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EFFICIENCY OF SOLAR ENERGY CONVERSION AS RELATED WITH GROWTH IN BARLEY

(Preliminary Communication)

by

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CONTENTS

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INTRODUCTION

Of great interest is the question how much the green plant profits from the radiant energy that falls upon it, and what part is stored as potential energy of the accumulated organic compounds.

Agriculture has been largely concerned only with the study of the 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 less than one to two per cent of the solar radiation usable in photosynthesis is converted into organic matter by higher plants, while under laboratory conditions the photosynthetic efficiency may reach 25 per cent corresponding to 8–12 photons of red light per molecule of CO_2. The low energy conversion observed under field conditions is due to the limited capacity of the photosynthetic apparatus and dissipation of energy absorbed in excess of this capacity.

Because of the lack of detailed information 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 important and fundamental tasks 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 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 variations in the density give another mean for varying the solar radiation, plant density has been also taken into consideration.

Besides, an extensive study has been made of the formative effects of shading on plant growth and development, aiming at the same time to determine the relationship between growth and light energy conversion efficiency.

In this laboratory, where all these studies were carried out, work on the efficiency of solar energy conversion has been in progess for a long time, both in algae and in higher plants. Periodic harvests of potatoes, e.g. with a view to determine the yield of energy conversion have been made in 1949, 1950, and 1951 (WASSINK, in course of publication). Data from literature have been discussed in view of this problem by GAASTRA in 1955 (Proc. World Symp. on Applied Solar Energy. Phoenix, Arizona, pp. 255–259).

In the present paper, the author intends to discuss, briefly, some of his results on this problem (efficiency of radiant energy and growth in leaf area and in weight as affected by time, shading and density, in barley).

A more detailed publication including all the results of the series of experiments performed in 1957 and 1958 on barley and mangolds, will appear in the near future.

REVIEW OF LITERATURE

I. Efficiency of solar energy conversion

Several investigators have attempted to determine the efficiency of plants in utilizing the light energy striking them. Brown and Escombe (1905) estimated the conversion yields to be of the order of 2.5 per cent of the visible radiation absorbed by plants. Purevich (1914) calculated efficiency values from 0.6–7.7 per cent of the incident energy. Transeau (1926) reported from his own results that the corn plant utilized about 1.25 per cent of the incident energy. Spoehr (1926) obtained much lower values for the practical efficiency (neglecting the stalks, husks and roots of wheat). Noddack and Komor (1937), studying the efficiency of grass in converting solar radiation in two successive periods and in two different plot sizes, stated that the efficiency tended to increase with time and to decrease as the experimental area increased. Rabinowitch (1945 and 1951) estimated the average solar energy conversion of field crops and forests to be about 2 per cent of the absorbed visible radiation. Wassink (1948) computed the efficiency of some crops in converting solar energy to range from 0.5 to 2.2 per cent. Wassink, Kok, and van Oorschot (1953) studied the efficiency under optimal conditions and reported values of 11–15 per cent. Van Oorschot (1955), growing algae under field conditions, obtained values ranging from 1–5 per cent of the visible radiation. He found also that decreasing the light intensity resulted in higher efficiency values.

II. Shading and growth

Besides the fact that light is the direct source of energy for the manufacture of food, light is the most important factor affecting the form of plants and plays a significant role in determining their structure. Although much work has been done on the effect of shading on plant growth and development, evidence is rather conflicting. Lubimenko (1908) found that the 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 sunlight. Leaf area was found to behave as dry weight, but attained maximum development at lower intensities. The dry matter percentage usually increased with increasing light intensity. Combes (1910) found the optimum light intensity for the production of dry matter in plants to increase with the age of the plants. Gregory (1921) stated that the average leaf area of cucumber plants over the growth period (about 30 days) is proportional to the total radiation received. Clements *et al.* (1929) found that the leaf area and dry weight per plant of wheat and sunflower crops increased with intensity. Shirley (1929) pointed out that 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 and the density of growth increased with increasing light intensity, while the leaf area was found to be maximum at light intensities of about 20 per cent of full summer sunlight. Milthorpe (1945) found that shading reduced the leaf area of flax by decreasing leaf number and leaf size. Blackman and Rutter (1948, 1950) on the other hand reported that the plants of *Scilla nonscripta* grown in the open under shades, produced larger total leaf area than plants grown under full daylight illumination. They demonstrated that in general plant weight increased with light intensity, and maximum growth was in full daylight. MONSELISE (1951) showed that also the leaf area of citrus seedlings was increased by shading. Although most investigators concluded that growth in leaf area under open air conditions decreased by increasing light intensity, the results of GREGORY and MILTHORPE indicate that in some cases, possibly at high temperature, leaf area may increase with increase in illumination. BLACKMAN and WILSON (1951) 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 thereafter decreased.

