesis, and thus affect the ultimate "efficiency of growth" as computed here.

To sum up, it seems that in shade plants (*versus* plants in the open), two controversial tendencies affect the efficiency of light energy conversion:

1. Increase of efficiency of photosynthesis by less excess of light.
2. Decrease of efficiency of growth by unfavorable balance between photosynthesis and respiration.

Aside of this, the morphogenetic reactions towards light intensity should be remembered.

In this connection, it is worth noting that leaves which are adapted to strong light are more efficient in strong light and have low efficiency in weak light (CURTIS and CLARK, 1950). WASSINK, RICHARDSON and PIETERS (1956) concluded that, in *Acer pseudoplatanus* grown at high light intensities, the saturating light intensity as well as the maximum rate of photosynthesis, increase. The leaves formed are thicker. However, the efficiency in using low light intensities was found to decrease. Conversely, in shade plants, the leaves formed are thinner and are more efficient in utilizing reduced light intensities.

RESULTS AND DISCUSSION – DENSITY EFFECTS

I. DENSITY AND GROWTH

A. Growth in shape, size, and number

1. *Shoot length and thickness*

Fig. 24 shows that in 1957 at all harvests, shoot length decreased with increasing density as a consequence of intense competition. In 1958, the reverse was true during the early stages of growth, but later on, owing to increased competition, the plants at the highest density were no longer in advance and failed to exceed those at the medium density. The present writer (KAMEL, 1954) found the height of sesame plants to decrease with increasing density. The differences induced by density increased with time and were maximal after 49 days in 1957, and after 70 days in 1958. By that time the shoot length varied from 91.0 cm for the dense planting to 100.5 cm for the normal one, in 1957; and from 115.1 cm for the dense planting to 99.1 cm for the thin one, in 1958. Statistical analysis showed that the differences induced by density at the final harvest were not significant.

Up to the 4th and 5th harvests in 1957 and in 1958 respectively, the plants increased rapidly in length with time till the maximum height was reached. At all densities, the growth curves were close to the S-shape.

Fig. 25 indicates that, with few exceptions, the length of separate internodes, especially the lower ones, increased with density. The fact that the internode length was greater in the highest density suggests that some factors other than the availability of water – which has been supposed earlier by CROWTHER (1934) – must come into play. It has been established for long that shading within certain limits increased internode extension and it would, therefore, seem that with increasing density competition for light is already in progress (HODGSON and BLACKMAN, 1956). Measurements of the relative light intensity reaching the ground level within each density showed that mutual shading increased with increasing number of plants per unit area, *viz.*, 40.8 per cent and only 11.0 per cent of the incident light reached the ground level after 42 days from planting at the lowest and highest densities, respectively.
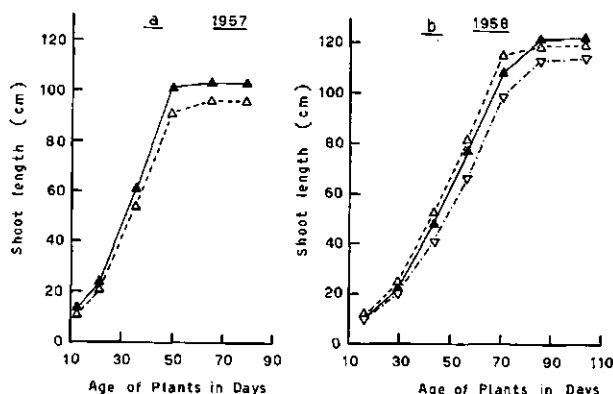

FIG. 24.
Density effect on shoot length (main axis) in cm, in barley, at successive harvests, in 1957 (a) and in 1958 (b).

△----△ : Dense planting
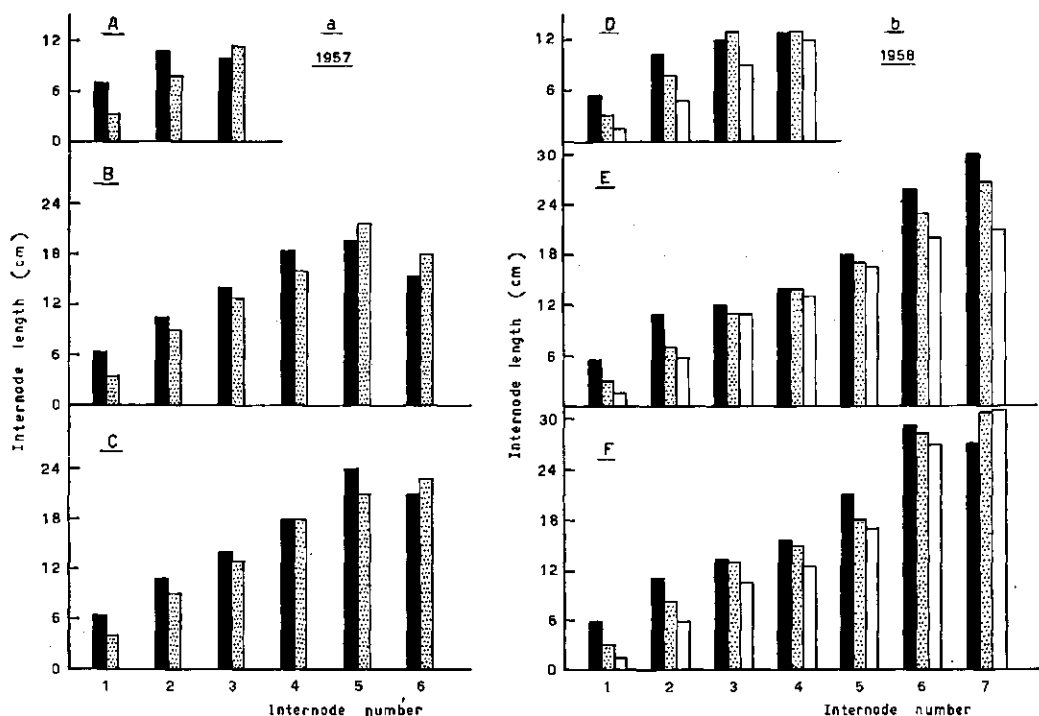▲———▲ : Normal planting
▽—·—·▽ : Thin planting

FIG. 25. Density effect on internode length (main axis) in cm, in barley, at three consecutive periods, in 1957 (a) and in 1958 (b).

■: Dense planting   ▓ : Normal planting   □ : Thin planting

a) A: 35 days after planting   B: 49 days after planting   C: 64 days after planting
b) D: 56 days after planting   E: 70 days after planting   F: 85 days after planting

It is evident also that the internodes increased in length as well as in number, as the plants developed.

Internode length in general increased with density, a tendency which – in 1958, in the first part of the season – was reflected also in total plant length. However, in the last two harvests, in 1958 and in almost the entire season of 1957, this relation was reversed at least at the higher densities. This may be due to several reasons, e.g. some increase in internode number with decreasing density, and to an increasing effect of competition in the course of the season, which may overcome the effect of shade in producing elongation. Rather variable results were also obtained by CLEMENTS et al. (1929) in wheat and sunflower.

Fig. 26 shows that, in both seasons, shoot diameter decreased with increasing density. In this, the increased competition, especially for light, seems to be the most critical factor. These results are in general agreement with those of CLEMENTS et al. (1929). The highest differences were found in the period from July 11 to 25 (39–49 days after sowing) in 1957, and on June 12 (56 days after sowing), in 1958. At the last harvest under investigation, the shoot diameter in 1957 varied from 2.6 mm for the dense planting to 3.1 mm for the normal
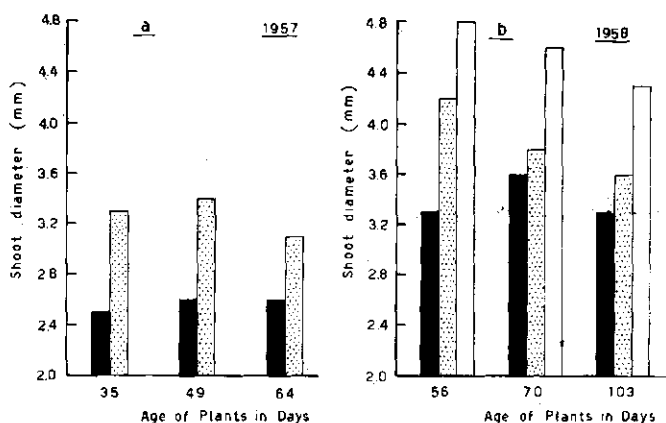
FIG. 26. Density effect on shoot diameter in mm (average of the first two or three internodes of the main axis), in barley, at successive harvests, in 1957 (a) and in 1958 (b).
■: Dense planting   ▨ : Normal planting   □ : Thin planting

one, and in 1958 from 3.3 mm for the highest density to 4.3 mm for the lowest one. The density effect was statistically analysed at the last harvest and was found to be highly significant.

2. *Tillering*

The results illustrated in Table 9 and fig. 27 indicate that, in both seasons, the number of living shoots per plant was greatly reduced by increased density (see also Plate 2a). This can be explained by the fact that each tiller not only reflects the suppression of the parent but also a suppression acting directly upon itself. In connection herewith we can, in general, use the word: competition. It is difficult to ascertain which factor under field conditions is the determining one in this competition. For instance, the pattern of development may be largely dependent on the availability of mineral nutrients, especially nitrogen, so that branching and tillering may be limited by the supply of nitrogen. On the other hand, it has been found that branching was greatly depressed by drought as well as by shading (MILTHORPE, 1945, see also this paper) indicating that water and light factors may also be liable to competition. The differences induced by variations in density were found to be less marked at the first stages of growth at which obviously competition was not yet very important. Later on, the plants respond greatly to density, and the differences in shoot number per plant increased to a maximum in the period from July 25 to August 9 (49–64

TABLE 9. Density effect on shoot number per plant, in barley, at successive harvests.

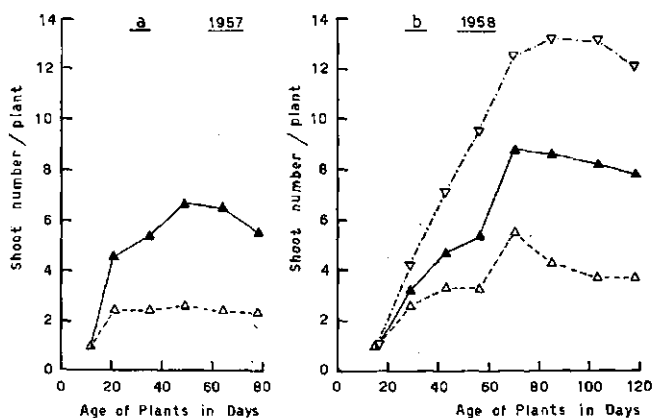| Plant density	1957					1957						
	Age of plants in days					Age of plants in days						
	21	35	49	64	78	29	43	56	70	85	103	118
Dense planting	2.4	2.4	2.6	2.4	2.3	2.6	3.3	3.3	5.5	4.3	3.7	3.7
Normal planting	4.6	5.4	6.7	6.5	5.5	3.2	4.7	5.3	8.8	8.6	8.2	7.8
Thin planting						4.2	7.1	9.5	12.5	13.2	13.1	12.1

FIG. 27. Density effect on shoot number per plant, in barley, at successive harvests, in 1957 (a) and in 1958 (b).

△-----△ : Dense planting ▲———▲ : Normal planting ▽—·—·▽ : Thin planting

days after sowing) in 1957, and from July 11 to 28 (85–103 days after sowing) in 1958. The differences were statistically analysed at the final harvest, and were found to be highly significant.

Similar results were obtained by ENGLEDOW (1925) in wheat, CLEMENTS *et al.* (1929) in wheat and sunflower, the present author (KAMEL, 1954) in sesame and HODGSON and BLACKMAN (1956) in *Vicia faba*.

At all densities, the number of living shoots per plant increased progressively with age – and more rapidly so at the lowest density – till a maximum, and then decreased sharply, especially at the higher densities owing to senescence associated with earlier maturity. The changes were less pronounced in 1957, especially at the dense planting, owing to the restricted number of shoots per plant from the beginning. In 1957, the maximum shoot number per plant, reached after 49 days from seeding, varied from 2.6 for the dense planting to 6.7 for the normal one. In 1958, the maximum was reached after 70 days from sowing in the highest density and about two weeks later in the lowest one, indicating that higher densities favor earlier maturity. The maximum shoot number differed from 5.5 for the dense planting to 13.2 for the thin one.

In 1957, the final shoot number per plant varied from 2.3 to 5.5 for the dense and normal plantings, respectively; in 1958 from 3.7 for the highest density to 12.1 for the lowest one.

Since the final yield in cereals greatly depends on the shoot number per unit area, it is of great interest to study shoot number on unit area basis. Fig. 28 shows that in both seasons up to a certain date (35 and 85 days after planting in 1957 and in 1958, respectively), the shoot number per unit area increased with increasing density. This can be explained by the fact that with increasing density during this period, competition was not yet intense, and the higher number of plants per unit area could easily counterbalance the reduction in shoot number per plant. Later on, competition had become so intense that increase in plant number over the "normal" density could not compensate for the depression in shoot number per plant. The values for the lowest density always were the lowest, indicating that their high capacity in producing tillers per plant was
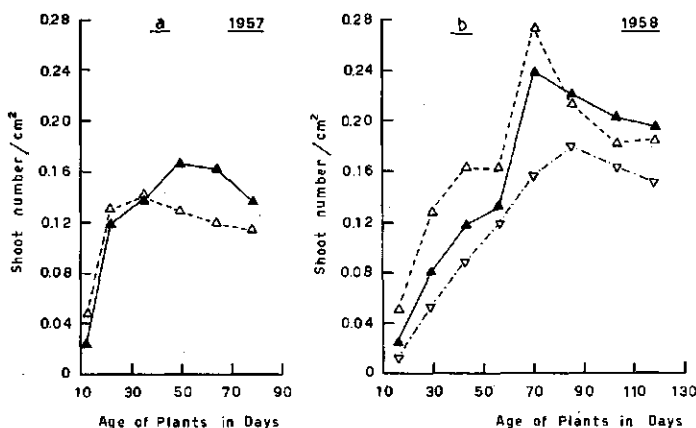
FIG. 28. Density effect on shoot number per cm², in barley, at consecutive harvests, in 1957 (a) and in 1958 (b).
△-----△ : Dense planting   ▲———▲: Normal planting   ▽—·—·▽ : Thin planting

not sufficient to overcome the reduction in plant number per unit area. The density effect on shoot number per cm² were statistically analysed at the last harvest, and were found to be insignificant.

In general, the age trend was the same as that based on individual plants with the only exception that in 1957 the maximum shoot number per unit area in the dense planting occurred two weeks earlier than the maximum shoot number per plant.

3. *Leaf production*

a. Leaf number

Since leaf number per plant was greatly dependent on shoot number per plant in the light intensity experiment, one would expect the same trend to be reflected here. Fig. 29a shows that, with increasing plant density, the number of green leaves per plant decreased. Similar results were obtained by CLEMENTS *et al.* (1929) in wheat and sunflower. The differences increased as the plants developed; obviously, at the early stages competition was not yet important. The largest differences were observed after 85 days from planting. The same trend was observed in 1957.

At all densities, the green leaf number per plant increased progressively with age – and more rapidly so at the lower densities – till a maximum was reached. After the maximum it decreased sharply, especially at the higher densities, owing to more rapid onset of senescence and earlier maturity. Although the maximum was attained after 70 days from planting at all densities, there was a tendency for the highest density to ripen earlier. The same trend was observed in 1957 with the only difference that the maximum was reached after 35 days from planting in the dense planting, and two weeks later in the normal one which indicates the density effect on accelerating ripening.

Dying off of leaves at the highest density started two weeks earlier than at the normal one, indicating that the effect of some factors other than light, especially water and nutrient factors, was responsible herefor, because in the shading
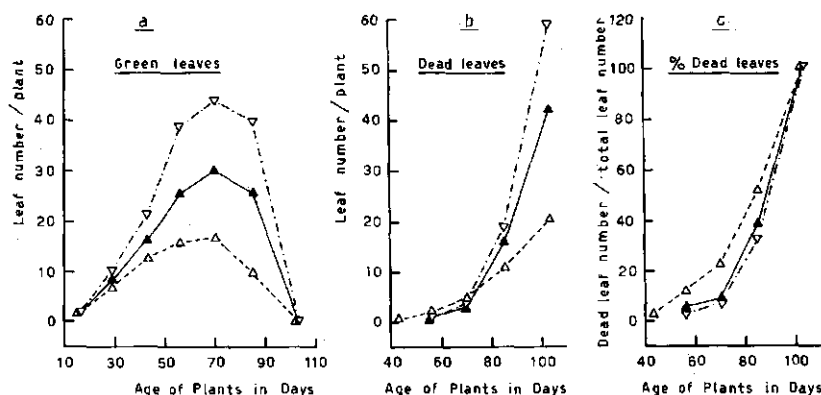
Fɪɢ. 29. Density effect on green leaf number per plant (a), dead leaf number per plant (b) and the percentage of dead leaves to total leaf number (c), in barley, at successive harvests, in 1958.

△----△ : Dense planting   ▲——▲ : Normal planting   ▽— — —▽ : Thin planting

experiment it was found that senescence started earliest at the highest light intensity. In the period from May 30 to June 26 (43–70 days after sowing), the number of dead leaves per plant increased with increasing density, indicating earlier maturity. Later on, the position was changed and the number of dead leaves per plant increased with decreasing density (fig. 29b). This, however, was not due to earlier maturity, but to increased number of total leaves per plant. This is clear from the percentage of dead leaves out of total leaf number which increased with increasing density (fig. 29c), indicating that light was not responsible herefor (cf. above).

At all densities, the number of dead leaves per plant as well as the percentage of dead leaves increased progressively with time, both were maximal at the last harvest under investigation.

With rare exceptions, the same trend was observed in 1957.

Fig 30 illustrates the effect of density on the number of green leaves per cm², at successive harvests. Up to 35 days and 70 days after planting in 1957 and in 1958, respectively, the green leaf number per unit area increased with density, indicating that the increase in plant number per unit area easily counterbalanced the reduction in leaf number per plant. Later on, the position was changed in favor of the normal planting, similar to what holds for the shoot number per unit area.

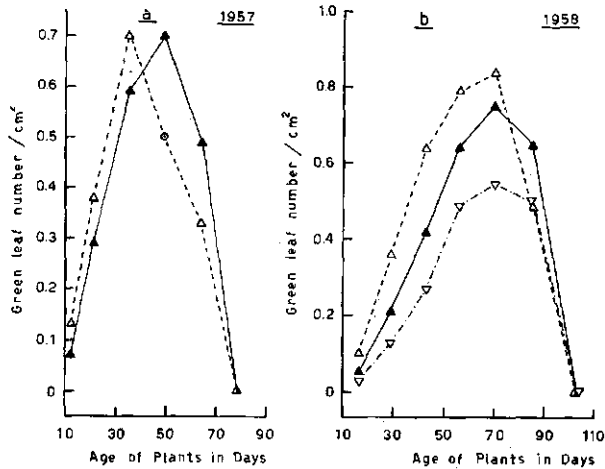In general, the time trend was the same as in the green leaf number per plant.

b. Leaf dimensions

Fig. 31 shows that up to 43 days after planting, the leaf length of the 2nd leaf from top increased with density, indicating that competition for light was responsible herefor. Later on, the situation was changed, and the highest density showed the lowest leaf length. This suggests that the effect of some factors other than light predominated, and masked the light effect. Earlier emergence of ears at the highest density may be responsible for such effect since it is well known that the presence of the growing inflorescence inhibits leaf expansion of the young leaves immediately below it.

