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THE PRODUCTION OF MATTER IN AGRICULTURAL PLANTS AND ITS LIMITATION

BY

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1. Introduction.

The amount of energy radiating from the sun makes up 3.10^{30} kg.cal. per year. Of this amount of energy only a very slight part, viz. 1.34×10^{21} kg.cal., will hit the earth. Most of this energy is transformed into heat, but a small part, namely 0.01 per cent. or 0.162×10^{18} kg.cal., is used for carbon dioxide assimilation in the green plants.

Table 1 (Schroeder 1919).

	Billion kg.cal.
Total solar radiation per year	3 000 000 000 000 000 000
Incident radiation at the edge of the atmosphere	1 340 000 000
Consumption of energy by assimilation	162 000

Through the carbon dioxide assimilation light energy is transferred into chemical energy, 6 molecules of carbon dioxide + 6 molecules of water being transformed into 1 molecule of sugar under the absorption of 708 kg.cal., and thereby elevated to a higher level of energy (fig. 1). The sugar formed is used in two different ways, first, as a source of matter, as the compounds found in the living organisms, plants as well as animals, are formed from the sugar which arises by the assimilation of carbon dioxide, in connection with small quantities of other elements; secondly, the sugar is used as a source of energy, as by means of enzymes it can by a voluntary process be split up into carbon dioxide + water, the latent chemical energy thereby being liberated. Part of the latter becomes free energy, which is used for the non-voluntary processes in plants and animals, for the building up of matter, for growth, movements, etc. This splitting up of the sugar takes place gradually and is regulated.

Consequently the living organisms are built into the run-down of the free energy of the solar radiation by its conversion

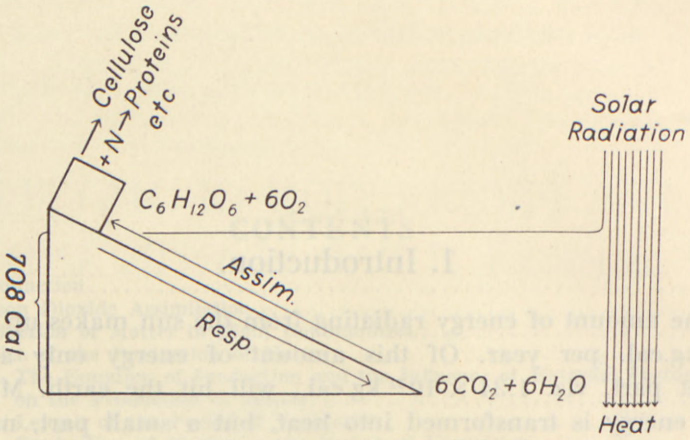

Fig. 1.

into heat, but the part of it which is transformed into chemical energy in the green plants is, as will be seen from the above, very slight.

The basis of all life on earth is consequently the process

carbon dioxide + water + radiant energy → sugar + oxygen
$6\,CO_2 + 6\,H_2O + 708$ kg.cal. → $C_6H_{12}O_6 + 6\,O_2$.

It is the quantity of organic matter formed annually by the carbon dioxide assimilation on the surface of the earth which determines how many heterotrophic organisms, heterotrophic plants, animals, and human beings can live on the earth.

II. Carbon Dioxide Assimilation.

If we want to analyze the annual production of matter per unit of area, we must begin by examining the carbon dioxide assimilation.

When examining the influence of light intensity on the rate of carbon dioxide assimilation in a horizontally placed leaf of *Sinapis alba* at 20° C. and the carbon dioxide tension of the atmosphere, we get a curve, which is represented in fig. 2*a*. The curve begins below the axis of abscissae. When the intensity of light is 0 (darkness), no intake of carbon dioxide will take place, but a giving off of carbon dioxide as a consequence of the respiration. At the intensity of light where the curve intersects the axis of abscissae, there is an equilibrium between carbon dioxide assimilation and respiration. This point is called the compensation point; as far as light leaves are concerned, it is between 500 and 1000 BJ-Lux, i. e. at 1—2 per cent. of the average intensity of light in the middle of the day in summer. Then the curve rises in a straight line with the intensity of light, until it turns over and reaches a maximum, whereupon it runs parallel to the axis of abscissae. The said maximum is reached at an intensity of light of 12.000—15.000 BJ-Lux, about 30 per cent. of the average intensity of light in the middle of the day.