III. DENSITY AND GROWTH

Density is one of the major factors determining the amount of growth per unit area. It is of great importance 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 planting up to muturity. CLEMENTS *et al.* (1929) reported that the average leaf area and dry weight of tops, roots, and entire plants decreased as the density increased. KONOLD (1940) found that, in general, the production of seed per plant decreased with density. IWAKI (1958) showed that with increasing the density of a buckwheat population a marked suppression in individual plant weight was observed. The differences induced by variation in density became more marked as the plants developed. He also found that the leaf area index increased as the density increased, especially at the early stages of growth. The maximum leaf area index was attained in all densities after 42 and after 30 days from planting in 1954 and 1955, respectively.

MATERIAL AND METHODS

Barley (*Hordeum distichum*, var. Heine 4804) was used in this study, and the work was carried out in the experimental garden of the Plant Physiological Research Laboratory, University of Agriculture, Wageningen/Holland, during the growing seasons 1957 and 1958.

SHADING EXPERIMENT

In order to study the shading effect, daylight was reduced by screens; 4 intensities were applied: 100 per cent (full daylight), 80 per cent, 50 per cent and 25 per cent. Only one density was employed in this experiment (250 plants/m^2). Planting was on June 6 in 1957, and on May 2 in 1958.

DENSITY EXPERIMENT

For studying the density effect 3 densities were applied in 1958: 500, 250 and 125 plants/m^2, while in 1957 only the first two densities were employed. Planting was on June 6 in 1957, and on April 17 in 1958.

GENERAL METHODS AND OBSERVATIONS

The plot size was 4 m^2. Two replicates were used in 1958. Plots were in reach of full daylight during most of the day (except those under screens which differed according to the treatment). Periodic harvests were taken during the growing season from seedling stage up to maturity. On the sampling days up to the 3rd harvest (after 39 and 43 days from planting in the shading and density experiments, respectively), top photographs were taken to determine the surface covered by the plants. In subsequent harvests this was no more necessary, since the cultivated area was completely covered. A sample of 30 plants within each treatment, from a closed area, was selected randomly at each interval. An area of 0.5 m^2 from the center of the plots was used for the determination of the average efficiency during the entire growing season.

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 the factor 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 sowing 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/gr), the efficiency of solar energy conversion in per cent is given by:

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

Fresh and dry weight determination

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

Leaf area estimation

At early stages of growth, an outline of a sample of leaf blades was drawn and its area was measured by planimeter. At later stages, 100 discs of 6 mm. diameter were punched. The dry weight of these measured blades or discs was determined. In this way an estimate of the leaf area: leaf dry weight ratio for each sample was obtained, and this multiplied by the dry weight of green blades per plant, gave the total green leaf area per plant.

Note: For simplicity and to save space, Tables are not given in this publication.

RESULTS AND DISCUSSION

I. Shading effects

1. Shading and Efficiency of Solar Energy Conversion

The effect of shading on the efficiency of solar energy conversion in barley, measured during the growth season of 1958, at successive intervals, is given in fig. 1. It is evident that the efficiency, in general, tended to be low at the early

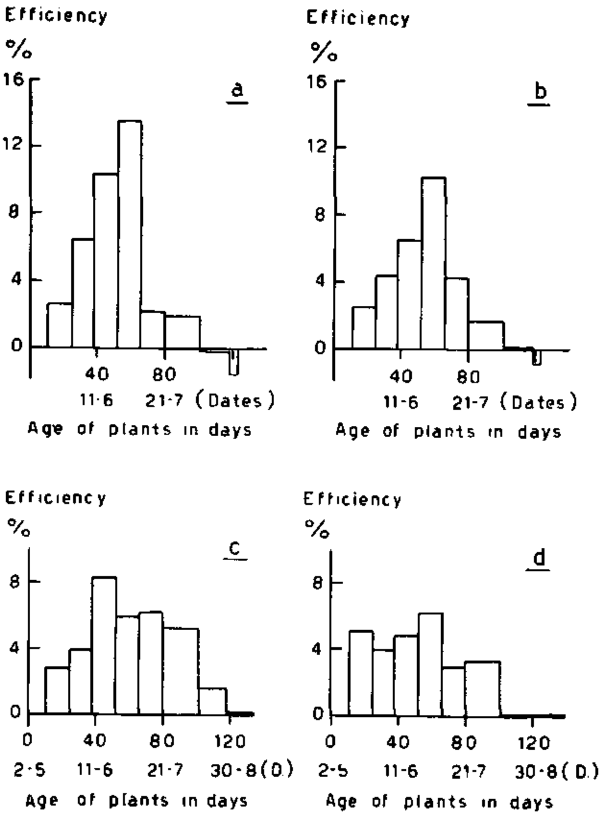


FIG. 1. Shading effect on the efficiency of solar energy conversion during growth (in per cent), in barley, at successive intervals, in 1958.
a: Full daylight b: 80 per cent c: 50 per cent d: 25 per cent