60

FIG. 30.
Density effect on green leaf
number per cm², in barley, at
successive harvests, in 1957
(a) and in 1958 (b).

△-----△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

At all harvests, leaf breadth of the 2nd leaf from top decreased with in-
creasing density. This suggests that light has played the major rôle. CLEMENTS
et al. (1929) found that both leaf length and breadth decreased with increasing
density.

The leaf length increased rapidly with age, especially at the highest density,
until a maximum was reached, and then decreased owing to the presence of the
ears, and more sharply so, and from an earlier date at the highest density.

In general, leaf breadth increased progressively with time.

Fig. 32a shows that, in general, leaf ratio (length/breadth) of the 2nd leaf
from top increased with increasing density. Since the ratio was found to in-
crease with reduced light intensity, as has been observed earlier in the shading
experiment, together with the results of BENSINK (1958) it may be suggested
that the light factor was responsible herefor.

At all densities, the leaf ratio increased with time to a maximum on May 30
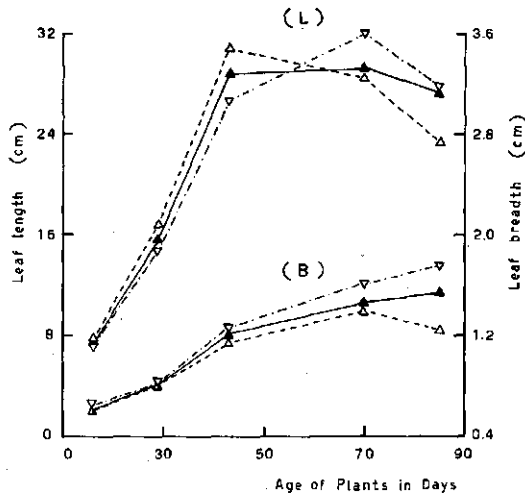

FIG. 31.
Density effect on leaf length (L) and
leaf breadth (B), in cm, of the 2nd
leaf from top, in barley, at succes-
sive harvests, in 1958.

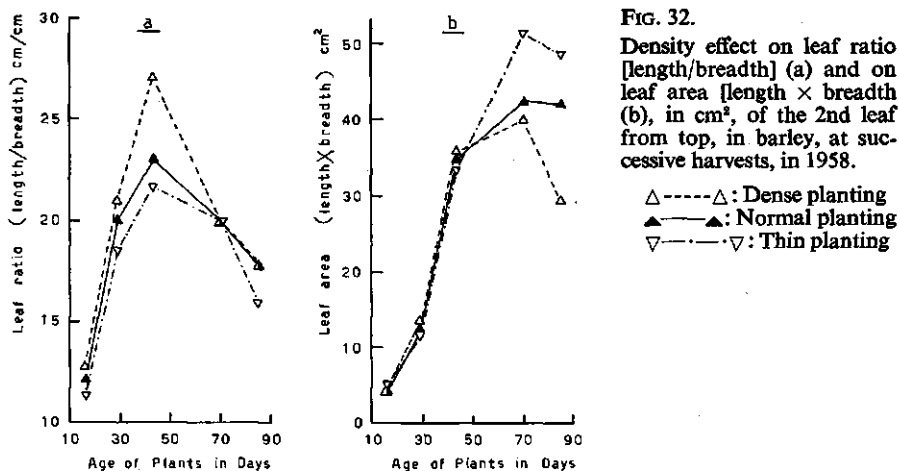△-----△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

FIG. 32.
Density effect on leaf ratio [length/breadth] (a) and on leaf area [length × breadth (b), in cm², of the 2nd leaf from top, in barley, at successive harvests, in 1958.

△-----△ : Dense planting
▲——▲ : Normal planting
▽—·—·▽ : Thin planting

(43 days after planting), and thereafter decreased. The maximum leaf ratio differed from 27 for the highest density to 22 for the lowest one.

Fig. 32b indicates that up to 43 days, the leaf area of the 2nd leaf from top increased with density, favoring the supposition that light may play the major rôle. At a more advanced age, the leaf area decreased with increasing density, supporting the suggestion that some factor other than light predominates.

The leaf area increased progressively with age till a maximum was reached on June 26 (70 days after planting), thereafter it decreased, and more sharply so at the higher density, owing to earlier ear emergence.

4. *Ear production*

In 1958, awn emergence had already started on June 13 (57 days after sowing) at the highest density, on June 16 at the medium one, and on June 18 at the lowest density. This suggests that, owing to increased competition for nutrients (especially nitrogen) and for water with increasing density, the vegetative growth was restricted, and the vegetative period shortened, ear emergence was accelerated while plants tended to terminate their growth cycle earlier. Micro-dissection studies of the growing points after 49 days from planting showed that increasing plant density induced earlier development of the spike. Light cannot well be the responsible factor herefor since, in the shading experiment, the earlier development of the spike was observed at the highest light intensity.
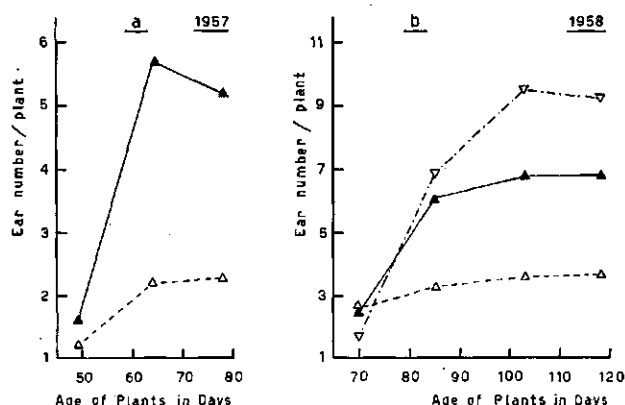
Table 10 shows that after 49 days in 1957, and after 70 days in 1958, the percentage of completely emerged ears to the total number of ears increased with increasing plant density. On the other hand, the ratio of the partly emerged ears decreased with increasing density, favoring the supposition previously given.

It is apparent from fig. 33 that, in general, the number of completely emerged ears per plant was found to decrease with increasing density. In 1958, at the first harvest (70 days after seeding) the reverse was true, owing to the fact that ears emerged earlier with increased density. The differences, normally induced by differences in density, increased with age and were maximal near the end of the season. Statistical analysis at the final harvest showed that the effect of

FIG. 33.
Density effect on ear number per plant, in barley, at successive harvests, in 1957 (a) and in 1958 (b).

△-----△: Dense planting
▲———▲: Normal planting
▽—·—·▽: Thin planting

density was highly significant. ENGLEDOW (1925) also found that the number of ears per plant decreased with increasing density. The same trend was observed by CLEMENTS *et al.* (1929) in wheat, the present author (KAMEL, 1954) in sesame, and HODGSON and BLACKMAN (1956) in *Vicia faba.*

TABLE 10. Density effect on completely and partly emerged ears per plant and on the percentage of completely emerged ears/total ear number, in barley, after 49 days and after 70 days from planting, in 1957 and in 1958, respectively.

Plant density	1957				1958			
	Ear number per plant			$\frac{Comp.}{Total} \times 100$	Ear number per plant			$\frac{Comp.}{Total} \times 100$
	Completely emerged	Partly emerged	Total		Completely emerged	Partly emerged	Total	
Dense planting	1.2	0.9	2.1	57.14	2.6	0.1	2.7	96.3
Normal planting	1.6	2.9	4.5	35.14	2.5	1.0	3.5	71.4
Thin planting					1.7	3.0	4.7	36.2

Since ear number per plant in cereals depends on shoot number, the variation in ear number per plant apparently is due to changes in shoot number per plant, induced by varying the density.

Owing to emergence of successive ears, ear number per plant increased progressively with time and was maximal at the end of the season. The increase tended to be less pronounced at increasing density. At the last harvest, ear number per plant ranged from 2.3 for the dense planting to 5.2 for the normal one in 1957, and from 3.7 for the highest density to 9.2 for the lowest one in 1958.

Table 11 and fig. 34 represent the effect of density on ear number per cm², at successive harvests in 1957 (a) and 1958 (b). In 1957, the ear number per unit area during the first harvest (49 days after sowing) increased with density. Later on, competition became so intense that the increased number of plants per unit area could not compensate the reduction in ear number per plant. Thus, the ear number per unit area, following closely the shoots in their reactions to density, decreased with increasing density. In 1958, the ear number per unit area in-
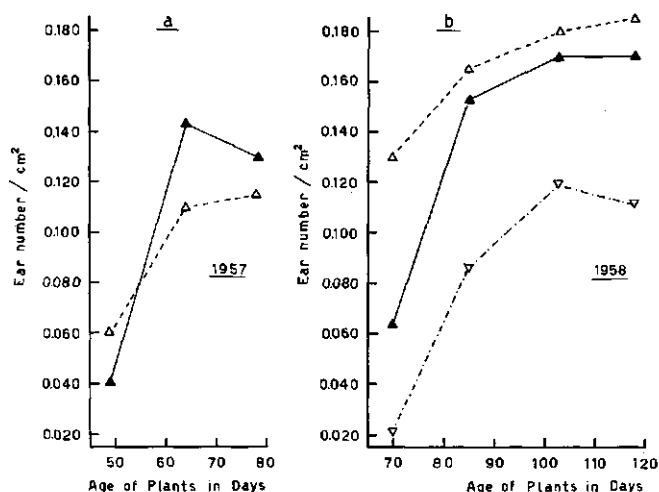
FIG. 34. Density effect on ear number per cm², in barley, at successive harvests, in 1957 (a) and in 1958 (b).

△-----△ : Dense planting   ▲———▲ : Normal planting   ▽—·—·▽ : Thin planting

creased with density, indicating that the depression in ear number per plant was easily overcome by the increase in plant number per unit area. In general, the differences induced by density decreased with time, owing to production of more ears at the lower densities. The differences were statistically analysed at the last harvest and were found to be highly significant. CLEMENTS *et al.* (1929) found that ear number per unit area increased with density.

The age trend was the same as in the ear number per plant.

TABLE 11. Density effect on ear number per cm², in barley, at successive harvests.

Plant density	1957			1958			
	Age of plants in days			Age of plants in days			
	49	64	78	70	85	103	118
Dense planting	0.060	0.110	0.115	0.130	0.165	0.180	0.185
Normal planting	0.040	0.143	0.130	0.063	0.153	0.170	0.170
Thin planting				0.021	0.086	0.119	0.111

Fig. 35 shows that, in 1958, ear length of the main axis was greatly depressed by density (see also Plate 2b). Similar results were obtained by CLEMENTS *et al.* (1929). The largest differences induced by density were observed at the end of the season. Statistical analysis by that time showed that the density effect was highly significant. The maximum length of ears was reached on June 26 (70 days after planting) at the highest density, on July 11 (about two weeks later) at the medium one, and on July 29 (about five weeks later) at the lowest one. These results support the foregoing and forthcoming findings that higher densities favor earlier ear emergence and maturity.

Since reduced light intensity resulted in shorter ears, one would suggest that

the light factor, to some extent, may be responsible herefor. In addition, drought and nitrogen deficiency also induce shorter ears.

5. *Seed production*

Fig. 36a and b show that, in 1958, the number of seeds per plant as well as per ear decreased with increasing density. The differences in seed number per plant became more marked with time owing to increased competition and were maximal at the end of the season. At the last harvest, the differences were statistically analysed, those in seed number per plant were highly significant, while those in seed number per ear were not significant. For seed number per ear, the highest differences were found 103 days after planting.

FIG. 35. Density effect on ear length, in cm, of the main axis, in barley, at successive harvests, in 1958.

△-----△: Dense planting
▲——▲: Normal planting
▽—·—·▽: Thin planting

At all densities, the number of seeds produced per plant increased progressively as the plants advanced towards maturity, and more rapidly so at the lower densities. The final seed number per plant varied from 72.7 for the highest density to 201.3 for the lowest one. In general, seed number per ear decreased with time, owing to formation of ears with lower seed number that brought the average down. On July 11 (85 days after sowing) the seed number per ear differed from 23.2 for the dense planting to 27.4 for the thin one, while at the final harvest it varied from 19.8 to 22.0 for the former and the latter, respectively.

Similar results were obtained in 1957. In a previous paper (KAMEL, 1954), the same trend was observed in sesame plants. HODGSON and BLACKMAN (1956)
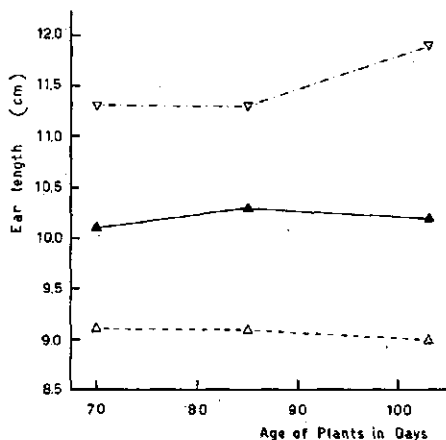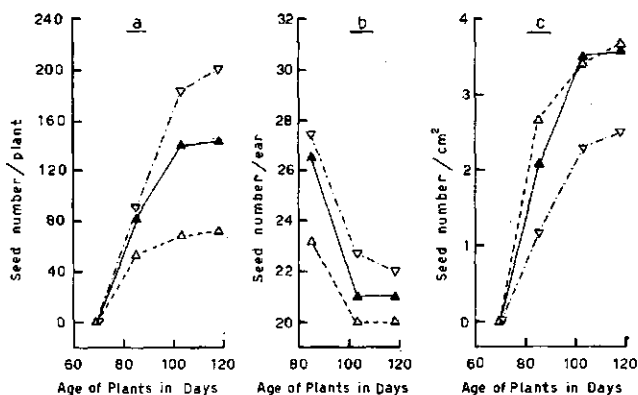

FIG. 36. Density effect on seed number per plant (a), per ear (b), and per cm² (c), in barley, at successive harvests, in 1958.

△-----△: Dense planting   ▲——▲: Normal planting   ▽—·—·▽: Thin planting

found that, in *Vicia faba*, seed production was greatly depressed by increasing density.

Fig. 36c indicates that, with rare exceptions, seed number per unit area increased with density, indicating that the increase in plant number per unit area easily counterbalanced the reduction in seed number per plant. The differences increased with time and were maximal after 85 days from planting. At the last harvest, the differences were statistically analysed and were found to be highly significant.

It is worth noting that reduction of the number of plants per unit area to the normal density (250 plants/m²), especially at the very advanced stages, had little effect on the number of seeds per unit area, but with further reduction the seed number per unit area was greatly depressed.

The seed number per unit area was found to increase rapidly with age, especially at the higher densities, and was maximal at the end of the season. At the final harvest, the number of seeds per cm² varied from 3.64 for the highest density to 2.52 for the lowest one.

In 1957, it was found that the number of seeds per unit area was greatly reduced when the number of plants per unit area was increased to 500 plants/m², indicating that competition had become so intense that the increase in plant number per unit area could not compensate for the reduction in seed number per plant.

6. *Efficiency of shoots in producing ears and of ears in forming seeds*

It has been shown above that shoot number as well as ear number per plant were greatly influenced by density. It is of practical importance to study the effect of density on the efficiency of shoots in producing ears (ear number/shoot number, in per cent) or of ears in forming seeds (number of ears forming seeds/total ear number, in per cent). Fig. 37a indicates that with increasing density the percentage ears per shoots increased, indicating that at higher densities the shoots are more efficient in producing ears.

At all densities, the percentage increased rapidly with time, especially so at the higher densities, and was maximal at the end of the season. In the period from 70 to 118 days after planting the percentage ears/shoots went from 47.3 to 100.0 for the highest density and from 13.6 to 76.0 for the lowest one.

Similar results were obtained in 1957.

Fig. 37b shows that also the efficiency of ears in forming seeds increased with density. The percentage increased progressively with age, and more rapidly so at the dense planting. The maximum efficiency, reached on July 29 (103 days after sowing), varied from 100 per cent for the highest density to 85 per cent for the lowest one.

B. Growth in weight

B'. On individual plant basis (fresh and dry weight)

The depressive effects of increased density on fresh and dry weight of the entire plant has already been demonstrated previously. Suggestions were put forward that these changes result from a greater degree of self-shading together with a more restricted supply of mineral substances. At the highest density there can be little or no assimilation by the lower leaves (the greater fraction), especially
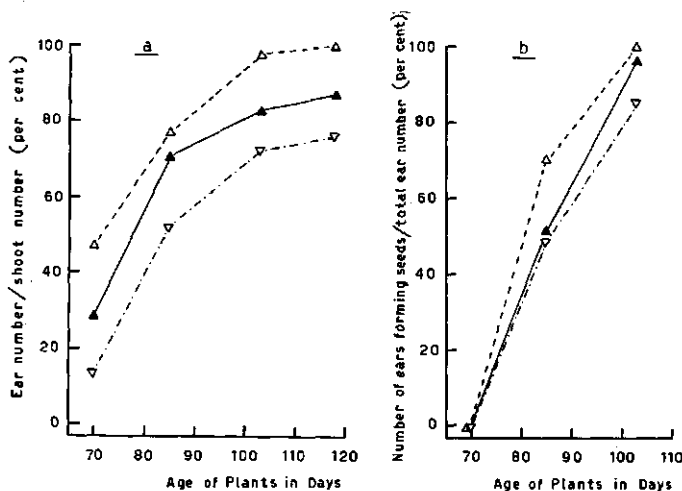
FIG. 37. Density effect on the efficiency of shoots in producing ears [ear number to shoot number, in per cent] (a) and on the efficiency of ears in forming seeds [number of ears forming seeds to total ear number, in per cent] (b), in barley, at successive harvests, in 1958.

△-----△ : Dense planting   ▲———▲ : Normal planting   ▽—·—·▽ : Thin planting

during the period of maximum growth (KAMEL, 1958).

It should be noted here that fresh weight or dry matter accumulation in a crop is only a partial measure of agricultural yield. Usually such yields refer only to a single morphological or chemical constituent of the plant, i.e. the grains of cereals, the tubers of potatoes, or the sucrose of sugar-beet roots, etc., the remaining part being of little or no economic value. For full analysis, consideration of the distribution of fresh weight or dry matter between different parts of the plant, as well as the total weight accumulation is required. It is, therefore, reasonable to follow the variations induced by density in the weight of each of the individual plant organs during their development. However, the weights of the component parts usually are highly correlated with the total dry weight of the plant. Variation in partition of assimilates between different organs rarely is sufficiently large to offset variation in total plant weight.

Table 12 and the following figures represent the effect of density on the weight of each of the individual plant organs, and on other growth characteristics.