It will be seen from the above statement that a horizontally placed leaf is unable to utilize the full daylight completely, because the maximum assimilation is reached already at an intensity of light far below that of the full daylight. We might therefore be inclined to conclude that in nature there is an excess of light. Such a conclusion will also be correct as far as solitarily growing plants are concerned, which have so few leaves that they do not shade each other. In natural plant communities, however, conditions are different.

In a field of grass or cereals the leaves are not placed horizontally, but more or less slanting. At the same time the leaf area is increased and becomes much larger than the ground area. Therefore the leaves are exposed to an intensity of light amounting only to a certain percentage of the free daylight, and a possibility is thereby created of far better utilization of the light than in the case of leaves fully illuminated.

If we therefore examine the intensity of assimilation of a plant community in various intensities of light, we must expect to get another shape of curve than the one which holds good of horizontal leaves. The result of an examination of this case is represented in fig. 2; as already mentioned *a* represents the assimilation curve for horizontal leaves of *Sinapis alba*, *b* represents the corresponding curve for the leaves in a stock of *Sinapis alba*, like *a* calculated per 50 sq.cm leaf area and hour. The rate of respiration is the same in both cases, but as the leaves in the stock partly shade each other, the slope of curve *b* is far less steep than that of curve *a*, and the compensation point for curve *b* will therefore be at a higher intensity of light. As the leaf area in the stock was 3.4 times that of the ground area, the rate of assimilation at the various intensities of light per 50 sq.cm ground surface can be calculated from curve *b*. The curve *c* is the light-assimilation curve of the stock. Its compensation point lies at the same intensity of light as for curve *b*, and therefore considerably higher than for curve *a*. The stock, therefore, demands more light than the horizontal leaf to get a positive result of the assimilation, on the other hand it is able to utilize a far higher intensity of light. Indeed, there is reason to believe that the maximum intensity of assimilation is only reached at an intensity of light of 40—50.000 BJ-Lux, i. e. the stock is able to completely utilize the daylight.

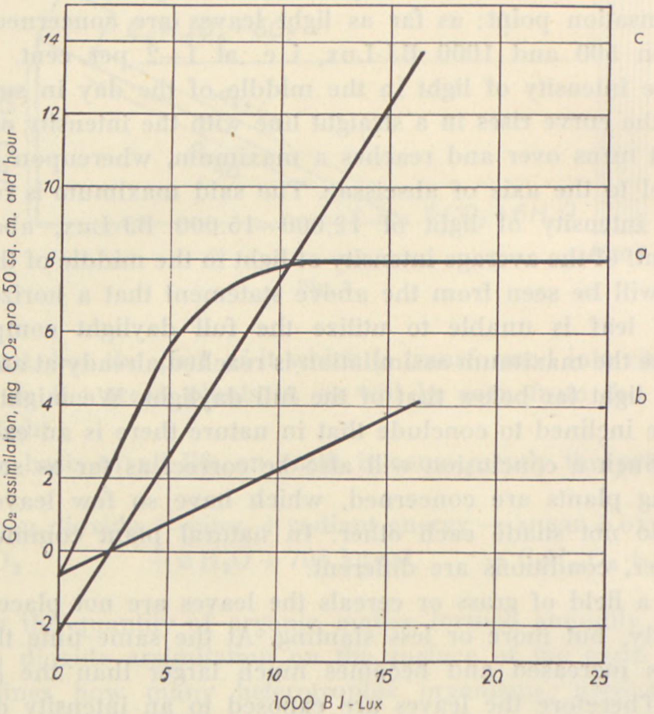

Fig. 2. Light-assimilation curve for horizontal *Sinapis* leaves, measured unilaterally per 50 sq.cm. and hour (a), and for a stock of *Sinapis*, partly per 50 sq.cm leaf area and hour (b), partly per 50 sq. cm. ground area and hour.

III. Production of Matter in Plant Communities.

The dry matter formed during the carbon dioxide assimilation is used either for an increase of the mass of the individual, or for the formation of reproductive organs, for instance seeds, which may develop into new individuals. With regard to the production of matter, two questions now arise, viz. what factors will determine (1) the course of the production of matter and its size, and (2) the distribution over the different organs of the plant of the matter produced and the nature of the same.

1. Size of the Production of Matter.

a. *The Equation of Production and the Influence of External Factors on the Production of Matter.*

The bulk of the dry matter of the plant is, as already mentioned, produced through the carbon dioxide assimilation. Therefore, when it is asked why a certain quantity of dry matter is produced by a certain plant or in a certain area during the period of vegetation, the answer must be: in the first instance because the said quantity of matter is produced through the carbon dioxide assimilation. The total quantity of dry matter produced in this process is called the gross production. However, the case is not simply that all the gross production becomes plant dry matter. Part of the dry matter produced in the leaves by the gross production is lost by the respiration in the leaves. When this loss of dry matter due to the respiration of the leaves, together with the dry matter that has been used for the formation of the leaves, is subtracted from the gross production, a quantity is obtained that may be called the net production of the leaves, i. e. the quantity of dry matter given off by the leaves to roots, stems, and reproductive organs.