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 4 to 6 weeks, from May 27 to July 7 (25 to 65 days after sowing) the plants 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 to 65 days after planting). The maximum of green leaf area, tiller number and fresh weight was reached also by that time. After this maximum, the efficiency dropped towards a minimum at the end of the growing season. It followed closely the trend of green leaf area and fresh weight. This time trend was also observed in 1957.

At certain periods the efficiency increased with decreasing light intensity. This was observed only in the first period (11 to 24 days after planting) 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 extending from May 27 to July 6 (25–65 days after seeding), 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 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 decrease in light intensity resulted in an increase in the efficiency of the solar energy conversion. Thus, the highest efficiency was obtained at the lowest light intensity (25 per cent daylight intensity).

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.

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.

At late stages of growth, the plants grown under full daylight profit little from the light owing to senescence, while those under shade, due to growth cycle prolongation, exhibited the highest efficiency values. Thus, at a light intensity of 50 per cent, the efficiency increased. But, at only 25 per cent of full daylight it decreased again, maybe due to a detrimental effect of heavy shading which increased with time. 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 full daylight intensity, respectively. 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 whole growing season was found to increase with increasing light intensity up to full daylight. The efficiency values ranged from 2.9 per cent for full daylight to 1.4 per cent for the 25 per cent daylight. The same trend was observed in 1957.

The decrease in the efficiency associated with the lowering of the light intensity may be attributed to the 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 restricted due to limited photosynthesis from the beginning. As a result, growth is greatly depressed as compared with that under full daylight. It seems that the lower degree of growth and development of shaded plants is not solely the result of the lower assimilation rate, but is due to some effect of light other than that directly on assimilation. Apart, however, from a possible effect of reduced light intensity of leaf thickness (light absorbing power of leaves), the modifications in leaf structure, stomatal number, etc, induced by shading may affect, indirectly, photosynthesis by changing the rate of gas exchange. Moreover, shading affects the formation of mechanical and conductive tissues and the root growth. This, in turn, may influence the uptake of nutrients and water as well as the translocation of food and water.

From our data, it is evident that the depression in growth due to shading is more effective than the reduction in light intensity. It appears that many internal and metabolic factors as well as external factors may directly or indirectly influence photosynthesis and thus 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 "health" and development of the plant and less favorable balance between photosynthesis and respiration.

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.

2. Shading and Growth

A. Growth in weight

a. Fresh weight per plant

The results illustrated graphically in fig. 2a indicate that in general, within the limits of experimental error, the fresh weight increased with increasing light intensity. The differences induced by shading increased as the plants advanced in growth and were maximal at midseason (on July 7) when the plants were 66 days old.

At all light intensities, the plants increased only slowly in weight during the first stages of growth, and the more so under heavy shading. From the 2nd harvest up to the 4th one, the fresh weight increased rapidly while the effect of shading remained the same. At more advanced age, it increased less rapidly till the maximum, and then decreased sharply due to maturity. It is of great interest that the maximum fresh weight was attained in the 100 and 80 percent daylight intensities when the plants were 66 days old. The maximum in the 50 per cent intensity was reached two weeks later (on July 21), while it was attained five weeks later (on August 11) in the 25 per cent intensity. This indicates that, in general, with decreasing light intensity the length of the vegetation period increased due to growth retardation induced by shading.