1. Roots

a. F r e s h w e i g h t

Fig. 38a shows that with increasing density (up to 500 plants/m²) the fresh weight of roots per plant was greatly depressed. The differences increased with time due, of course, to increased competition, and were maximal in the period from June 26 to July 11 (70–85 days after planting). Later on, owing to maturity, they became progressively smaller with the development of the plants, although they were still significant.

The time trend was the same at all densities, showing exponential growth in earlier developmental stages, but nevertheless, between densities there were

TABLE 12. Density effect on fresh weight and dry weight per plant (in grams) of entire plant, roots, leaves, ste stems + leaves percentage, and seeds/ears percentage (on dry weight basis), in barley, at succes:

Plant density	Date	Age of plants in days	Entire Plant			Roots		
			Fresh	Dry	%	Fresh	Dry	%
Dense Normal Thin	3 V	16	0.195 0.170 0.177	0.025 0.022 0.022	12.8 12.9 12.4	0.026 0.026 0.029	0.006 0.006 0.006	23. 23. 20.
Dense Normal Thin	16 V	29	1.171 1.364 1.458	0.117 0.148 0.164	10.0 10.9 11.2	0.020 0.028 0.057	0.008 0.010 0.017	40. 35. 29.
Dense Normal Thin	30 V	43	6.454 7.861 8.198	0.591 0.738 0.839	9.2 9.4 10.2	0.059 0.096 0.122	0.023 0.034 0.044	39. 35. 36.
Dense Normal Thin	12 VI	56	11.019 18.891 25.435	1.608 2.410 3.170	14.6 12.8 12.5	0.069 0.140 0.278	0.035 0.061 0.107	50. 43. 38.
Dense Normal Thin	26 VI	70	19.369 30.317 52.013	3.535 5.090 7.855	18.3 16.8 15.1	0.129 0.250 0.554	0.069 0.116 0.237	53. 46. 42.
Dense Normal Thin	11 VII	85	11.538 30.207 46.271	3.936 8.158 11.412	34.1 27.0 24.7	0.115 0.291 0.528	0.075 0.171 0.295	65. 58. 55.
Dense Normal Thin	29 VII	103	11.444 26.211 41.627	5.285 10.081 13.309	46.2 38.5 32.0	0.102 0.216 0.388	0.078 0.149 0.243	76. 69. 62.
Dense Normal Thin	13 VIII	118	6.616 17.726 28.970	4.970 10.690 14.523	75.1 60.3 50.1	0.055 0.203 0.341	0.044 0.153 0.225	80. 75. 66.

Plant density	Date	Age of plants in days	Tops					
			Ears					
			Seeds			Total		
			Fresh	Dry	%	Fresh	Dry	%
Dense Normal Thin	3 V	16	0.000 0.000 0 000	0.000 0.000 0 000	0.0 0.0 0 0	0.000 0.000 0 000	0.000 0.000 0 000	0 0 0
Dense Normal Thin	16 V	29	0.000 0.000 0.000	0.000 0.000 0.000	0.0 0.0 0.0	0.000 0.000 0.000	0.000 0.000 0.000	
Dense Normal Thin	30 V	43	0.000 0.000 0.000	0.000 0.000 0.000	0.0 0.0 0.0	0.000 0.000 0.000	0.000 0.000 0.000	
Dense Normal Thin	12 VI	56	0.000 0.000 0.000	0.000 0.000 0.000	0.0 0.0 0.0	0.000 0.000 0.000	0.000 0.000 0.000	
Dense Normal Thin	26 VI	70	0.000 0.000 0.000	0.000 0 000 0.000	0.0 0 0 0.0	1.775 2.216 3.519	0.541 0.669 0.876	3(3(2.
Dense Normal Thin	11 VII	85	2.438 3.682 3.945	0.950 1.310 1.271	39.0 35.6 32.2	3.370 6.223 7.692	1.360 2.204 2.624	4(3: 3.
Dense Normal Thin	29 VII	103	4.034 7.377 10.060	2.362 4.088 4.844	58.6 55.4 48.2	4.588 8.627 12.885	2.733 4.843 6.016	5! 5. 4.
Dense Normal Thin	13 VIII	118	2.894 5.975 7.500	2.472 4.966 6.094	85.4 83.1 81.2	3.288 6.897 8.566	2.822 5.770 7.032	8 8 8

stems + leaves, seeds, ears, and tops; and on dry weight/fresh weight percentage, root/top ratio, ears/harvests, in 1958.

Tops											
Stems + Leaves											
Leaves (Blades)						Stems + Sheaths			Total		
Green			Total								
Fresh	Dry	%	Fresh	Dry	%	Fresh	Dry	%	Fresh	Dry	%
0.100	0.013	13.0	0.100	0.013	13.0	0.064	0.006	8.7	0.169	0.019	11.2
0.086	0.011	12.8	0.086	0.011	12.8	0.058	0.005	8.6	0.144	0.016	11.1
0.090	0.011	12.2	0.090	0.011	12.2	0.058	0.005	8.6	0.148	0.016	10.8
0.746	0.078	10.5	0.746	0.078	10.5	0.405	0.031	7.7	1.151	0.109	9.5
0.860	0.098	11.3	0.860	0.098	11.3	0.476	0.040	8.4	1.336	0.138	10.3
0.946	0.107	11.3	0.946	0.107	11.3	0.455	0.040	8.8	1.401	0.147	10.5
3.085	0.337	10.9	3.096	0.341	11.0	3.299	0.227	6.9	6.395	0.568	8.9
3.995	0.426	10.7	3.945	0.426	10.8	3.820	0.278	7.3	7.765	0.704	9.1
4.296	0.483	11.2	4.296	0.483	11.2	3.780	0.312	8.3	8.076	0.795	9.8
3.854	0.562	14.6	3.890	0.581	14.9	7.060	0.992	14.1	10.950	1.573	14.4
7.115	0.971	13.6	7.143	0.982	13.7	11.608	1.367	11.8	18.751	2.349	12.5
0.394	1.451	14.0	10.438	1.464	14.0	14.719	1.599	10.9	25.157	3.063	12.1
4.233	0.684	16.2	4.349	0.762	17.5	13.116	2.163	16.5	17.465	2.925	16.7
7.148	1.132	15.8	7.245	1.180	16.3	20.606	3.125	15.2	27.851	4.305	15.5
4.109	1.978	14.0	14.255	2.035	14.3	33.685	4.707	14.0	47.940	6.742	14.1
0.676	0.272	40.2	0.899	0.460	51.2	7.154	2.041	28.5	8.053	2.501	31.1
3.239	1.007	31.1	3.771	1.370	36.3	19.922	4.413	22.2	23.693	5.783	24.4
6.371	1.552	24.4	7.125	2.021	28.4	30.926	6.472	20.9	38.051	8.493	22.3
0.000	0.000	0.0	0.457	0.389	85.1	6.297	2.085	33.1	6.754	2.474	36.6
0.000	0.000	0.0	0.924	0.754	81.6	16.444	4.335	26.4	17.368	5.089	29.3
0.000	0.000	0.0	2.044	1.222	59.8	26.310	5.828	22.2	28.354	7.050	24.9
0.000	0.000	0.0	0.285	0.244	85.6	2.988	1.860	62.2	3.273	2.104	64.3
0.000	0.000	0.0	0.707	0.585	82.7	9.919	4.182	42.2	10.626	4.767	44.9
0.000	0.000	0.0	1.241	0.969	78.1	18.822	6.297	33.5	20.063	7.266	36.2

Total			Root/Top Ratio	% Ears/Stems + Leaves	% Seeds/Ears
Fresh	Dry	%			
0.169	0.019	11.2	0.3158	0 0	0.0
0.144	0.016	11.1	0.3750	0.0	0.0
0.148	0.016	10.8	0.3750	0.0	0.0
1.151	0.109	9.5	0.0734	0.0	0.0
1.336	0.138	10.3	0.0724	0.0	0.0
1.401	0.147	10.5	0.1156	0.0	0.0
6.395	0.568	8.9	0.0405	0.0	0.0
7.765	0.704	9.1	0.0483	0.0	0.0
8.076	0.795	9.8	0.0553	0.0	0.0
10.950	1.573	14.4	0.0223	0.0	0.0
18.751	2.349	12.5	0.0260	0.0	0.0
25.157	3.063	12.1	0.0349	0.0	0.0
17.240	3.466	18.0	0.0199	18.5	0.0
27.067	4.974	16.5	0.0233	15.5	0.0
47.459	7.618	14.8	0.0311	13.0	0.0
8.423	3.861	33.8	0.0194	54.4	69.8
23.916	7.987	26.7	0.0214	38.1	59.4
38.743	11.117	24.3	0.0265	30.9	48.4
11.342	5.207	45.9	0.0150	110.5	86.4
28.995	9.932	38.2	0.0150	95.2	84.4
44.239	13.066	31.7	0.0186	85.3	80.5
6.561	4.926	75.1	0.0089	134.1	87.6
17.523	10.537	60.1	0.0145	121.4	86.1
28.629	14.298	49.9	0.0158	96.8	86.6

marked differences in growth rate during the same period; the highest rate was observed at the lowest density. The maximum fresh weight of roots was reached after 70 days from planting at the highest and lowest densities, and after 85 days from planting at the medium one. It ranged from 0.129 g for the dense planting to 0.554 g for the thin one. After the maximum, the fresh weight of roots decreased to a minimum towards the end of the season.

The same trend was observed in 1957.

b. Dry weight

Fig. 38b indicates that also the dry weight of roots decreased with increasing density, and the greatest differences were found in the period from 70 to 85 days after sowing. Similar results were obtained by CLEMENTS et al. (1929) in wheat and sunflower.

In general, the age trend was the same as that of the fresh weight. The reduction in dry weight of roots at the late stages may be due to dying off of the absorbing roots and to loss of most of them. The maximum dry weight of roots was attained after 103 days from planting at the highest density, and after 85 days from sowing at the medium and lowest densities. It ranged from 0.078 g for the highest density to 0.243 g for the lowest one.

Similar results were obtained in 1957.

c. Dry weight

Fig. 38c shows that, in general, the dry weight percentage of roots increased with density. This indicates a competition while, moreover, and probably as a result of this, the plants at the higher densities tended to terminate their growth cycle or to mature earlier. For this competition, the light factor may not be primarily responsible since, in the shading experiment, maturation was earliest at the highest light intensity. The highest differences induced by density were found at the end of the season.

At all densities, the dry weight percentage of roots increased with time – and more rapidly so at the higher densities – till the maximum was reached at the final harvest. By that time, the percentage differed from 80 for the highest density to 66 for the lowest one.

These results are in general agreement with those obtained in 1957.
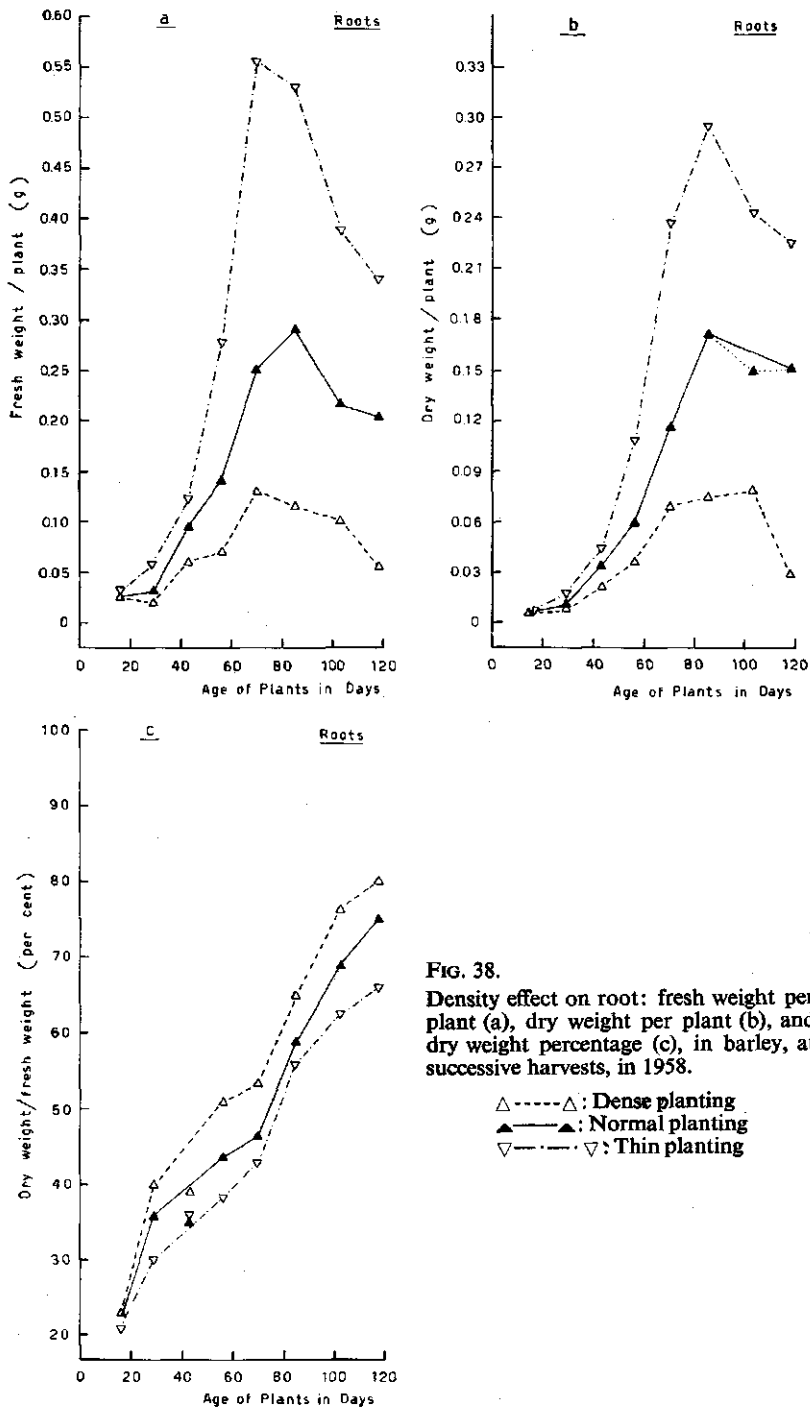
2. *Leaves*

a. Fresh weight

Fig. 39a indicates that, at all harvests, the fresh weight of total leaves (green and dead) per plant increased with decreasing density. The differences increased as the plants developed, obviously at the early stages differences in competition were not yet well pronounced. The maximum differences were found after 70 days from planting.

At all densities, fresh weight of total leaves per plant increased with age, was maximal on June 26 (70 days after sowing), then decreased to a minimum towards the end of the season. The curve decreased more sharply at the dense planting, owing to increased mutual shading and, consequently, more rapid senescence and earlier maturity. The maximum fresh weight of total leaves per plant ranged from 4.35 g for the highest density to 14.26 g for the lowest one.

The same trend was observed for the fresh weight of the green leaves only.

b. Dry weight

Fig. 39b shows that, as a result of a greater degree of mutual shading together with a more restricted supply of mineral substrates, the dry weight of the total

FIG. 38.
Density effect on root: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.

△------△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

leaves per plant was greatly depressed by increased density. The differences induced by density increased as the plants advanced in growth, and were maximal after 85 days from planting. In this connection, IWAKI (1958) found the maximum assimilation of buckwheat leaves in densely planted stands to be lower than that in stands with lower densities.

At all densities, the dry weight of the total leaves increased to a maximum, and more rapidly so at the highest density, and then decreased and more gradually so at the lowest density. The reduction in dry weight of total leaves per plant after the maximum is attributed to absence of photosynthesis in the lower part of the plant (as a result of mutual shading and increased senescence of the lower leaves) and, consequently, a larger fraction of the products of photosynthesis in these leaves passed into the grain after ear emergence. This was more pronounced at the highest density, indicating earlier maturity. The maximum dry weight of the leaves was reached after 70 days from seeding for the dense planting, and in the period from 70–85 days after planting for the thin one. The maximum dry weight of leaves per plant ranged from 0.762 g for the highest density to 2.035 g for the lowest one in 1958.

In this connection, it is of great interest to follow the density effects on the dry weight of the green leaves, as well as on that of the dead leaves, and on the percentage of dead leaves in total dry weight of leaves. Dry weight of green leaves per plant was greatly depressed by increased density. The differences increased with time and were maximal after 70 days. The age trend was the same as in the total dry weight of leaves per plant, with the only difference that the maximum dry weight of green leaves was attained at all densities after 70 days. Although in the 6th harvest (103 days after planting) the plants at all densities no longer possessed green leaves, there was a tendency for the higher densities to mature earlier.

In the period from 43 to 70 days, the dense planting had the highest dry weight of dead leaves per plant, owing to earlier onset of senescence (about two weeks earlier at the highest density). Later on, the position changed and the dry weight of dead leaves increased with decreasing density, which is not due to earlier maturity, but to increased number of leaves per plant. This can be shown from the percentage of dead leaves per total leaf dry weight. The differences increased with time and were maximal at the end of the season.

At all densities, the dry weight of dead leaves per plant increased progressively with age till the maximum was reached after 103 days, and thereafter decreased owing to translocation of cell constituents to ears, together with losses through over-ripening.

The percentage of dead leaves per total leaves on dry weight basis followed closely that on number basis; it increased with increasing density, indicating that increased plant number per unit area induced earlier maturity, and that some factors other than light are responsible herefor, since, in the shading experiment, maturity is earliest at the highest light intensity. Full ripening was reached after 124 days from planting at the highest density, and 10 days later at the lowest one.

The percentage of dead leaves increased with age – and more rapidly so at the higher densities – till all leaves had died after 103 days from seeding.

A few words may be said here about density effects on leaf thickness (on dry weight basis). During the first harvest (16 days after planting), leaf thickness decreased with increasing density, indicating that competition for light was responsible herefor. Later on, the situation changed and leaf thickness increased
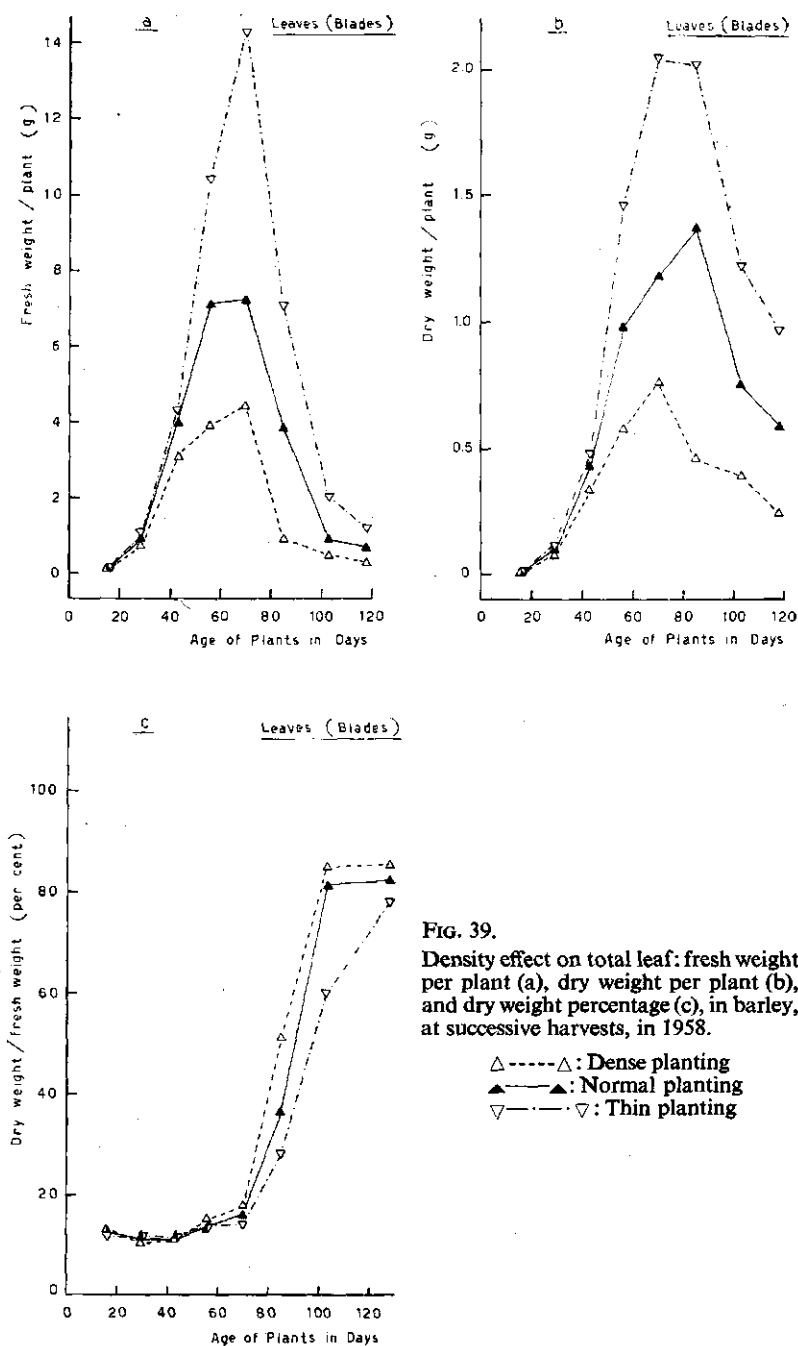
FIG. 39.
Density effect on total leaf: fresh weight
per plant (a), dry weight per plant (b),
and dry weight percentage (c), in barley,
at successive harvests, in 1958.

△-----△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

with density. This suggests that, by that time, the effect of some factors other than light, especially water and mineral nutrient supply, predominated and masked the light effect. The differences induced by density increased with age and were maximal at the last harvest which still includes green leaves. By that time (85 days after sowing), leaf thickness (dry weight/sample area [28.3 cm^2]) varied from 0.125 g for the highest density to 0.110 g for the lowest one.

At all densities, leaf thickness increased progressively as the plants developed, and was maximal at the last harvest still including green leaves.

Similar results were obtained in 1957.

c. Dry weight percentage

Fig. 39c shows that up to 43 days, the differences induced by density were not yet well marked. At more advanced age, the dry weight percentage of the total leaves increased with density. This may be considered as another indication of the effect of density on inducing earlier maturity. Since with increasing density, self-shading increased, and since in the shading experiment it has already been demonstrated that reduced light intensity resulted in lower dry weight percentage and later maturity, it can be concluded that this effect may be attributed to some factors other than light, viz., water and nutrient factors. The greatest differences induced by density were found after 103 days from planting. By that time, the dry weight percentage of leaves differed from 85.0 for the dense planting to 59.8 for the thin one.

The dry matter percentage of total leaves decreased during the early stages of growth up to the 2nd harvest in the highest density, and to the 3rd one in the medium and lowest densities. This may be due to increased uptake of water connected with extension growth. After this reduction, the dry matter percentage of the total leaves increased progressively with time until the last harvest; the values for the dense planting always were highest as they were for the entire plant.

The same trend was observed if the dry weight percentage of green leaves only was taken into account.

3. *Stems and sheaths*

a. Fresh weight

Fig. 40a indicates that, at all harvests, the fresh weight of stems and sheaths per plant was greatly suppressed by density. The differences increased as the plants advanced in growth; obviously at the early stages competition was not yet marked. The highest differences in fresh weight of stems and sheaths were observed 85 days from planting.

At all densities, the fresh weight of stems and sheaths increased with time till a maximum was reached 70 days from sowing – at the same time at which maximum fresh weight of the entire plant was reached – then dropped to a minimum towards the end of the season. This drop was more pronounced at the higher densities, owing to earlier maturity. Maximum fresh weight of stems and sheaths per plant varied from 13.12 g for the dense planting to 33.69 g for the thin one.

b. Dry weight

From fig. 40b it is evident that also the dry weight of stems and sheaths per plant decreased with increasing density. The differences, owing to increased competition, increased with time and were maximal in the period from July 11 to August 14 (85–118 days after sowing).

The dry weight of stems + sheaths increased progressively with time till a
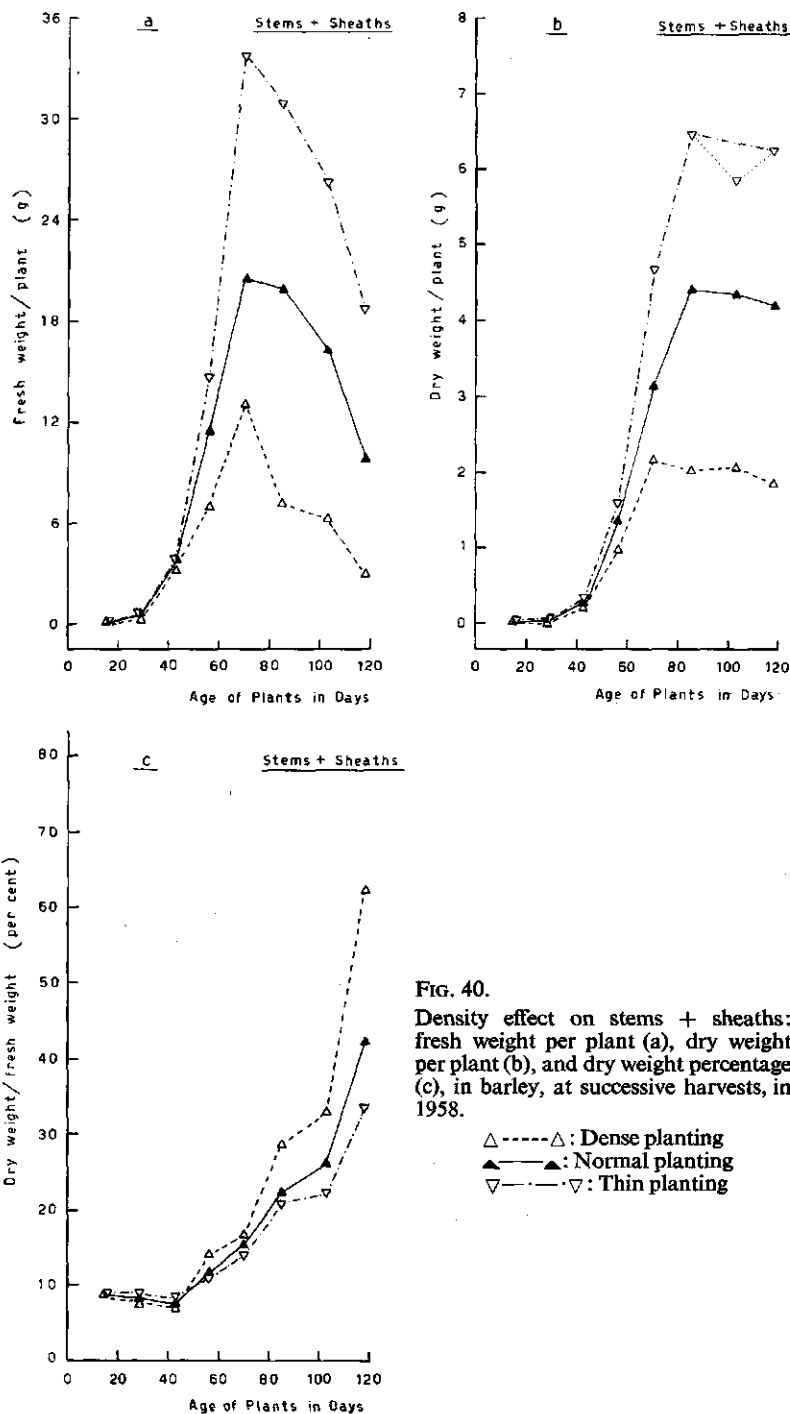
74

FIG. 40.
Density effect on stems + sheaths: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.

△-----△ : Dense planting
▲——▲ : Normal planting
▽—·—▽ : Thin planting

maximum was reached, and thereafter even decreased somewhat owing to maturity; it should be observed that, in the later stages, the assimilates produced in the shoots were mainly translocated to the ears. The reduction in dry weight of stems and sheaths was somewhat more marked at the highest density and started two weeks earlier, *viz.*, on June 26 (70 days after planting) in the dense planting, and on July 11 (85 days after seeding) in the thin one. The maximum dry weight of stems and sheaths per plant differed from 2.16 g for the highest density to 6.47 g for the lowest one. At the final harvest, it ranged from 1.86 g to 6.30 g for the highest and lowest densities, respectively. It is clear that the decrease in dry weight after the maximum was less pronounced in stems than in leaves (cf. figs. 39b and 40b).

c. Dry weight percentage

Fig. 40c shows that up to 43 days, the dry weight percentage of stems and sheaths decreased with increasing density, indicating that during this period competition for light seems to be more important. From the 4th interval up to the end of the season, the percentage increased with density, indicating that the increase in plant number per unit area favors earlier maturity. This is, of course, due to increased competition for water and nutrients which masked the light effect. The differences induced by varying the density became more marked with time and were maximal at the end of the season. By that time the dry weight percentage of stems and sheaths ranged from 62.2 for the highest density to 33.5 for the lowest one.

The dry matter percentage of stems and sheaths, as that of the entire plant, decreased during the early stages, up to the 3rd harvest, and thereafter increased progressively with time. This was most pronounced for the highest density. It is worth noting here again that with increasing density ripening was accelerated.

4. *Leaves and stems*

If stems and leaves together were taken into consideration, their fresh weight, dry matter and dry matter percentage tended to follow closely those of stems and sheaths in their reactions to varying density, since the latter represents the largest fraction of the entire plant during most of the season.

The same trend was observed in 1957.

5. *Ears*

a. Fresh weight

Fig. 41a indicates that, at all harvests, the fresh weight of ears per plant was greatly depressed by increasing density. The differences increased with age and were maximal after 103 days from planting.

The fresh weight of ears per plant increased progressively with time – and more rapidly so at the lowest density – till a maximum was reached after 103 days from sowing, and then decreased. The maximum ear fresh weight produced per individual plant varied from 4.95 g for the highest density to 12.89 g for the lowest one.

Similar results were obtained in 1957.

b. Dry weight

Fig. 41b shows that, with increasing density, the dry weight of ears per plant decreased. Competition became more marked as the plants advanced in growth, and the differences induced by density were maximal at the end of the season.
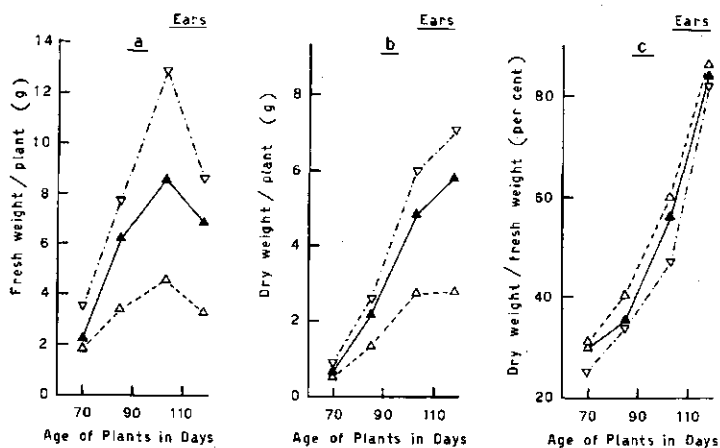
FIG. 41. Density effect on ears: fresh weight per plant (a), dry weight per plant (b), and dry weight percentage (c), in barley, at successive harvests, in 1958.
△-----△ : Dense planting   ▲——▲ : Normal planting   ▽—·—·▽ : Thin planting

At all densities, the dry weight of ears per plant increased rapidly with age, especially at the lowest density. Owing to earlier maturing, induced by increasing density, the highest dry weight of ears was obtained two weeks earlier at the dense planting, *viz.*, on July 29 (103 days after planting) at the highest density, and on August 14 at the lowest one. The final dry weight of ears per plant varied from 2.82 g for the dense planting to 7.03 g for the thin one.

The same trend was observed in 1957.

c. Dry weight percentage

Fig. 41c indicates that the dry weight percentage of ears, on the contrary, increased with increasing density. This suggests that competition for light was not responsible herefor. The highest differences induced by density were found on July 29 (103 days after sowing). By that time the dry weight percentage of ears varied from 59.6 for the highest density to 46.7 for the lowest one.

The dry matter percentage of ears increased rapidly with age, especially at the lower densities, till a maximum was reached at the end of the season.

Similar results were obtained in 1957.

6. *Seeds*

Since seeds represent the most important fraction of the plant for human use, it is of great interest to follow the effect of density on their development. Our data show that the effects of density and age on fresh weight as well as on dry weight and dry weight percentage of seeds followed closely those on the ears; the fresh and dry weight increased while dry matter percentage decreased with decreasing density. The differences in seed fresh and dry weight were statistically analysed at the last harvest and were found to be highly significant.

Similar results were obtained in 1957. These results confirm those of CLEMENTS *et al.* (1929) on wheat and sunflower, KONOLD (1940) on *Vicia faba*, SOPER (1952) on *Vicia faba*, the present author (KAMEL, 1954) on sesame, and HODGSON and BLACKMAN (1956) on *Vicia faba*.

1000-grain dry weight

Although at the final harvest in 1958, the seed number per unit area was

found to increase with density (cf. fig. 36b), yet the highest dry weight of seeds per unit area was obtained at the medium density (cf. Table 13 and page 81) This can be explained if the variations in 1000-grain dry weight induced by density are studied. According to our data, it was found that up to July 29 (103 days after planting), the 1000-grain dry weight increased with increasing density, mainly owing to earlier emergence of ears connected with rapid development of seeds at the highest density. The greatest differences between the highest and lowest densities which are found at that time, varied from 33.0 g for the former to 26.5 g for the latter. At the final harvest under investigation, owing to increased competition at the dense planting, and to completion of seed development at the normal one, the 1000-grain dry weight at the latter was highest. It can be concluded, therefore, that the predominance of the normal density in the production of seeds per unit area is primarily due to increase in seed size and seed weight and not in seed number.

At all densities, the 1000-grain dry weight increased with age to a maximum at the end of the season.

7. *Tops*

It has been demonstrated earlier that the fresh weight as well as the dry weight of leaves, stems and ears were greatly depressed by increasing density, wheil the dry matter percentage of these organs increased. And since these organs together compose the top of the plant, the variations induced by density in their fresh and dry weights and dry matter percentage may well be expected to be reflected in these characteristics of the entire tops.

a. Fresh weight

Fig. 42a indicates that, at all harvests, the fresh weight of tops per plant increased with decreasing density. The differences increased with age; obviously, at the first stages of growth competitition was not yet important. The largest differences in fresh weight of tops were observed in the period from June 26 to July 29 (70–103 days after planting). The differences were statistically analysed at the last harvest, and were found to be highly significant.

At all densities, the fresh weight of tops increased with time, was maximal after 70 days from sowing, and then decreased. The curve declines more sharply in the dense planting, indicating earlier maturity. The maximum fresh weight of tops per plant ranged from 19.24 g for the highest density to 51.46 g for the lowest.

The same trend was observed in 1957.

b. Dry weight

Fig. 42b shows that also the dry weight of tops per plant increased with decreasing density. The differences became more marked as the plants advanced towards maturity, and were maximal at the end of the season. The differences were statistically analysed by that time, and were found to be highly significant. Similar results were obtained by CLEMENTS *et al.* (1929).

Dry weight of tops per plant increased progressively with time, and more rapidly so at the lowest density. The maximum dry weight of tops was reached at the end of the season in the lowest and medium densities, and about two weeks earlier in the highest one, indicating earlier maturity. Owing to over-ripening and loss of dead leaves, the dry weight of tops at the dense planting tended to decrease in the period from July 29 to August 14 (103–118 days after seeding).

78   *Meded. Landbouwhogeschool, Wageningen* **59** *(5), 1–101 (1959)*

Values ranging from 4.926 g for the highest density to 14.298 g for the lowest one were obtained for the dry weight of tops per plant at the final harvest in 1958.

The same trend was observed in 1957.

c. Dry weight percentage

Fig. 42c indicates that, up to 43 days, the dry weight percentage of tops tended to increase with decreasing density. From this date up to maturity, the position was changed, and the percentage of dry matter in tops increased with density. This suggests that the effect of water and nutrient factors prevailed and masked the light effect. The differences induced by density increased with time, and were maximal at the end of the season, due to increased competition, obviously inducing earlier maturation. CLEMENTS et al. (1929) found that the available water, the nitrogen content of the soil, and the light intensity within the population decreased with increasing density. It seems that the prevalence of each depends not only on plant organs or characters, but also on the stage of growth.

The dry matter percentage of tops decreased during the early stages of growth, up to the 3rd harvest. This occurred at all densities but was most pronounced for the dense planting. Later on, the percentage increased progressively with age until the final harvest, the values for the dense planting always were the

TABLE 13. Density effect on dry weight per cm², in mg, of entire plant, roots, leaves, stems and ears, in barley, at successive harvests, in 1958.