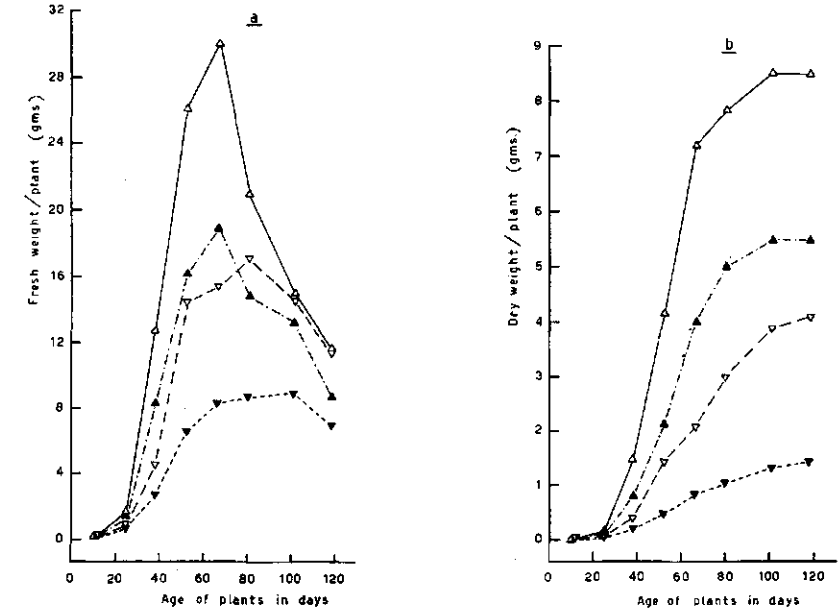
It has already been pointed out that the highest efficiencies were obtained at those periods of greatest growth in fresh weight (cf. fig. 1).

b. Dry weight per plant

It is apparent from fig. 2b that also the dry weight increased with increasing light intensity up to full daylight. The differences induced by shading were found to be less marked at the first stages of growth at which obviously the injurious effect of reducing the intensity was not yet very marked. Later on, the plants respond greatly to shading, and the differences in dry weight increased to a maximum at the end of the growing season. It was found that the maximum dry weight per plant in full daylight was about 6 times that at 25 per cent intensity, being 8.5 gr. and 1.4 gr., respectively.

These results are in accordance with those obtained by LUBIMENKO (1908), SHIRLEY (1929), CLEMENTS *et al.* (1929) and BLACKMAN and RUTTER (1948, 1950) who stated that cultivated plants always had maximum dry weight when grown in the open.

At the beginning the plants increased slowly in dry weight, then increased more rapidly, especially in the unshaded plot. The increase in weight came to a standstill at a moment which differed according to the treatment, *viz.*, on August 11 (101 days after planting) in the 100 per cent and 80 per cent intensi-



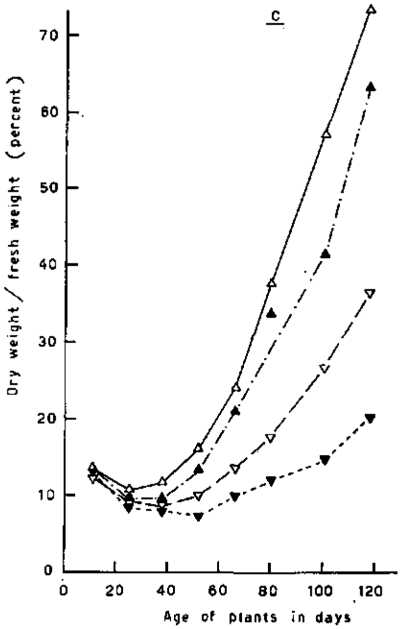


FIG. 2. Shading effect on entire plant: fresh weight (a), dry weight (b), and dry weight percentage (c), in barley, at successive intervals, in 1958.

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

ties, and only at the end of the growing reason in the 50 per cent and 25 per cent intensities. To some extent the same was observed in 1957.

It is clear that the shading effect on dry weight increment was reflected closely in the efficiency of solar energy conversion.

c. Dry weight percentage

Fig. 2c shows that the percentage of dry weight/fresh weight increased with increasing light intensity at all intervals under investigation. The differences induced by shading increased as the plants advanced in growth and were maximal at the end of the season. The decrease in dry matter percentage associated with lowering of the intensity may be due to the shading effect on increasing the water content of the plants. These results confirm those of LUBIMENKO (1908) and SHIRLEY (1929).

During further development, the dry matter percentage decreased due to extension growth, and more sharply so, and for a longer period, at the lower light intensities. After this drop the dry matter percentage increased progressively with age – and more rapidly so at the high light intensities – till a maximum was reached at the end of the growth period. This increase may be attributed also in part to maturing. The maximum dry weight per cent reached at full daylight intensity was about three times that at the lowest intensity, namely 73.3 and 20.4 per cent, respectively.

The percentage of dry weight/fresh weight may be considered a good indicator of the shading effect on prolonging the vegetation period. It may be mentioned in addition that shading also prolonges the vegetative period and retards the appearance of the ears.