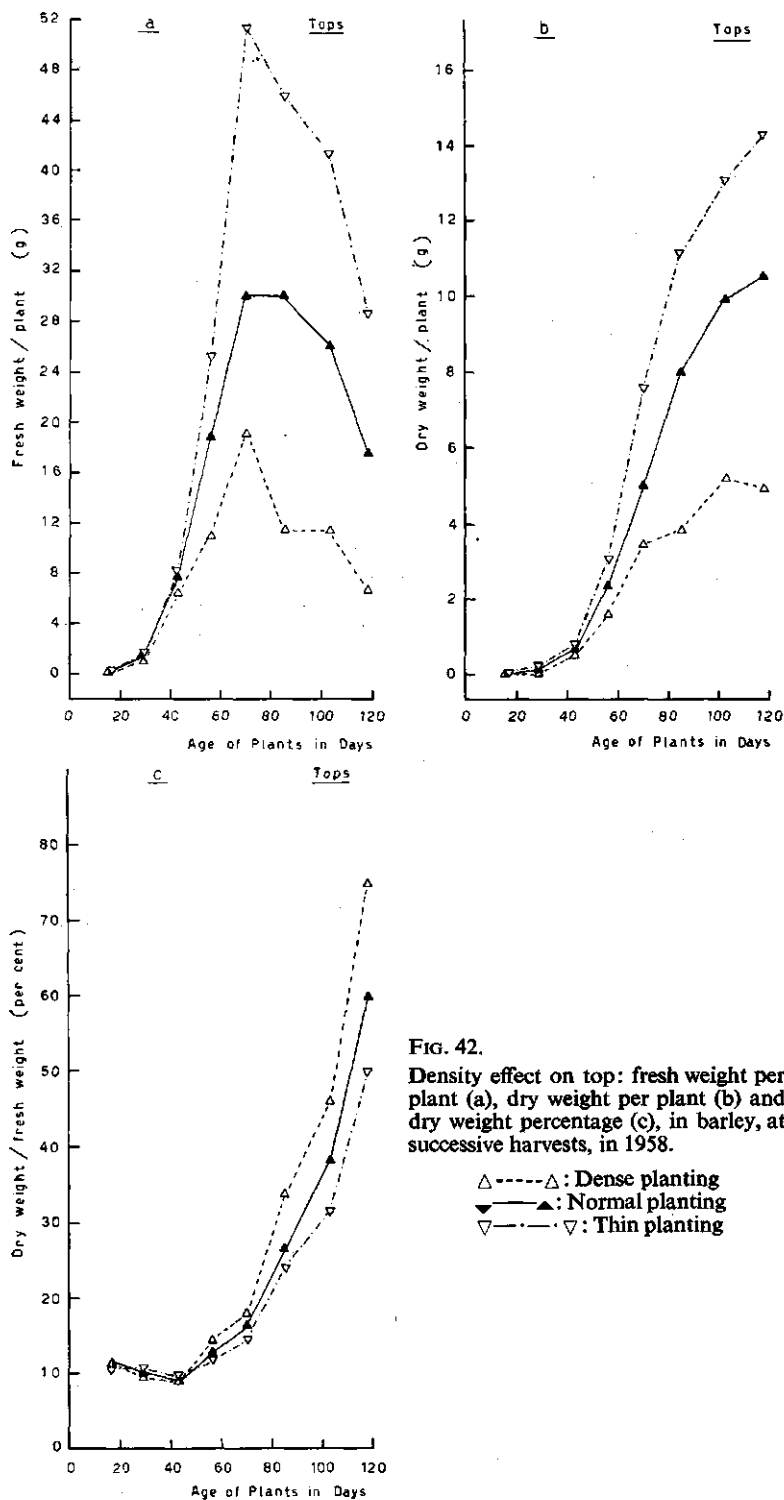| Plant density	Age of plants in days	Entire plant	Roots	Tops							
				Stems + Leaves				Ears		Total
				Leaves (Blades)		Stems + Sheaths	Total	Seeds	Total	
				Green	Total					
Dense	16	1.25	0.30	0.65	0.65	0.30	0.95	0.00	0.00	0.95
Normal		0.55	0.15	0.27	0.27	0.13	0.40	0.00	0.00	0.40
Thin		0.28	0.08	0.14	0.14	0.06	0.20	0.00	0.00	0.20
Dense	29	5.85	0.40	3.90	3.90	1.55	5.45	0.00	0.00	5.45
Normal		3.70	0.25	2.45	2.45	1.00	3.45	0.00	0.00	3.45
Thin		2.05	0.21	1.34	1.34	0.50	1.84	0.00	0.00	1.84
Dense	43	29.55	1.15	16.85	17.05	11.35	28.40	0.00	0.00	28.40
Normal		18.45	0.85	10.65	10.65	6.95	17.60	0.00	0.00	17.60
Thin		10.49	0.55	6.04	6.04	3.90	9.94	0.00	0.00	9.94
Dense	56	80.40	1.75	28.10	29.05	49.60	78.65	0.00	0.00	78.65
Normal		60.25	1.52	24.28	24.55	34.18	58.73	0.00	0.00	58.73
Thin		39.63	1.34	18.14	18.30	19.99	38.29	0.00	0.00	38.29
Dense	70	176.75	3.45	34.20	38.10	108.15	146.25	0.00	27.05	173.30
Normal		127.25	2.90	28.30	29.50	78.13	107.63	0.00	16.72	124.35
Thin		98.19	2.96	24.73	25.44	58.84	84.28	0.00	10.95	95.23
Dense	85	196.80	3.75	13.60	23.00	102.05	125.05	47.50	68.00	193.05
Normal		203.95	4.27	25.18	34.25	110.33	144.58	32.75	55.10	199.68
Thin		142.65	3.69	19.40	25.26	80.90	106.16	15.89	32.80	138.96
Dense	118	248.50	2.20	0.00	12.20	93.00	105.20	123.60	141.10	246.30
Normal		267.26	3.83	0.00	14.63	104.55	119.18	124.15	144.25	263.43
Thin		181.53	2.81	0.00	12.11	78.11	90.82	76.18	87.90	178.72

FIG. 42.
Density effect on top: fresh weight per plant (a), dry weight per plant (b) and dry weight percentage (c), in barley, at successive harvests, in 1958.

△-----△ : Dense planting
▼———▲ : Normal planting
▽—·—▽ : Thin planting

highest. This indicates that, with increasing density, ripening was accelerated by a more rapid translocation of cell constituents, owing to the absence of photosynthesis in the lower part of the plant. The lower leaves being unable to photosynthize due to increased mutual shading died off, and we may assume that before that all cell constituents translocated to the upper part. Several of the lower leaves then died, connected with early senescence and death. The maximum dry weight percentage of tops, attained at the end of the season, varied from 75 for the highest density to 50 for the lowest one. Notwithstanding all plots surely were to be considered as ripe at the last harvest, since all leaves were dead, there may have been a difference in the degree of maturity which, i.a., finds its expression in the above figures and in the date of full ripening. Full ripening was reached after 124 days from planting at the highest density and after 134 days at the lowest one.

With rare exceptions, the same trend was observed in 1957.

B." Growth in dry weight (on unit area basis)

In comparing various populations, any final analysis of the nature of competition must include an investigation of the interrelation between the growth of the individuals and the growth of the entire population. It was, therefore, decided, as next step, to follow the variations in growth in dry weight at each density on unit area basis.

The variations with time in dry weight of the entire plant, as well as of each of its individual organs, as affected by density, are brought out in Table 13 and fig. 43 for the 1958 experiment. It can be seen that up to 70 days, the dry weight per unit area of roots, leaves, stems (or stems and leaves), tops, and entire plant increased with increasing density, indicating that the increase in plant number could easily counterbalance the depression in dry weight per plant. Similarly, the dry weight per cm^2 of both ears and seeds showed the same trend during their first stages of development. Later on, the situation was changed in favor of the normal planting, indicating that the competition had become so intense that the increase in plant number per unit area above the normal density could not compensate the reduction in the dry weight per plant. In general, the differences induced by density increased progressively with time for roots, leaves, stems, ears, seeds, tops, and entire plant.

With few exceptions, the age trend on unit area basis was the same as that on
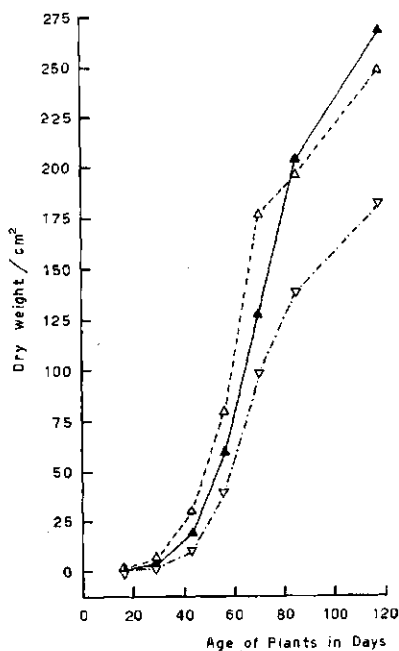

Fig. 43.
Density effect on dry weight per cm^2 of the entire plant, in barley, at successive harvests, in 1958.

△-----△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

individual plant basis (disregarding, for the moment, the density effects). At the final harvest, the dry weight per cm² of the entire plant was 248.5 mg for the highest density, 267.3 mg for the medium one, and 181.5 mg for the lowest one, while for seeds it was 123.6 mg in the dense planting, 124.2 mg in the normal one, and 76.2 mg in the thin one.

In 1957, with few exceptions, the same trend was observed. During that season competition was so intense that the prevalence of the normal planting started earlier, *viz.*, on July 11 (35 days after planting). The values for ears and seeds for the normal planting always were the higher ones.

ENGLEDOW (1925) found that the yield of cereal crops is positively correlated with plant number per unit area, CLEMENTS *et al.* (1929) on wheat and sunflower, KONOLD (1940) and SOPER (1952) on *Vicia faba* obtained similar results. HODGSON and BLACKMAN (1956) pointed out that with increasing density the yield of seeds per unit area rose to a maximum after which there was no significant change. There was some overall indication that at plant densities above the medium density, yield may decrease. In this connection, SMITH (1937) re-
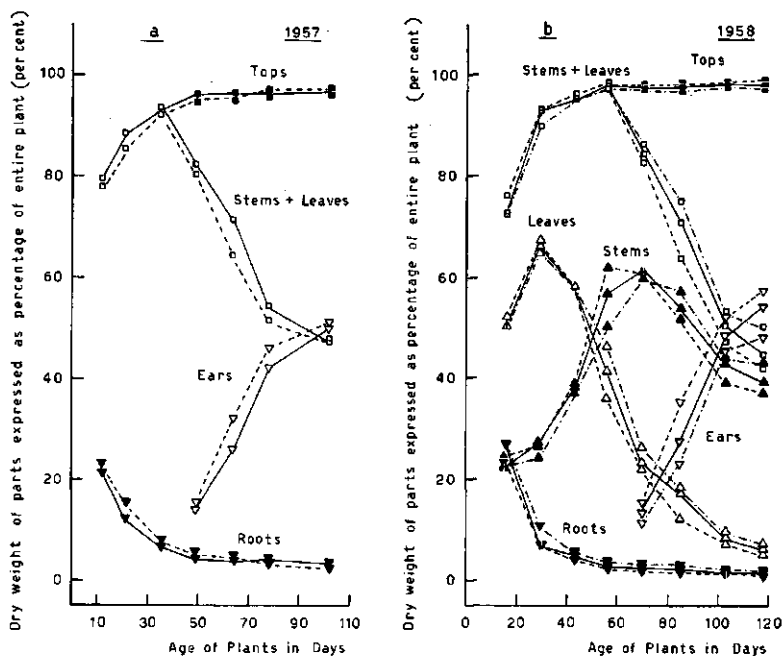
TABLE 14. Density effect on root and top growth expressed as a percentage of the total dry weight of the plant, in barley, at successive harvests, in 1958.

Plant density	Age of plants in days	Roots	Tops							
			Stems + Leaves					Ears		
			Leaves (Blades)		Stems + Sheaths	Total		Seeds	Total	Total
			Green	Total						
Dense		24.0	52.0	52.0	24.0	76.0		0.0	0.0	76.0
Normal	16	27.3	50.0	50.0	22.7	72.7		0.0	0.0	72.7
Thin		27.3	50.0	50.0	22.7	72.7		0.0	0.0	72.7
Dense		6.8	66.7	66.7	26.5	93.2		0.0	0.0	93.2
Normal	29	6.8	66.2	66.2	27.0	93.2		0.0	0.0	93.2
Thin		10.4	65.2	65.2	24.4	89.6		0.0	0.0	89.6
Dense		3.9	57.0	57.7	38.4	96.1		0.0	0.0	96.1
Normal	43	4.6	57.7	57.7	37.7	95.4		0.0	0.0	95.4
Thin		5.2	57.6	57.6	37.2	94.8		0.0	0.0	94.8
Dense		2.2	35.0	36.1	61.7	97.8		0.0	0.0	97.8
Normal	56	2.5	40.3	40.8	56.7	97.5		0.0	0.0	97.5
Thin		3.4	45.8	46.2	50.4	96.6		0.0	0.0	96.6
Dense		2.0	19.4	21.6	61.2	82.8		0.0	15.2	98.0
Normal	70	2.3	22.2	23.1	61.4	84.5		0.0	13.2	97.7
Thin		3.0	25.2	25.9	59.9	85.8		0.0	11.2	97.0
Dense		1.9	6.9	11.7	51.9	63.6		24.1	34.5	98.1
Normal	85	2.1	12.3	16.7	54.1	70.8		16.1	27.1	97.9
Thin		2.6	13.6	17.7	56.8	74.5		11.1	22.9	97.4
Dense		1.5	0.0	7.4	39.4	46.8		44.7	51.7	98.5
Normal	103	1.5	0.0	7.5	43.0	50.5		40.5	48.0	98.5
Thin		1.8	0.0	9.2	43.8	53.0		36.4	45.2	98.2
Dense		0.9	0.0	4.9	37.4	42.3		49.8	56.8	99.1
Normal	118	1.4	0.0	5.5	39.1	44.6		46.5	54.0	98.6
Thin		1.5	0.0	6.7	43.4	50.1		41.9	48.4	98.5

FIG. 44. Density effect on root and top growth expressed as a percentage of the total dry weight of the plant, in barley, at successive harvests, in 1957 (a) and in 1958 (b).
-----: Dense planting   ——: Normal planting   —·—·: Thin planting
▼: roots   △: leaves   ▲ : stems   □: stems + leaves   ▽: ears   ■: tops

ported that if a uniform distribution of plants in cereal crops was established at the higher densities in a normally variable crop, competition would be more severe, and the yield of the crop would not necessarily be increased.

C. Relative root and top growth

Table 14 and fig. 44b give the variation with time in root and top growth expressed as a percentage of the total dry weight of the plant as affected by density, at successive harvests, in 1958. It is evident that the percentage of roots, in accordance with the absolute values, increased with decreasing density while, on the contrary and in contrast to the actual dry weights, the percentage of tops increased with density. This suggests that competition for light was responsible herefor and that increasing density favors shoot growth relative to root growth.

In 1957, up to 64 days the reverse was true (fig. 44a), indicating that some factor other than light prevailed and masked its effect. It seems that in this season because of delay of sowing date, the plants obviously escaped the period during which light intensity was still low (planting was on June 6, while March is the proper time in sandy soils). As a consequence, competition for light was not so serious as that for water and nutrients. At a more advanced age (from 78 days after planting up to the end of the season), the same trend was observed as in 1958.

Up to the second harvest (29 days after sowing), in 1958, the percentage taken

by total leaves, in constrast to the actual values, tended to increase with density. This indicates that competition for light may be responsible herefor, since it has been established in the shading experiments that reduced light intensity favors leaf production. In the 3rd harvest, the percentage of total leaves seems to be unaffected by density, while that of the green leaves tended to decrease with increasing density following the absolute dry weight values. Later on, the percentage of total leaves as well as those of green leaves decreased with increasing density. Up to the last harvest still including green leaves (6th harvest), the percentage of dead leaves increased with density, indicating earlier maturity. During the last two harvests the dead leaf percentage decreased with increasing density.

During early stages of growth, up to 70 days, the percentage of stems and sheaths generally increased with density, but at more advanced age the reverse was true. It has been demonstrated previously that the absolute dry weight of stems and sheaths always decreased with increasing density. If stems and leaves were taken together, it was found that up to 56 days from planting, their percentage, in contrast to the actual weights, increased with density. Later on, it decreased with increasing density.

In 1957, the percentage of stems and leaves, in accordance with the absolute values, decreased with increasing density over the entire growth period.

In both seasons, the percentage of ears as well as of seeds, in contrast to the absolute values, increased with increasing density, indicating that the light factor is not responsible herefor and that increasing density favors seed production.

The results of 1958 show that with increasing density preference is given to leaf and stem formation during the first stages of growth, and to ear or seed production during more advanced age. The percentage of seed dry weight/total ear dry weight was found to increase with density and with age in both seasons, indicating that at higher densities ears are more efficient in forming seeds. Values ranging from 70 per cent for the highest density to 48 per cent for the lowest one were obtained after 85 days in 1958. It should, however, be observed that the reason for this result is in the fact that at lower densities more ears are being initiated which do not all develop many seeds.

Another interesting feature is to follow the variations in the percentage of each of the different organs with time. The percentage of roots, being maximal at the beginning, decreased progressively with time, and was minimal at the end of the season. Accordingly, the percentage of tops, being minimal at first, increased consistently with age and was maximal at the end of the season. The percentage of leaves increased till a maximum was reached after 29 days from planting in 1958, and thereafter decreased to a minimum towards the end of the season. This reduction in the percentage of leaves after the maximum is due at first to development of stems and later on to production of ears (cf. the curves for leaves, stems and sheaths, stems and leaves, ears and tops).

The percentage of stems increased progressively with time till the maximum was reached after 56 days at the highest density and two weeks later in the medium and lowest ones, in 1958, and then decreased, due to formation of ears.

The percentage of stems and leaves together increased progressively with age till a maximum was reached after 35 days in 1957 and after 56 days in 1958, thereafter it decreased owing to development of ears. The percentage of ears as well as of seeds increased rapidly with age, especially at the
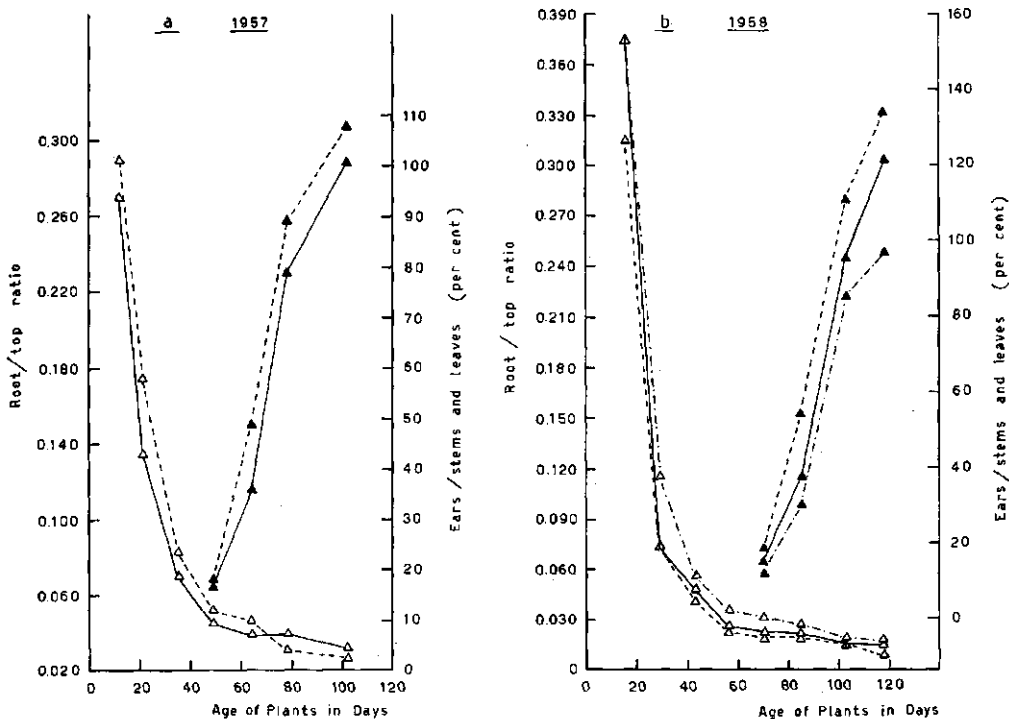
84

FIG. 45. Density effect on root/top ratio (root dry weight to top dry weight) and on ear/stem and leaf percentage (ear dry weight to stem and leaf dry weight, in per cent), in barley, at successive harvests in 1957 (a) and in 1958 (b).

-----: Dense planting   ——: Normal planting   —·—·: Thin planting

△ : root/top ratio ▲ : ears/stems and leaves in per cent

highest density, till the maximum was reached at the end of the season.

In 1957, the root/top ratio increased with increasing density during all harvests except the last two where the reverse was true (fig. 45a). In 1958, the ratio decreased with increasing density during the entire season (fig. 45b). HARRIS (1914) on corn seedlings and BARNES (1936) on carrots pointed out that the root/top ratio varied inversely with water supply while relative shoot growth decreased with decreasing water supply. In addition, many investigators have reported data like these showing a marked increase in relative root growth in drier soils. TURNER (1922), on barley, and BARNES (1936), on carrots, stated that the dry weight of roots, tops and entire plants decreased with an increase in (N), while the root/top ratio increased. MAXIMOV and LEBEDINCEV (1923), on bean, and MITCHELL and ROSENDAHL (1939), on white pine seedlings, found that the root/top ratio increased with increasing light intensity. This suggests that, in general, competition for water and nutrients was more pronounced in 1957, while that for light was more important in 1958. Regardless this fact, it is worth noting here that during certain stages of growth, the reverse was true, or all of these factors may act in the same direction.

A point of special interest is the efficiency of stems and leaves in producing ears (on dry weight basis). Fig. 45 illustrates also the efficiency of shoots (the

percentage of ear dry weight/stem and leaf dry weight) as affected by density, at successive harvests. It is clear that, in both seasons, the efficiency of shoots in producing ears increased with density.

At all densities, the percentage of ear dry weight/stem and leaf dry weight increased progressively with age, and more rapidly so at the higher densities – till a maximum was reached at the end of the season. Values ranging from 134 per cent for the dense planting to 97 per cent for the thin one were obtained at the last harvest, in 1958.

D. C/F ratio

Table 15 shows that, up to 29 days after planting, the C/F ratio tended to decrease with increasing density, indicating that the dry matter losses through respiration increased with decreasing density. The differences induced by density were not so marked, owing to the fact that by that time competition was not yet important. At more advanced age, the ratio increased with density due to increased mutual shading and consequently to increased senescence of the lower leaves, owing to absence of photosynthesis in the lower part of the plant at the higher densities. This favors earlier maturity. The differences induced by density increased with time, and were maximal at the last harvest still including green leaves (85 days after sowing), owing to increased competition. During this period, with increasing density, the proportion of the dry matter losses by respiration increased in a relative measure.

TABLE 15. Density effect on the C/F ratio, the ratio of non-photosynthetic system (roots, stems, dead leaves and reproductive organs) to the photosynthetic system (leaves), in barley, at successive harvests, in 1958.

Plant density	Age of plants in days					
	16	29	43	56	70	85
Dense planting	0.92	0.50	0.75	1.86	4.14	3.47
Normal planting	1.04	0.51	0.73	1.48	3.50	7.10
Thin planting	1.00	0.54	0.74	1.18	2.97	6.35

At all densities, the C/F ratio generally increased progressively as the plants advanced towards maturity. This is due to the increasing dominance of non-photosynthetic tissues over the photosynthetic system. C/F values, ranging from 13.47 for the highest density to 6.35 for the lowest one, were obtained after 85 days from planting, in 1958. IWAKI (1958) found that the C/F ratio in buckwheat tended to increase with density in the earlier stages of growth, but in the later stages no apparent correlation was observed. The ratio increased consistently with time.

E. Daily growth rate

Table 16 and fig. 46 show that, at all intervals, the daily growth rate per plant (dry matter increase in mg/day/plant) increased with decreasing density. The differences increased with time, and were maximal in the period from June 12 to 25 (56–70 days after sowing).

At all densities, the daily growth rate per plant increased rapidly with age – and the more so at the lowest density – till the maximum was reached in the
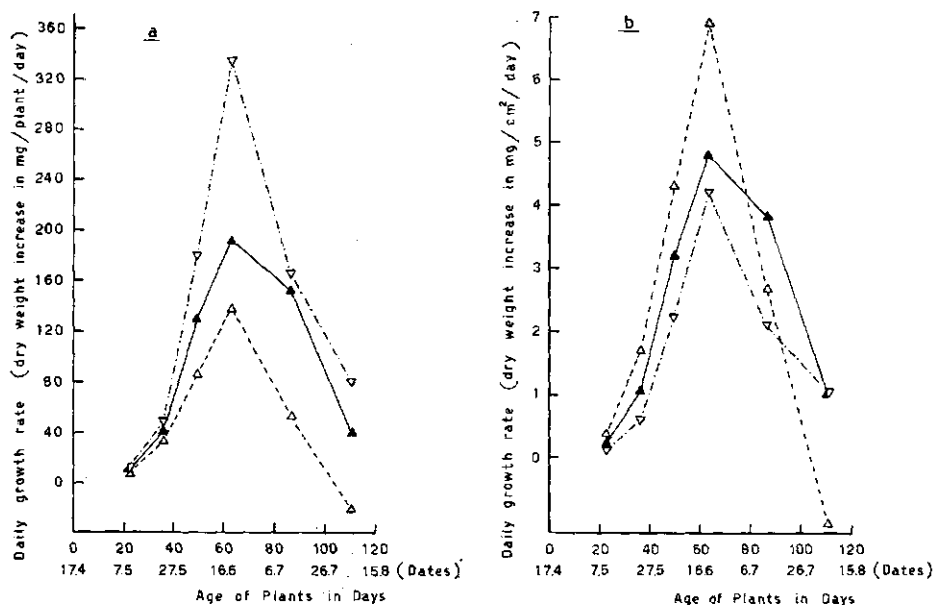
FIG. 46. Density effect on daily growth rate (dry weight increase in mg/day) per plant (a) and per cm² (b), in barley, at successive intervals, in 1958.
△-----△ : Dense planting   ▲———▲ : Normal planting   ▽—·—·▽ : Thin planting

TABLE 16. Density effect on daily growth rate (dry weight increase in mg/day) per plant and per cm², in barley, at successive intervals, in 1958.

Growing period	Daily growth rate/plant			Daily growth rate/cm²		
	Dense	Normal	Thin	Dense	Normal	Thin
May 3–May 15	7.1	9.7	10.9	0.36	0.24	0.14
May 16–May 29	33.9	42.1	48.9	1.70	1.05	0.61
May 30–June 11	85.9	128.6	179.3	4.30	3.22	2.24
June 12–June 25	137.4	191.4	334.6	6.87	4.80	4.18
June 26–July 28	53.0	151.2	165.3	2.65	3.78	2.07
July 29–Aug. 13	–21.0	40.6	80.9	–1.05	1.02	1.01

period from June 12 to 25, thereafter it decreased more sharply at the highest density. The maximum dry matter increase per day per plant varied from 137.4 to 334.6 mg for the dense and thin plantings, respectively.

On the contrary, the daily growth rate per unit area (fig. 46b) increased with density up to the period from June 12 to 25, indicating that the higher plant number per unit area could easily counterbalance the reduction in daily growth rate per plant. Later on, the situation was changed in favor of the medium density. Owing to earlier maturity, the highest density exhibited the lowest final daily growth rate per unit area. By that time, the plants at the dense planting not only ceased to increase in dry weight, but also suffered from losses in their capital dry weight, indicating earlier ripening.

In general, the age trend was the same as in the daily growth rate per plant. The maximum increase in dry weight per cm² per day varied from 6.9 mg for the highest density to 4.2 mg for the lowest one.

With rare exceptions, the same trend was observed in 1957.

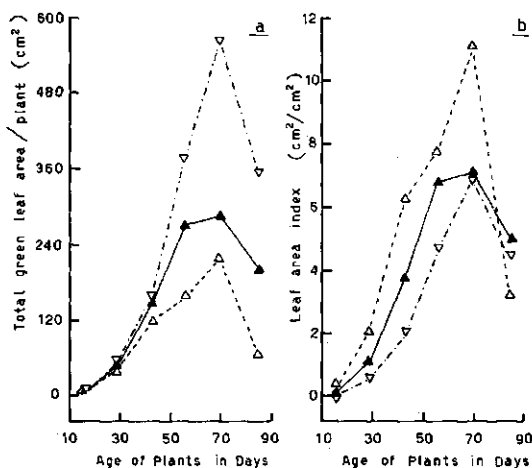## F. Growth in leaf area

Fig. 47 gives the mean leaf area per plant and the leaf area index, as affected by plant density, in 1958. Leaf area per plant increased with decreasing density; the differences became more marked with time.

At all densities, the leaf area per plant increased rapidly as the plants developed till the maximum was reached by late June (70 days after sowing) at the same time as the maximum fresh weight, after which it decreased. The maximum green leaf area per plant varied from 220.5 cm² for the dense planting to 562.3 cm² for the thin one. The last harvest still including green leaves was 85 days after planting, at which the green leaf area ranged from 66.5 cm² for the highest density to 353.8 cm² for the lowest one.

In contrast to the leaf area per plant, the leaf area index increased with density up to 70 days after seeding. This indicates that with increasing density, the higher plant number per unit area easily counterbalanced the reduction in leaf area per plant. Later on, this situation was changed in favor of the medium density. Owing to the higher degree of mutual shading of leaves, and consequently to early senescence, the dense planting had the least final green leaf area index.

In general, the age trend was the same as in the leaf area per plant. The same age trend was also observed by BOONSTRA (1929, 1937) and WATSON (1952). The maximum leaf area index was 11.0 for the highest density, 7.2 for the medium one and 7.0 for the lowest one. At 85 days, the leaf area index was 3.3 for the dense planting, 5.0 for the normal one, and 4.4 for the lowest one. These results, to some extent, are similar to those obtained by IWAKI (1958) on buckwheat.

G. Leaf-area ratio

Clearly, in fig. 48, two critical periods were noticed. In the early stages of growth, up to 47 days, the ratio increased with density, indicating that the light factor has played the major rôle. In the second period, from 47 to 85 days after sowing, the ratio decreased with increasing density. WATSON (1958) found that thinning the crop (or in other words decreasing density) caused a decrease in leaf-area ratio. And since BLACKMAN and WILSON (1951) reported that the leaf-

88   *Meded. Landbouwhogeschool, Wageningen 59 (5), 1–101 (1959)*
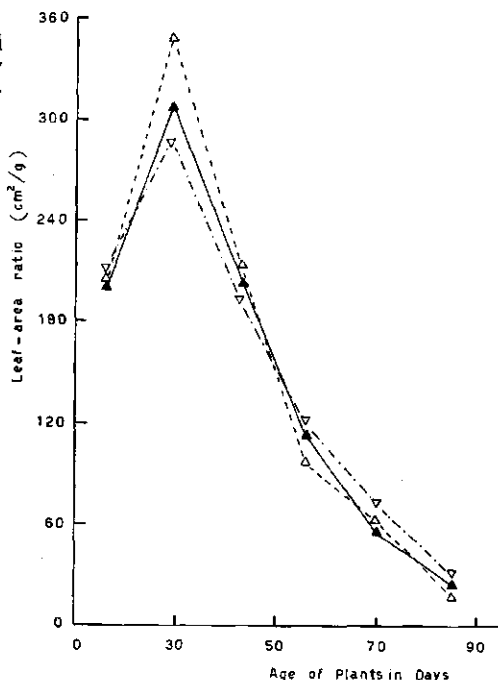
FIG. 48.
Density effect on leaf-area ratio (total green leaf area to entire plant dry weight), in barley, at successive harvests, in 1958.

△-----△ : Dense planting
▲———▲ : Normal planting
▽—·—·▽ : Thin planting

area ratio increased with increasing nutrient supply, it may be supposed that the severe competition for nutrients, induced by density at that time, has masked the light effect and was responsible for the observed decrease in the ratio.

It is clear from fig. 48 and from the preceding comments that, with the exception of the rise in the second harvest, the leaf-area ratio decreased with age. It is worth noting here again that, primarily, the rise in the second harvest – indicating that the increase in leaf area is relatively more rapid than that in dry weight – is just an expression of the fact that, obviously, in this stage of growth most of the acquired dry matter is converted into leaves. The plant, obviously, is now building its food factory, while, later on, the products of this factory are converted to a larger degree into other useful structures.

In this connection, it may still be observed that in the very first period, preference is given to root formation (cf. fig. 44).

II. DENSITY AND EFFICIENCY OF SOLAR ENERGY CONVERSION

Barley

The density effect on the efficiency of solar energy conversion, in barley, at successive periods, in 1958, is illustrated in fig. 49. At all densities, the efficiency was found to increase rapidly with time till it reached a maximum between June 12 and July 10, *viz.*, in the period from June 12 to June 25 (56–70 days after planting) for the dense and thin plantings, and from June 26 to July 10 (70–85 days after sowing) for the normal planting. Thereafter, it decreased to a minimum at the end of the season. The rise and fall before and after the maximum are sharpest in the dense planting, and tended to be more flattened as the density decreased. This may be due, in part, to the more rapid growth per unit area before reaching the maximum, and to early senescence after the maximum in the dense planting.

From May 16 to June 25 (29–70 days after planting) the efficiency increased with density, which may be attributed to increased mutual shading together
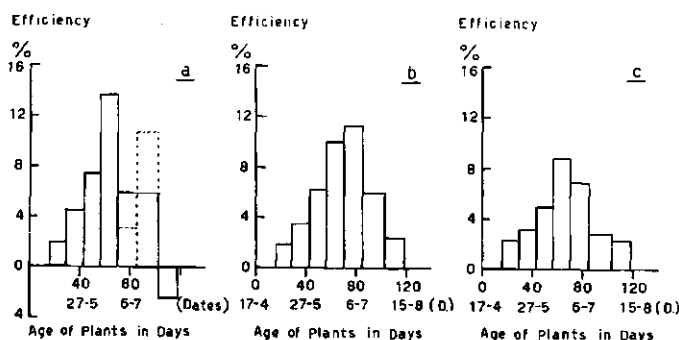
FIG. 49. Density effect on the efficiency of solar energy conversion during growth (in per cent), in barley, at successive intervals, in 1958.
a: Dense planting   b: Normal planting   c: Thin planting

with some other growth attributes favorable for higher efficiency. Later on, in the period from June 26 to July 28 (70–103 days after seeding), owing to increased competition and senescence, connected with a higher degree of mutual shading unfavorable for a healthy state of the lower part of the plant, the position was changed in favor of the normal planting, followed by the dense one while the thin planting came at the end.

The dotted lines in fig. 49a give the efficiency values in the dense planting during the periods from June 26 to July 10 and from July 11 to July 28, as actually observed. The sudden drop (after the maximum) in the first period, and the sharp rise in the second one seem to be incomprehensible as compared with the other densities in the same part of the season or with the same density in the previous parts of the season. An exceedingly unhappy variation in sampling may have been responsible for these deviations. If the first of the two harvests in question is disregarded, we obtain the full-drawn line which has been taken as a base for the previous discussion.

During the last period, extending from July 29 to August 13 (103–118 days after sowing) the efficiency again was minimal. It was still positive in the medium and thin densities in favor of the former, while it was negative in the dense one owing to over-maturing and to loss of dry leaves and smaller shoots.

The maximum efficiency value was 13.7, 10.0 and 8.8 per cent for the dense, normal and thin plantings, respectively. In 1957, nearly the same trend was observed with the only exception that the normal planting always exceeded the dense one.

The average efficiency during the entire growing season increased with increasing density up to the normal planting, and decreased with further increase in density, following closely the final dry weight per unit area. The average efficiency value was 2.3 per cent for the dense planting, 2.9 per cent for the normal one, and 1.8 per cent for the thin one. Statistical analysis showed that the differences induced by density were highly significant. With increasing density, up to the normal planting (250 plants/m²) the depression in growth owing to competition was overcome by the increase in plant number per unit area. With further increase up to 500 plants/m², competition had become so intense that the increase in plant number obviously could not counterbalance the decrease in the final yield per plant. Since seeds represented 49.8 per cent of the entire plant in the highest density, 46.5 per cent in the medium one and 41.9 per cent

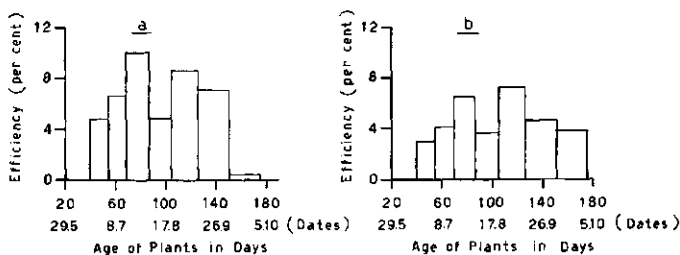90   *Meded. Landbouwhogeschool, Wageningen 59 (5), 1–101 (1959)*

FIG. 50. Spacing effect on the efficiency of solar energy conversion during growth (in per cent), in mangold, at successive intervals, in 1958.
a: Close spacing   b: Wide spacing

in the lowest one, the practical efficiency was 1.16, 1.37 and 0.77 per cent for the dense, normal and thin plantings, respectively.

As far as dense and normal plantings are concerned, similar results were obtained in 1957.

Mangold

The spacing effect on the efficiency of solar energy conversion, in mangold, at successive intervals, in 1958, is brought out in fig. 50. Although fodder-beet plants remain in a vegetative state in the first season and continue to grow until harvest, yet an age trend was observed, obviously less pronounced than that in barley. In general, the efficiency tended to increase progressively with age up to a maximum in the period from July 17 to August 3 (69–87 days after planting) for the close spacing, and in the period from August 22 to September 11 (105–126 days after sowing) for the wide spacing; thereafter it decreased to a minimum at the end of the season. It was found that the increase and the decrease in the efficiency were less pronounced for the wide spacing, where the figure tends to be more flattened. This may be attributed, to some extent, to the fact that the plants in the wide spacing increased less rapidly in dry weight per unit area, reached their maximum growth later and remained in a vigorous state for a longer time as compared with those in the close spacing. In this connection, it may be mentioned that TAKEDA and MARUTA (1956) found that in rice, light saturation was reached first in the thickest stand of plants. With customary spacing (12 × 12 cm), the maximum rate extended from full tillering to the booting stage and then decreased, while with wide spacing (24 × 24 cm or wider), maximum photosynthesis was found at the stage of active tillering, and then decreased.

At all intervals but the last one, the efficiency increased with density. During the last period, from October 7 to 31 (151–176 days after sowing), the efficiency decreased with increasing density. By that time a higher number of leaves were in a state of senescence, and little growth would take place in the dense planting. Most of the photosynthetic products were lost through respiration, and the efficiency of solar energy conversion was greatly depressed.

The maximum efficiency was 10.0 and 7.2 per cent for the close and wide spacings, respectively.