B. Growth in leaf area

The variations in total green leaf area per plant with time, in barley, as affected by shading are brought out in fig. 3 for the 1958 experiment. It can be seen that, up to July 7 (66 days after planting), the green leaf area increased with increasing light intensity and the greatest differences between the highest and lowest intensities were found at that time. The maximum leaf area, reached after 66 days from planting, was 280 cm^2/plant in full daylight and 146 cm^2/plant at 25 per cent light intensity. It was attained by June 23 (two weeks earlier) at the medium intensities. These results are in accordance with those of GREGORY (1921) and MILTHORPE (1945) with the only difference that in our case the decrease in leaf area induced by shading was due mainly to depression in leaf number and not in leaf size. 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 similar to those of SHIRLEY (1929) and BLACKMAN and RUTTER (1948, 1950).

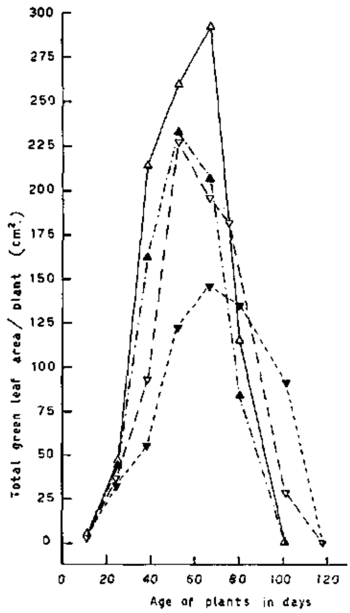
Turning next to the age effect, the leaf area increased to a maximum more rapidly at the higher light intensities, and when dropping, it decreased more gradually at the lower light intensities. This may be considered as another indication of the shading effect on the extension of the vegetation period.

With reference to the efficiency, it is evident that since the green leaf area represents the greatest part of the photosynthetic apparatus, the responses of the leaf area to shade and age are reflected in the capacity of plants in converting the solar radiation (cf. figs. 1, 3).

C. Leaf-area ratio

Fig. 4 shows that, in general, the leaf-area ratio increased with decreasing light intensity. With the exceptional rise observed at the second period, the leaf-area ratio in all cases decreased with age. Thus, the ratio increased from

FIG. 3. Shading effect on total green leaf area per plant, in barley, at successive intervals, in 1958.
△—△ : Full daylight ▲- . - ▲ : 80 per cent
▽--▽ : 50 per cent ▼---▼: 25 per cent



208 in the first period to 273 in the second one under full daylight intensity, and from 233 to 502 in the heaviest shading. Thus, for unexplicable reasons, the tendency of the leaf-area ratio to decrease with age was masked at the early stages. 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 in each interval. 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 (cf. curves 2b and 3). After the second interval, the amount of leaves still strongly increases (cf. fig. 3) together with a still more pronounced increase in dry weight. Fig. 4 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 (cf. fig. 3, and also p. 10).

II. DENSITY EFFECTS

1. Density and Efficiency of Solar Energy Conversion

The density effect on the efficiency of solar energy conversion, in barley, at successive periods, in 1958, is illustrated in fig. 5. At all densities, the efficiency

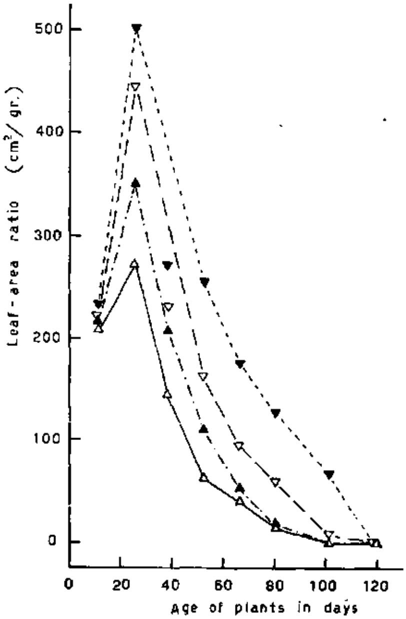


FIG. 4. Shading effect on leaf-area ratio (total green leaf area/entire plant dry weight), in barley, at successive intervals, in 1958.

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

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 to 70 days after planting) for the dense and thin plantings and from June 26 to July 10 (70–85 days after seeding) 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 more sharp in the dense planting. 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.

The experimental data on growth measurements show that the age trends of shoot number, green leaf number, leaf area, fresh-weight etc. per unit area are well reflected in the age trend of the efficiency of solar energy conversion. Thus, the maximum efficiency was reached by the time of highest tiller and leaf number, leaf area and fresh weight per unit area (see later).

From May 16 to June 25 (29–70 days after planting), the efficiency increased with increasing density. In the period from June 26 to July 28 (70–103 days after seeding) the position was changed in favor of the normal planting, followed by the dense one, while the thin planting came at the end. By that time, leaf area, shoot number, green leaf number, and dry weight per unit area, as well as plant length showed a similar trend. This indicates that the efficiency followed closely these growth aspects in their reactions to plant density.

The dotted lines in fig. 5a give the efficiency values in the dense planting during the periods from June 26 to July 10 and from July 11 to July 28. This sudden drop (after the maximum) in the first period and the sharp rise in the second one for the dense planting 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 season. An exceedingly unhappy variation in sampling may have been responsible for this 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.

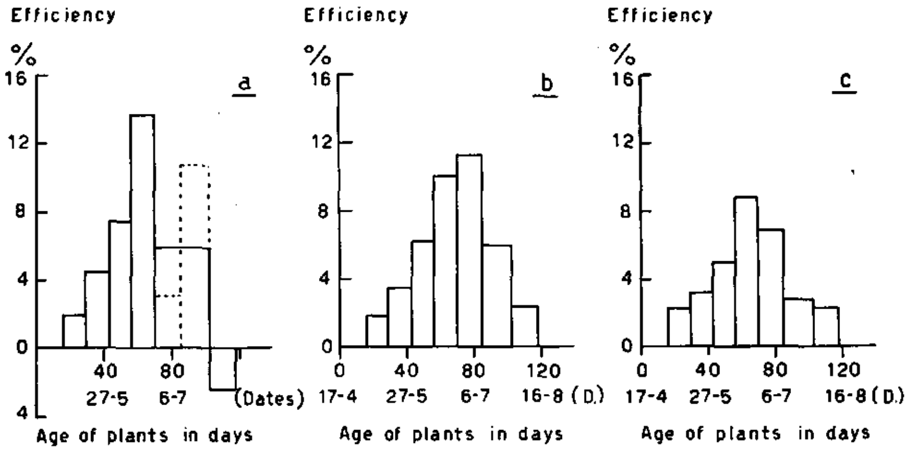


FIG. 5. Density effect on the efficiency of solar energy conversion during growth (in per cent), in barley, at successive intervals, in 1958.
a: *Dense planting* b: *Normal planting* c: *Thin planting*

During the last period, extending from July 29 to August 13 (103–118 days after seeding), 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 due to overmaturing 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. It seems that with increasing density up to the normal planting (250 plants/m^2) the depression in growth due to competition is overcome by the increase in plant number per unit area. With further increase up to 500 plants/m^2, the increase in plant number obviously could not counterbalance the decrease in the final yield per plant.

The average efficiency value was 2.33 per cent for the dense planting, 2.94 per cent for the normal one and 1.84 for the thin one.

Similar results were obtained in 1957.

2. Density and Growth

A. Growth in weight

a. Fresh weight per plant

Fig. 6a indicates that with increasing density fresh weight per plant decreased. The differences increased as the plants developed; obviously at the early stages competition was not yet important. The highest differences in fresh weight were observed in the period from June 26 to July 29 (70–103 days after sowing).

At all densities, fresh weight increased with time and was maximal on June 26, then it decreased towards a minimum at the end of the season. It was found that in the dense planting the curve decreased more sharply owing to early maturing. The maximum fresh weight per plant varied from 52 gr. for the thin planting to 19.4 gr. for the dense one.

b. Dry weight per plant

Fig. 6b shows that the dry weight per plant decreased with increasing density. The differences increased with time and the greatest differences were found at the end of the season.

Dry weight per plant, increased progressively with time for the normal and thin plantings while in the dense one, the plants tended to decrease in dry weight during the last two weeks, owing to over-ripening. The maximum dry weight, reached on August 14, was 14.7 gr. for the thin planting and 10.7 gr. for the normal one. In the dense planting it was attained on July 29 (103 days after seeding) and was 5.3 gr.

Similar results were obtained in 1957. These findings confirm those of CLEMENTS *et al.* (1929). KONOLD (1940) and IWAKI (1958).

c. Dry weight percentage

From fig. 6c it is evident that the dry weight percentage up to May 30 (43 days after planting) tended to increase with decrease in density, indicating that the competition for light was responsible herefor. From this date up to maturity the position was changed, and the percentage of dry matter increased with increasing number of plants per unit area. This suggests that the effect of some factors other than light especially 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.