The average efficiency during the entire growing season, in contrast to that of barley, was found to increase with density up to three times the normal density, following closely the final dry weight per unit area. Similar results were obtained

by BERNARD (1956) on several plant species. It is clear that with increasing density, the suppression in growth per plant due to competition was easily counterbalanced by the increase in plant number per unit area. The average efficiency value was 4.4 per cent for the close spacing and 3.0 per cent for the wide one; the differences were highly significant. These values are much higher than those found for barley. Such difference between barley and mangold may be due primarily to differences in the form of the two plants. In barley, the leaves are situated along a tall stem, and so are distributed over a wide range above the ground (except in the very early stages of growth), while in mangold they are produced in a narrow zone near the ground on an axis that does not elongate in the first season. As a result, the leaves of the fodder-beet stand, during most of the stages, especially that of maximum growth, seem to be more uniformly illuminated than that of a barley stand. Thus, with increasing density, a general reduction in light intensity over the whole leaf surface of the mangold crop may occur, while in barley its main effect may be to increase the fraction that receives light of low intensity near or below the compensation point, without much affecting the illumination of the upper surface.

Since a smaller fraction of the leaf surface of mangold plants is exposed to light intensities below the compensation point or to those above saturation, it can be concluded that mangold (a short crop) is more efficient in utilizing daylight intensity in photosynthesis than barley. Moreover, because of the fact that radiation is distributed more efficiently over the leaf area, the advantage of the short crop increases with increasing density. As a result, the periodic, as well as the average efficiency in mangold increased with increasing density up to three times the normal planting, while in barley the average efficiency was greatly depressed by increasing the density above the normal planting.

It may be also suggested here that in root crop (*vs.* grain crop) competition is less intense so that increase in number of plants, even to three times the normal planting, could easily compensate for the reduction in growth per individual plant.

CHAPTER VI

GENERAL DISCUSSION

The results of the present study furnish some information on the time trend of solar energy conversion efficiency, as connected with growth, from planting up to maturity. Shading and density effects were also taken into consideration to test the validity of the supposition that excessive solar radiation in summer may be one of the chief reasons for the low average efficiency under natural conditions. It has been established from our shading and density experiments that light was in great excess of plant requirements during the early and the late stages of growth in barley, and during most of the growing season in mangold.

Under normal field conditions, the efficiency of solar energy conversion was low during the early stages. It was found also from our experimental data on the growth of barley that, by that time, the plants were still less active, with short stems, few tillers and leaves, small leaf size, and small total green leaf area, low fresh and dry weight and low daily growth rate, thin leaves with low absorbing capacity, etc. As the plants developed, the efficiency increased till the maximum was reached at the same time of maximum shoot and leaf number, growth rate,

fresh weight (of roots, leaves, stems, tops, and entire plant), and total leaf area. Round this period, leaves and stems attained their highest dry weight. Maximum height and leaf thickness was not yet reached. Because of death and senescence after the vigorous growth in annual plants, the efficiency decreased with time and with increased senescence following the reduction in leaf area, fresh weight, growth rate and shoot or leaf number. This was less pronounced at the lower light intensities and the thinner densities owing to extension of the growth season connected with less pronounced senescence.

Growth was greatly affected by reduction of the light intensity and the responses of the plants to shading with time were well reflected in their efficiency as converters of solar radiation. Thus, the plants at the lower intensities, owing to extension of the growth period, and to their predominance in daily growth rate, fresh weight, leaf area, shoot and leaf number, etc. exhibited the higher efficiency values during later stages. The average efficiency was found to decrease with reduction of light intensity, although the periodic efficiency increased with shading at the early and the late stages of growth. It was advanced that in shade plants (vs. plants in the open) two controversial tendencies influence the efficiency: 1. Increase of efficiency of photosynthesis by less excess of light. 2. Decrease of the efficiency of growth by unfavorable balance between photosynthesis and respiration. It was suggested that the decrease in the efficiency of growth induced by the detrimental effect of shading may prevail and offset the beneficial effect of reduction of light intensity in increasing the efficiency of solar energy conversion.

With reference to density, it has been established for a long time that for efficient use of light by the vegetation on an area of land, the first requirement is that all radiation should be intercepted by photosynthetic tissues. In higher plant communities in which this occurs the total leaf area surface is far greater than that of the land on which the plants are growing. The upper part of the plants receives light at full daylight intensity, while the remainder receives largely reflected and diffuse light at a much lower level of intensity. Since, in general, the individual leaves utilize the light more efficiently when they receive it at relatively low intensity, and since increasing density increased mutual shading, it follows that, within limits, the larger the area or the amount of photosynthetic tissue over which the light can be scattered, the greater will be the production of dry matter formed per unit light energy on a given area of land. But with increasing density of any given crop, especially cereal crops, increase in its efficiency of utilizing light would be offset by an increase in the relative importance of other limiting factors, and by acceleration of death. The density and the stage of growth at which the other limiting factors over-ride gains from increased mutual shading seems to depend on the form of the plant. In barley (a grain, tall crop) increasing the density up to two times the normal planting (500 plants/m^2) favored the production of dry matter per unit area and lead to higher efficiency values only during the first stage of growth. Later on, owing to increased competition for water, light and nutrients, this was no more true, and increase in the number of plants per unit area only up to the normal density (250 plants/m^2) induced higher yield and efficiency values. The responses of the plants to density during this period influenced the final yield and the average efficiency over the entire growing season. It must be kept in mind that the reactions with time of the individual plants, as well as, of whole the population to variations in density are well reflected in their efficiencies as converters of radiant energy.

In mangold (a root, short crop) increasing the density up to three times the normal planting (25 plants/m²) induced maximum yield and higher efficiency values per period during all intervals but the last one, and over the entire growing season.

Finally, it can be concluded that the efficiency of solar energy conversion following closely the age trend of growth, is not constant and dependable on the stage of growth.

SUMMARY

The growth and the efficiency of solar energy conversion, in barley and mangold, as affected by shading or density, at successive intervals, were studied under field (natural) conditions at Wageningen, during the growing seasons 1957 and 1958.

SHADING EFFECTS

A. The growth of barley was greatly affected by shading.

1. At the early stages, plant height increased with shading, but later on maximum height was obtained under full daylight illumination, in 1957, and under 80 per cent intensity, in 1958. With increasing light intensity, internode length decreased and shoot diameter increased.

2. In 1957, shoot and leaf number per plant decreased with shading, while in 1958 this was no more true at the late stages. Shoot and leaf number increased to a maximum and then decreased. The maximum was retarded by shading, and senescence started earlier at the higher light intensities. The number of dead leaves and the dead leaf percentage (on number and dry weight basis) decreased with shading, and increased with time. With decreasing light intensity leaf length, leaf ratio, and leaf area increased, while leaf breadth decreased.

3. Spike development and awn emergence were delayed by shading. Ear length, ear number per plant, seed number per ear or per plant, and efficiency of shoots in producing ears or of ears in forming seeds (on number and dry weight basis) increased with increasing light intensity and with time. Maximum ear length was reached earlier at the higher light intensities.

4. With decreasing light intensity, there were reductions in fresh and dry weight of roots, ears, seeds, tops, and entire plant. This was also true for dry weight of leaves and stems during the entire season, and for their fresh weight during all harvests but the late ones. The fresh and dry weight of roots, leaves and stems, and the fresh weight of ears, tops, and entire plant increased with time to a maximum, and then decreased. The dry weight of ears, seeds, tops, and entire plant increased progressively with time. The dry weight percentage, in general, increased with increasing light intensity. It dropped at first, then increased with time (except in ears and seeds, where it is increased progressively).

5. Leaf thickness, root/top ratio, 1000-grain dry weight, root percentage, and seed or ear percentage decreased with shading, while leaf percentage, stem and leaf percentage and top percentage increased. During the first stages, stem percentage decreased with shading, while later on the reverse was true. Root/top ratio and root percentage decreased with time, while the 1000-grain dry weight, leaf thickness, and the percentage of either seeds, ears, or tops increased. Leaf percentage and stem percentage increased to a maximum, and then decreased.

6. The C/F ratio, the ratio of non-photosynthetic tissues (roots, stems, dead leaves and reproductive organs) to photosynthetic tissues (green leaf blades) increased with increasing light intensity and with time. The daily growth rate and the green leaf area increased with increasing light intensity up to 66 days, while the reverse was true at the late stages. They increased with time to a maximum and then decreased. The leaf-area ratio decreased with increasing light intensity and with time.

7. Shading prolongs the vegetative and the vegetation period, and is unfavorable for seed production.

B. The efficiency of solar energy conversion, in barley, was greatly affected by shading. At the early stages and the late stages, the efficiency increased with decreasing light intensity, while at the middle stages the reverse was true. The average efficiency during the entire growing season increased with increasing light intensity up to full daylight. Values ranging from 2.9 per cent for full daylight intensity to 1.4 per cent for the 25 per cent light intensity were obtained in 1958 for the average efficiency.

It has been demonstrated that the efficiency of solar energy conversion under normal field conditions increased with time to a maximum (nearly at mid-season), then decreased to reach a minimum at the end of the season. It followed closely the time trend of growth, and as a result its value is extremely dependent on the stage of growth. The highest efficiency values were attained, in general, at the stages of vigorous growth for a period of about 4 to 6 weeks. In 1958, a maximum of 13.6 per cent of the photosynthetic radiation for the full daylight intensity was obtained.

DENSITY EFFECTS

A. The growth of barley was greatly influenced by density.

1. Up to 70 days, in 1958, shoot length increased with density, but at late stages and also during the entire season in 1957 it decreased with further increase in density above the normal one. With increasing density internode length increased, and shoot diameter decreased.

2. Shoot and leaf number per plant decreased with density, while that per unit area increased with density up to 35 days in 1957, and to 85 days in 1958; later on the higher number was attained at the medium density. Maximum shoot number and leaf number was reached earlier, and senescence started earlier at the higher densities. The dead leaf percentage increased with density. At the early stages, leaf length and leaf area increased with density, while at late stages it decreased in this order. Leaf breadth decreased, while leaf ratio (length/breadth) increased with density.

3. Spike development and awn emergence were speeded up by increase in density. Ear length, ear number per plant, and seed number per ear or per plant increased with decreasing density. Maximum ear length was obtained earlier at the dense planting. Ear and seed number per unit area increased with density in 1958, while, in 1957, this was not true for seeds, and for ears only at the late stages. The efficiency of shoots in producing ears, or of ears in forming seeds, increased with density.

4. With increasing density, there were reductions in fresh and dry weight per plant of roots, leaves, stems, or stems + leaves, ears, seeds, tops, and entire plant. In 1958, up to 70 days, the dry weight per unit area of roots, leaves, stems,

stems + leaves, tops, and entire plant increased with density. Seed and ear dry weight per unit area showed the same trend up to 85 days. Later on, the situation was changed in favor of the medium density. The dry weight percentage of roots, ears, and seeds increased with density. In the first stages, the dry weight percentage of leaves, stems, stems + leaves, tops, and entire plant decreased with density, later on the reverse was true.

5. Leaf thickness increased with density. The 1000-grain dry weight increased with density at all harvests, except the last one. Root percentage decreased, and top percentage increased with density in 1958; in 1957 the reverse was true up to 64 days. At the first stages, in 1958, leaf percentage and stem percentage increased with density, while at the late stages they decreased; in 1957, leaf and stem percentage decreased with increasing density during the entire season. In both seasons, seed or ear percentage increased with density. Root/top ratio, in general, increased with density in 1957, and decreased with increasing density in 1958.

6. The C/F ratio, the ratio of the non-photosynthetic system (roots, stems, dead leaves and reproductive organs) to photosynthetic one (green leaf blades) decreased in the early stages, and increased in the late ones with increasing density. With increasing density, daily growth rate, and green leaf area per plant were reduced. The daily growth rate, and the leaf area per unit area increased at first with increasing density, but the final values were highest for the medium density. The leaf-area ratio increased with density in the first stages, while the reverse was found in the late stages.

7. The time trend was the same as for shading.

8. Maximum growth occurred earlier, and ripening was accelerated at the higher densities.

B. The efficiency of solar energy conversion was greatly influenced by density. In barley, up to the period from 56 to 70 days, the efficiency increased with density, later on the position was changed in favor of the medium density. The average efficiency over the entire season increased with density up to the normal planting, and was lower again at the highest density. Values of 2.3 per cent for the dense planting, 2.9 per cent for the normal one, and 1.8 per cent for the thin one were obtained in 1958 for the average efficiency.

In mangold, the periodic as well as the average efficiency increased with density. Values of 4.4 per cent for the close spacing, and 3.0 per cent for the wide one were obtained in 1958. The maximum efficiency was reached earlier at the close spacing.

The age trend was the same as for shading, being less pronounced in mangold. The highest efficiency values also covered a longer period in this crop. A maximum of 13.7 and 10.0 per cent of the photosynthetic radiation for the dense planting in barley and mangold, respectively, was reached in 1958.

In general, the responses of the plants with time, to shading and density are well reflected in their efficiencies as converters of solar radiation.

ACKNOWLEDGEMENTS

SAMENVATTNIG

Te Wageningen werd bij gerst en voederbiet onder natuurlijke omstandigheden (in het veld) gedurende het seizoen 1957 en 1958 in opeenvolgende perioden de invloed van lichtverzwakking en plantdichtheid op de groei en het rendement van de omzetting van de zonne-energie bestudeerd.

DE INVLOED VAN LICHTVERZWAKKING

A. Verzwakken van het licht had een sterke invloed op de groei van gerst.

1. In de vroege stadia nam de hoogte van het gewas toe bij lichtverzwakking, doch later – althans in 1957 – werd de maximum hoogte bereikt bij volle natuurlijke belichting, terwijl deze in 1958 werd verkregen bij een intensiteit van 80 % van het natuurlijke daglicht. Bij toenemende lichtintensiteit nam de lengte der internodiën af en de diameter van de spruit toe.

2. In 1957 nam bij lichtverzwakking het aantal spruiten en bladeren per plant af, terwijl dit in 1958 niet meer opging voor de late stadia. Het aantal spruiten en bladeren nam toe tot een maximum bereikt werd om dan af te nemen. Het bereiken van het maximum werd vertraagd door lichtverzwakking. Ouderdomsverschijnselen traden eerder op bij de hogere lichtintensiteiten. Het aantal afgestorven bladeren en het percentage afgestorven bladeren (betrokken op aantal en op drooggewicht) nam af bij verzwakken van het licht en nam toe in de tijd. Bij afnemende lichtintensiteit namen de lengte van de bladeren, de verhouding lengte/breedte en het bladoppervlak toe, terwijl de breedte van de bladeren afnam.

3. De ontwikkeling van de aar en het tevoorschijn komen van de kafnaalden werden door lichtverzwakking vertraagd. De lengte van de aar, het aantal aren per plant, het aantal korrels per aar of per plant en de productiviteit van de spruiten bij het vormen van aren of van de aren bij het vormen van korrels (betrokken op aantal en drooggewicht) nam toe bij toenemende lichtintensiteit en in de tijd. De grootste lengte van de aar werd bij de hogere lichtintensiteiten eerder bereikt.

4. Bij afnemende lichtintensiteit traden lagere vers- en drooggewichten op bij wortels, aren, korrels, bovengrondse delen en gehele planten. Dit gold ook voor het drooggewicht van bladeren en stengels gedurende de gehele teeltperiode en voor hun versgewicht gedurende alle perioden behalve de latere. Het vers- en drooggewicht van wortels, bladeren en stengels en alleen het versgewicht van aren, bovengrondse delen en gehele planten nam toe in de tijd tot een maximum,

om vervolgens af te nemen. Het drooggewicht van aren, korrels, bovengrondse delen en gehele planten nam versneld toe in de tijd. Het drooggewicht-percentage nam in het algemeen toe bij toenemende lichtintensiteit; na een aanvankelijke daling nam het mettertijd toe.

5. De bladdikte, de verhouding wortel/bovengrondse delen, het duizend-korrel-drooggewicht, het percentage wortels, en het percentage korrels of aren, nam af bij verzwakken van het licht, terwijl de bladeren, de stengels en bladeren samen, en de bovengrondse delen procentueel toenamen. Gedurende de eerste stadia namen de stengels procentueel af bij lichtverzwakking, terwijl later het omgekeerde het geval was.

De verhouding wortels/bovengrondse delen en het percentage wortels namen af in de tijd, terwijl het duizendkorrel-drooggewicht, de bladdikte en de percentages korrels, aren en bovengrondse delen toenamen. Bladeren en stengels namen procentueel toe tot een maximum en namen vervolgens af.

6. De C/F verhouding (niet-photosynthetisch actief weefsel/photosynthetisch actief weefsel) nam toe bij toenemende lichtintensiteit en tevens in de tijd. De dagelijkse groeisnelheid en het groene bladoppervlak namen de eerste 66 dagen toe bij toenemende lichtintensiteit, terwijl in de late stadia het omgekeerde het geval was. Deze groodheden namen in de tijd toe tot een maximum, en namen vervolgens af. De verhouding bladoppervlak/totaal drooggewicht nam af bij bij toenemende lichtintensiteit en tevens in de tijd.

7. Verzwakken van het licht verlengt de vegetatieve fase en de vegetatie-periode en is ongunstig voor de korrelproduktie.

B. Het rendement van de omzetting van de zonne-energie stond bij gerst sterk onder de invloed van lichtverzwakking. In de vroege en in de late stadia nam het rendement toe bij afnemende lichtintensiteit, terwijl in de midden-stadia het omgekeerde zich voordeed.

Het gemiddelde rendement over de gehele teeltperiode nam bij toenemende lichtintensiteit toe tot de intensiteit van vol daglicht bereikt was. Er werden in 1958 waarden voor het gemiddelde rendement verkregen die zich uitstrekten van 2.9 procent voor de vol-daglicht intensiteit tot 1.4 procent voor de intensiteit van 25 % vol daglicht. Er werd aangetoond, dat het rendement van de omzetting van de zonne-energie onder normale veldomstandigheden in de tijd toenam tot een maximum (bijna in het midden van de teeltperiode), vervolgens afnam om een minimum aan het einde van de teeltperiode te bereiken. Het rendement volgde ten naaste bij het groeiverloop en dientengevolge is de grootte ervan uitermate afhankelijk van het groeistadium. De hoogste waarden voor het rendement werden in het algemeen in de stadia van krachtige groei, gedurende een periode van ongeveer 4 tot 6 weken, bereikt. In 1958 werd een maximum van 13.6 procent van de photosynthetisch actieve straling verkregen voor de vol-daglicht intensiteit.

DE INVLOED VAN DE PLANTDICHTHEID

A. De plantdichtheid had een grote invloed op de groei van gerst.

1. In de eerste 70 dagen nam in 1958 de lengte van de spruit met de dichtheid toe, maar in de late stadia en ook gedurende de gehele teeltperiode in 1957, nam deze af bij verdere vergroting van de dichtheid boven de normale. Bij toenemende dichtheid nam de lengte der internodiën toe en de diameter van de spruit af.