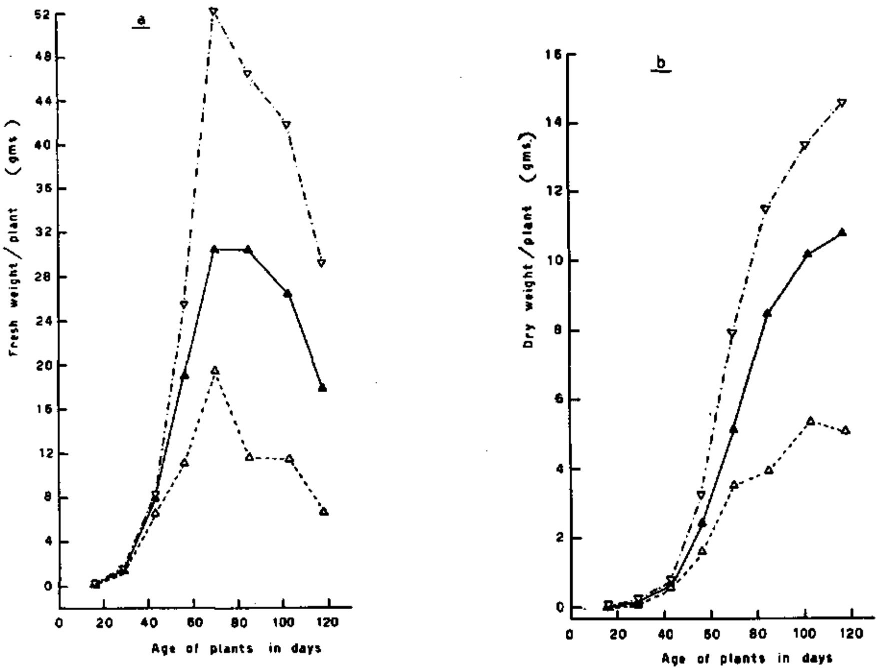
The dry matter percentage decreased, during the early stages of growth up to the 3rd period. This may be due to increased uptake of water connected with extension growth; this was most pronounced for the dense planting. From May 30 up to the end of the season the dry weight/fresh weight in per cent increased progressively with time until harvest; the values for the dense planting always were the 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. Several of the lower leaves then die, connected with early senescence and death. The final dry weight percentage was 75 for the dense planting, 60 for the normal one and 50 for the thin 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.

With few exceptions the same trend was observed in 1957.

B. Growth in leaf area

Fig. 7 gives the mean leaf area per plant and the leaf area index in barley 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 maximum fresh weight, after which it decreased. The maximum green leaf area per plant



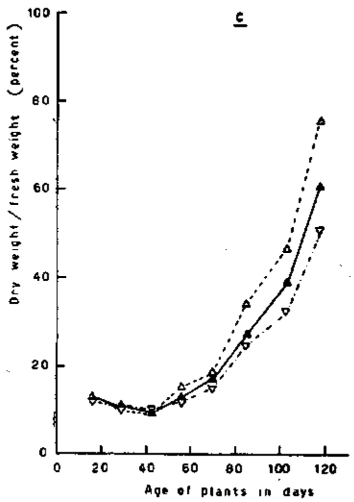


FIG. 6. Density effect on entire plant: fresh weight (a) dryweight (b) and dry weight percentage (c), in barley, at successive intervals, in 1958.

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

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 differed from 66.5 cm² for the highest density to 353.8 cm² for the lowest one.

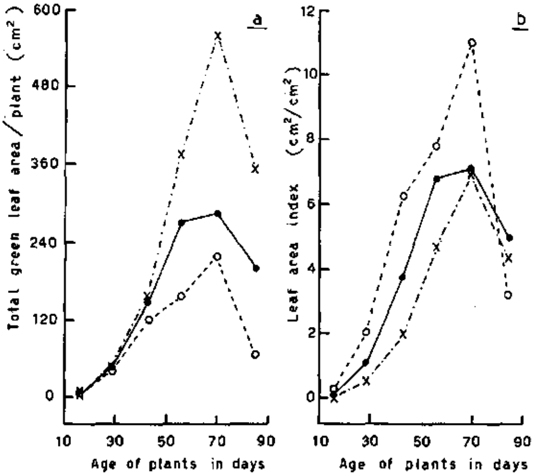


FIG. 7.
Density effect on total green leaf area per plant (a) and leaf area index (b), in barley, at successive intervals, in 1958.
o-----o: Dense planting
●——●: Normal planting
x-·-·-x: Thin planting

In contrast to the leaf area per plant, the leaf area index increased with density up to 80 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. From 80 to 85 days after sowing this situation was changed in favor of the medium density. Owing to higher degree of self-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 WATSON (1952). The maximum leaf area index was 11.0 for the dense planting, 7.2 for the normal one and 7.0 for the thin one. At 85 days the leaf area index was 3.3 for the highest density, 5.0 for the medium one and 4.4 for the lowest one.