98

2. De aantallen spruiten en bladeren per plant namen met de dichtheid af, terwijl die per eenheid van oppervlakte gedurende de eerste 35 dagen in 1957 en de eerste 85 dagen in 1958 met de dichtheid toenamen; later werden de grootste aantallen bij middelgrote dichtheid bereikt. De maximum aantallen spruiten en bladeren werden eerder bereikt bij grotere plantdichtheid, waarbij tevens eerder ouderdomsverschijnselen optraden. Het percentage afgestorven bladeren nam met de dichtheid toe. In de vroege stadia namen de bladlengte en het bladoppervlak met de dichtheid toe, terwijl ze in de late stadia bij toenemende dichtheid afnamen. De breedte der bladeren nam af, terwijl de lengte/breedte-verhouding der bladeren met de dichtheid toenam.

3. De ontwikkeling van de aar en het verschijnen van de kafnaalden werden versneld door grotere dichtheid.

De lengte van de aar, het aantal aren per plant en het aantal korrels per aar of per plant namen toe bij afnemende dichtheid. De maximum lengte van de aar werd eerder bereikt bij dicht planten. Het aantal aren en korrels per eenheid van oppervlak nam in 1958 tegelijk met de dichtheid toe, doch in 1957 gold dit niet voor de korrels, en voor de aren alleen in de late stadia. De productiviteit van de spruiten bij het vormen van aren, of van de aren bij het vormen van korrels nam met de dichtheid toe.

4. Bij toenemende dichtheid waren de vers- en drooggewichten per plant van wortels, bladeren, stengels of stengels + bladeren, aren, korrels, bovengrondse delen en gehele planten lager. In 1958 nam gedurende de eerste 70 dagen bij toenemende dichtheid het drooggewicht per oppervlakteeenheid van wortels, bladeren, stengels, stengels + bladeren, bovengrondse delen en gehele planten toe. Het drooggewicht per oppervlakte-eenheid van korrels en van aren vertoonde de eerste 85 dagen hetzelfde verloop. Later veranderde de situatie ten gunste van de middelgrote dichtheid. Het drooggewichtpercentage van wortels, aren en korrels nam met de dichtheid toe. In de eerste stadia nam het drooggewichtpercentage van bladeren, stengels, stengels + bladeren, bovengrondse delen en gehele planten af bij toenemende dichtheid; later gold het omgekeerde.

5. De bladdikte nam toe met de dichtheid. Het duizendkorrel-drooggewicht nam met de dichtheid toe bij iedere oogst behalve de laatste. Het percentage wortels nam in 1958 bij toenemende dichtheid af, terwijl het percentage bovengrondse delen toenam; het omgekeerde trad op gedurende de eerste 64 dagen in 1957. In de eerste stadia in 1958 namen bladeren en stengels, met de dichtheid, procentueel toe, terwijl ze in de late stadia afnamen. In 1957 namen bij toenemende dichtheid bladeren en stengels procentueel af gedurende de gehele teeltperiode.

In beide jaren namen korrels of aren procentueel toe met de dichtheid. De verhouding wortel/bovengrondse delen nam in 1957 in het algemeen met de dichtheid toe en nam in 1958 bij toenemende dichtheid af.

6. De C/F verhouding (niet-photosynthetisch actief weefsel/photosynthetisch actief weefsel) nam bij toenemende dichtheid in de vroege stadia af, doch nam in de late stadia toe. Bij toenemende dichtheid namen de dagelijkse groeisnelheid en het groene bladoppervlak per plant af. De dagelijkse groeisnelheid en het bladoppervlak per eenheid van bodemoppervlakte namen aanvankelijk toe bij toenemende dichtheid, maar de uiteindelijke waarden waren het grootst voor de middelgrote dichtheid. De verhouding bladoppervlak/totaal drooggewicht nam in de eerste stadia met de dichtheid toe, terwijl in de late stadia het omgekeerde werd gevonden.

7. Het verloop in de tijd was hetzelfde als bij lichtverzwakking.

8. Bij de grotere plantdichtheden trad de maximum groei eerder op, terwijl het rijpen versneld werd.

B. De plantdichtheid oefende in hoge mate invloed op het rendement van de omzetting van de zonne-energie. Bij gerst nam gedurende een periode van 56–70 dagen dit rendement bij toenemende dichtheid toe; later wijzigde de toestand zich ten gunste van de middelgrote dichtheid. Het gemiddelde rendement over het gehele seizoen nam bij toenemende dichtheid toe tot de normale dichtheid, en daalde weer bij de grootste dichtheid. In 1958 werden voor het gemiddelde rendement waarden verkregen van 2.3 procent voor grote plantdichtheid; 2.9 procent voor normale en 1.8 procent voor geringe plantdichtheid.

Bij de voederbiet namen zowel het periodieke als het gemiddelde rendement bij toenemende dichtheid toe. In 1958 werden waarden van 4.4 procent voor dicht planten en 3.0 procent voor meer gespreid planten verkregen. Het maximum rendement werd bij dicht planten eerder bereikt.

Het verloop in verband met de leeftijd was hetzelfde als bij lichtverzwakking, hoewel bij de voederbiet minder uitgesproken. De waarden voor het hoogste rendement strekten zich bij dit gewas over een langere periode uit.

Een maximum rendement van 13.7 en 10.0 procent van de photosynthetische actieve straling werd bij resp. gerst en voederbiet in 1958 bij dicht planten bereikt.

In het algemeen werden de reacties van de planten op lichtverzwakking en plantdichtheid goed weerspiegeld in het rendement waarmee zij zonnestraling omzetten.

LITERATURE CITED

ARCHBOLD, H. K. (1938). Ann. Bot. N.S. 2, 403–436.

BENSINK, J. (1958). Proc. Kon. Akad. v. Wetensch. A'dam C61, 1, 89–100.

BERNARD, E. A. (1956). Public. Inst. National pour l'Étude Agronomique du Congo Belge (INEAC), Série Scientifique 68, 70–82.

BLACKMAN, G. E., and W. G. TEMPLEMAN (1940). Ann. Bot. N.S. 4, 15, 533–587.

BLACKMAN, G. E., and A. J. RUTTER (1948). Ann. Bot. N.S. 12, 1–26.

BLACKMAN, G. E., and A. J. RUTTER (1950). Ann. Bot. N.S. 14, 487–520.

BLACKMAN, G. E., and G. L. WILSON (1951a). Ann. Bot. N.S. 15, 63–94.

BLACKMAN, G. E., and G. L. WILSON (1951b). Ann. Bot. N.S. 15, 373–408.

BOONSTRA, A. E. H. R. (1929) Meded. Landbouwhogeschool Wageningen 33, 3–23.

BOONSTRA, A. E. H. R. (1937) Meded. Inst. Suikerbietenteelt 7, 79–102.

BOSE, J. C. (1924). Physiology of Photosynthesis. Longmans, Green, London.

BOYSEN–JENSEN, D. (1932). Stoffproducktion der Pflanzen. Fisher, Jena.

BROWN, H. T., and F. ESCOMBE (1905). Proc. Roy. Soc. London, B 76, 29–112.

CLEMENTS, F. E., J. E. WEAVER, and H. C. HANSON (1929). Plant Competition. Carnegie Institution of Washington, pp. 202–289.

COMBES, R. (1910). Ann. Sci. Nat. Bot. 9, 11, 75.

CROWTHER, F. (1934). Ann. Bot. 48, 877–913.

CURTIS, O. F., and D. G. CLARK (1950). An Introduction to Plant Physiology, pp. 10–77.

ENGLEDOW, F. L. (1925). Jour. Agric. Sci. 15, 125–146.

GARNER, W. W., and H. A. ALLARD (1920). Jour. Agric. Res. 18, 580.

GLAS, P., and P. J. GAASTRA (1953), Unpublished results, quoted in Wassink, Kok and van Oorschot (1953).

GREGORY, F. G. (1921). Ann. Bot. 35, 93–123.

GREGORY, F. G., and P. K. SEN (1937). Ann. Bot. N.S. 1, 521.

HARRIS, F. S. (1914). Jour. Amer. Soc. Agron. 6, 65–75.

HODGSON, G. L., and G. E. BLACKMAN (1956). J. Expt. Bot. 7, 147–165.

IWAKI, H. (1958). Jap. Jour. Bot. 16, 210–226.

KAMEL, M. S. (1954). Thesis for the M. Sc. (Agr.) degree, Cairo University.
KAMEL, M. S. (1958). Meded. Landbouwhogeschool, Wageningen/Netherlands **58** (8), 1–19.
KHALIL, M. S. H. (1956). Meded. Landbouwhogeschool, Wageningen/Netherlands **56** (7), 1–73.
KOK, B. (1952). Acta Botan. Neerl. **1**, 446–467.
KONOLD, O. (1940). Forschungsdienst **10**, 41–57.
LEOPOLD, A. (1949). Amer. J. Bot. **36**, 437.
LUBIMENKO, W. (1908). Ann. Sci. Nat. Bot. **9**, 7, 321–415.
MAXIMOV, N. A., and E. L. LEBEDINCEV (1923). Deut. Bot. Gesell. Ber. **41**, 292–297.
MAXIMOV, N. A. (1938). Plant Physiology, pp. 178.
MILTHORPE, F. L. (1945). Ann. Bot. N.S. **9**, 31–53.
MITCHELL, H. L., and R. O. ROSENDAHL (1939). Black Rock Forest papers **1**, 88–93.
MITCHELL, K. J. (1953). Physiologia Plantarum **6**, 21–46.
MONSELISE, S. P. (1951). Palestine J. Bot., Rehovot Series **8**, 54–75.
NODDACK, W., and J. KOMOR (1937). Angew. Chem. **50**, 271–277.
OORSCHOT, J. L. P. VAN (1955). Meded. Landbouwhogeschool, Wageningen/Netherlands **55**, 225–276.
POP, H. W. (1926). Amer. Jour. Bot. **13**, 706–736.
POP, H. W. (1926). Bot. Gaz. **82**, 306–319.
PORTER, A. M. (1937). Plant Physiol. **12**, 225.
PURIEWITSCH, K. (1914). Jahrb. Wiss. Botan. **53**, 210–254.
PÜTTER, A. (1914). Naturwissenschaffen **2**, 169–174.
RABINOWITCH, E. I. (1945). Photosynthesis and Related Processes, Vol. I, Interscience Publishers, New York (a), pp. 9, 50.
RABINOWITCH, E. I. (1951). Photosynthesis and Related Processes, Vol. II, Interscience Publishers, New York, pp. 998–1007.
RICHARDS, F. J. (1938). Ann. Bot. N.S. **2**, 491.
RICHARDSON, S. D. (1957). Acta Bot. Neerl. **6**, 445–457.
RIELY, G. A. (1941). Bull. Bengham Oceanogr. Coll. **7**, (4), 1.
ROSÉ, E. (1913). Ann. Sci. Nat. Bot. **9**, 17, 1–110.
SAUBERER, F. (1937). Planta **27**, 269–277.
SHANTZ, H. L. (1913). Effect of artificial shading on plant growth in Louisiana. U.S. Dep. Agr. Bur. Pl. Ind. Bull. 279.
SHIRLEY, H. L. (1929). Amer. Jour. Bot. **16**, 354–390.
SKOOGI, F., and CH. TSUI (1951). In "Plant Growth Substances" F. Skoog. Univ. of Wisconsin Press.
SMITH, H. F. (1937). Australia Council Sci. Ind. Res. Bull. 109.
SOPER, M. H. R. (1952). Jour. Agric. Sci. **42**, 41–57.
SPOEHR, H. A. (1926). Photosynthesis. Chemical Catalog. Co., New York, pp. 315–337.
TAKEDA, TOMOSHIRO, and HIROSHI MARUTA (1956). Proc. Crop. Sci. Soc. Japan **24** (4), 331–338.
THIMANN, K. V. (1937). Amer. J. Bot. **24**, 407.
THOMAS, M. D., and G. R. HILL (1937). Plant Physiol. **12**, 285–307.
TRANSEAU, E. N. (1926). Ohio Jour. Sci. **26**, 1–10.
TURNER, J. W. (1922). Amer. Jour. Bot. **9**, 415–445.
VERKERK, K. (1955) Meded. Landbouwhogeschool, Wageningen/Netherlands **55** (4), 175–224.
WASSINK, E. C. (1948) Med. Dir. Tuinbouw, Netherlands **11**, 503–513.
WASSINK, E. C., B. KOK, and J. L. P. VAN OORSCHOT (1953). Algal culture. From laboratory to pilot plant. Publ. 600, Carn. Inst. Wash., pp. 55–62.
WASSINK, E. C., S. D. RICHARDSON and G. A. PIETERS (1956). Acta Bot. Neerl. **5** (3), 247–256.
WATSON, D. J., and A. G. NORMAN (1939). Jour. Agric. Sci. **39**, 3, 321–346.
WATSON, D. J. (1952). Advances in Agron. **4**, 101–145.
WATSON, D. J. (1958). Ann. Bot. N.S. **22**, 85, 37–54.
WENT, F. W. (1939). Amer. J. Bot. **71**, 77.
ZILLICH, R. (1926). Fortsch. Landwirtschaft. **1**, 461–470.

PLATE 2a. Shading effect on the development of barley after 66 days from planting in 1958.
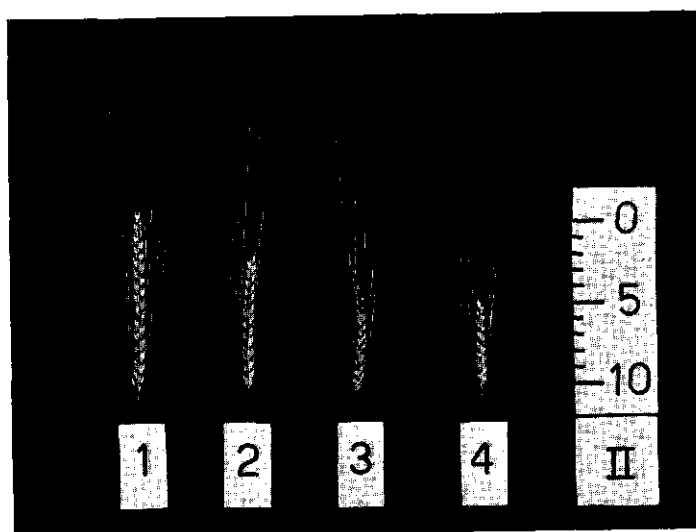1: Full daylight 2: 80 per cent 3: 50 per cent 4: 25 per cent

PLATE 2b. Shading effect on ear length of barley after 80 days from sowing, in 1958.
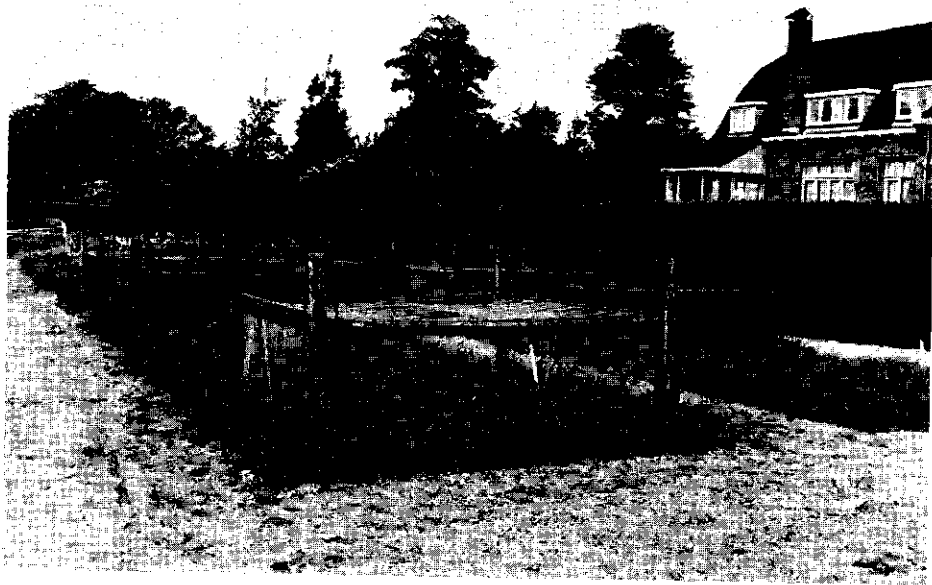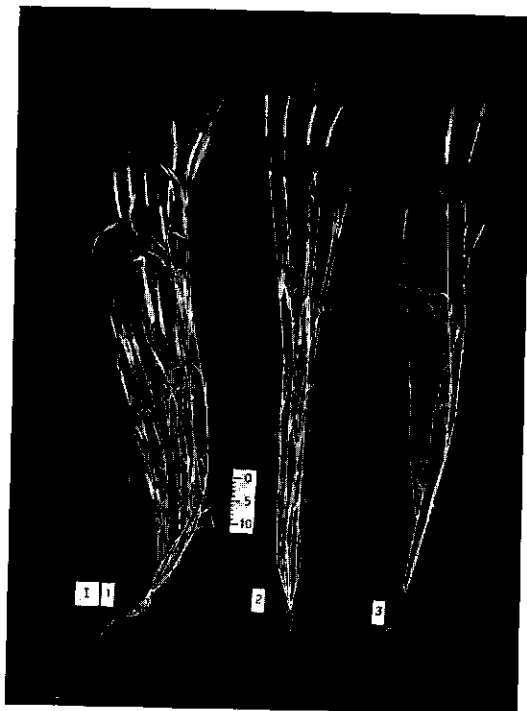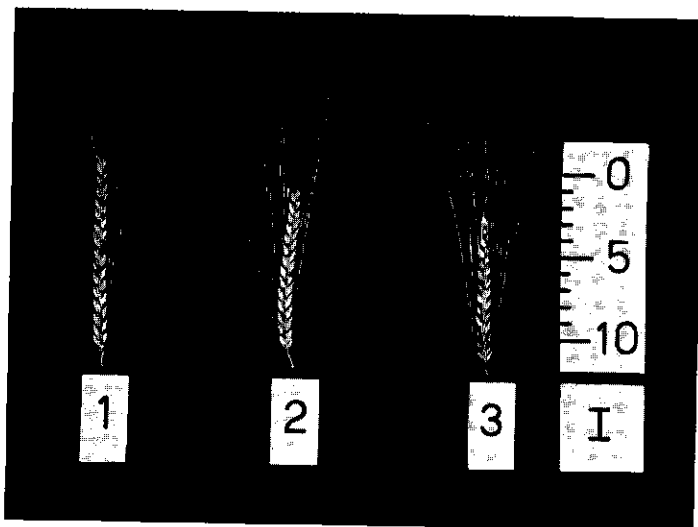1: Full daylight 2: 80 per cent 3: 50 per cent 4: 25 per cent

PLATE 1   General view of barley shading experiment showing the construction of the screen cages, in 1958. Photograph taken 30.5.1958, 28 days after sowing. In as much as the plants grew higher the top and side screens were lifted together, side screens were not made any longer than shown in the picture.

PLATE 3a. Density effect on the development of barley after 103 days from planting, in 1958.
1: Thin planting　　2: Normal planting　　3: Dense planting

PLATE 3b. Density effect on ear length, in barley, after 103 days from planting, in 1958.
1: Thin planting　　2: Normal planting　　3: Dense planting