These results, to some extent, are similar to those obtained by IWAKI (1958) on buckwheat.

C. Leaf-area ratio

Clearly, in fig. 8 two critical periods were noticed. In the early stages of growth, up to 47 days old, the ratio increased with increasing density, indicating that the light factor has played the major role. In the second period, from 47 to 85 days after sowing, the ratio decreased with increasing density. Since BLACKMAN and WILSON (1951) reported that the leaf-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. 8 and from the preceding comments that, with the exception of the rise in the second period, the leaf-area ratio decreased with age. It is worth noting here again that, primarily, the rise in the second period – indicating that the increase in leaf area is relatively more rapid than that in dry

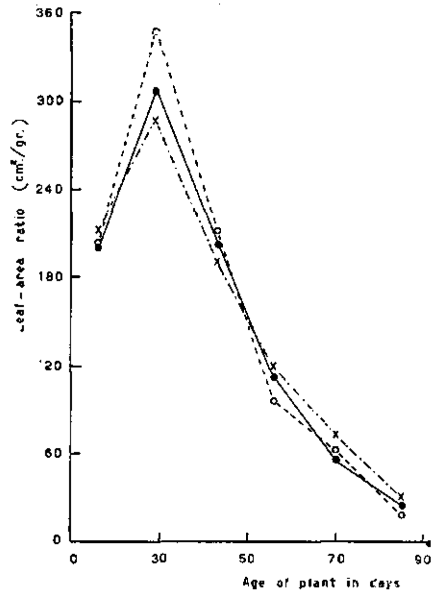


FIG. 8. Density effect on leaf-area ratio (total green leaf area/entire plant dry weight), in barley, at successive intervals, in 1958.

o-----o: Dense planting
●——●: Normal planting
x-·-·-x: Thin planting

weight – is only 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. Data on this development will be supplied in detail in the following, more extensive paper.

SUMMARY

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

It has been established that the efficiency of solar energy conversion under field conditions increased with time to a maximum (at mid-season), then decreased to reach a minimum at the end of the season. It followed closely the time trend of growth in leaf area, fresh weight, etc. Thus, its value is extremely dependent on the stage of growth. The highest efficiency values were attained at the middle stages of growth (for a period of about 4 to 6 weeks). A maximum of 13.6 per cent of the photosynthetic radiation for the full daylight intensity was obtained in the shading experiment, while in the density experiment a maximum of 13.7 per cent for the dense planting was reached.

I. Shading effects

1. Shading greatly affected the efficiency. At the early stages and at the late stages the efficiency increased with decreasing light intensity, at the middle stages the reverse was true. The average efficiency during the whole growing

season increased with increasing light intensity up to full daylight. Values ranged from 2.9 per cent for the full daylight intensity to 1.4 per cent for the 25 per cent intensity as obtained in 1958.

2. The fresh and dry weights per plant as well as the dry weight percentage decreased, in general, with increased shading. The maximum fresh weight was reached at mid-season in full daylight and in 80 per cent light intensity, and later with increased shading. At all intensities, the dry weight per plant and dry weight percentage were maximal at the end of the season.

3. Fresh weight increased with time to a maximum, then it decreased, while dry weight increased progressively as the plants grew up. Dry weight percentage dropped at first, then increased with time.

4. The green leaf area per plant increased with time up to a maximum, then decreased. At early stages of growth, up to 66 days, the leaf area increased with increasing light intensity, while at late stages it decreased with increasing light intensity.

5. The leaf-area ratio decreased with age and with increasing light intensity.

6. The length of the vegetation period increased with shading.

II. Density effects

1. The number of plants per unit area greatly influenced the efficiency. Up to the time of maximum efficiency, the efficiency increased with density. Later on the position changed in favor of the medium (normal) planting. The average efficiency over the entire season increased with density up to the normal planting and was lower again at the highest density. Efficiency 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.

2. Fresh weight, dry weight and green leaf area per plant decreased with density. In contrast, the dry weight percentage increased with density with the exceptions observed at early stages of growth.

3. With increasing density, the leaf area index increased, but the final leaf area index, 85 days after planting, was highest for the normal planting.

4. The leaf-area ratio increased with density in the first half of the growing season, while the reverse was found in the second half.

5. The age trend was the same as for shading.

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

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