The said quantity of dry matter has then been used partly to build up axial organs and roots as well as reproductive organs, partly to cover the loss of dry matter that has taken place by the respiration in the organs mentioned. When the loss of dry matter by the respiration in axial organs and roots, as well as in the reproductive organs, is subtracted from the net production of the leaves, the result will be the total weight of dry matter of these organs.

We then get the following balance sheet of the production of dry matter in the plants (Table 2).

Table 2.

Gain of dry matter by carbon dioxide assimilation in the leaves (gross production)

— Loss of dry matter by respiration in the leaves

— Dry matter, used for the formation of leaves

Net production of dry matter by the leaves

Loss of dry matter by respiration in	Dry matter present in
Axial organs	Axial organs
Roots	Roots
Reproductive organs	Reproductive organs (flowers, seeds)

According to the above survey, the total production of dry matter comprises all the dry matter formed in leaves, axial organs, roots, and reproductive organs.

As to their significance for the production of matter the organs of the plants fall into two groups, the matter-producing organs which, in general, practically comprise the leaves only, and the rest of the organs, such as stems, roots, flowers, and fruits, which are built up of the matter produced by the leaves, and in which dry matter is also lost by respiration.

From the point of view of economy a distinction must be made between the parts utilized, and the parts left in the field of growth (Table 3).

Table 3.

	Parts utilized	Parts left behind
Cereals	Leaves + Stems, Seeds	Roots
Sugar beets	Leaves, Roots	

We are now able to record which factors are of importance to the size of the production of matter. They may be divided into 6 groups: (1) Temperature with regard to its effect on the growth and thereby as a determining factor for the length of the period of vegetation. (2) Factors which influence the size of the carbon dioxide assimilation, viz. light, temperature, and carbon dioxide tension. (3) Temperature with regard to its effect on the respiration in leaves, axial organs, and roots, as well as in the reproductive organs, and thereby on the loss of matter by respiration in the said organs. (4) Factors that are of importance with regard to the water balance. Under this heading belongs, first, the quantity of water available, which is determined partly by the size of the rainfall, partly by the properties of the soil; here also belong the factors influencing the transpiration especially the saturation deficit of the air, and winds. (5) The edaphic factors or the properties of the soil; to these belong chiefly the mineral nutrients, but also the hydrogen ion concentration, the contents of air in the soil, etc. The edaphic factors may often, when unfavourable for the plants, be altered by the intervention of man, and that is the reason why those factors have preferably been considered in connection with investigations on the production of matter. (6) The pathological factors. The latter comprise not only attacks from parasitic fungi and animals, but also certain climatic factors, for instance hail.

The factors 1—5 will now be examined with regard to their effect on the size of the production of matter.

b. *Length of the Period of Vegetation.*

The length of the period of vegetation will be of the very greatest importance to the size of the production of matter in the course of a year. By the period of vegetation is understood the the time of the year during which the development of plants is not limited by external factors. It will now be investigated what external factors can limit the period of vegetation.

In regions with uniform, constantly warm and humid weather, the period of vegetation will extend over the whole year.

In regions with seasonally changing temperature and rainfall, it will in many cases, e. g. in North and Central Europe, be the temperature that determines the length of the period of vegetation by its influence on the growth. In the early spring, towards the end of March and all through April, there is sufficient light in Denmark for enabling a rather vigorous carbon dioxide assimilation, but the production of matter is nevertheless slight, e. g. in fields with winter cereals. This is due to the fact that the temperature is too low to enable growth. There is, therefore, no consumption of matter in the growth processes; the plants are filled with assimilates, and the carbon dioxide assimilation stops. Not until May does the temperature become so high that growth commences, and development is given an impetus.

c. *Production of Matter in the Period of Vegetation.*

(*a*) When a closer examination of the production of matter is made, it will be natural to begin by considering the case in which water and mineral substances are present in optimum, and no pathological factors are acting on the plants. It will now be examined how it is possible to measure the individual quantities determining the size of the production of matter per ha. As object is chosen a stock of *Solanum nodiflorum*. (POUL LARSEN 1941).

(1) *Gross Production.* It will first be shown how the size of the gross production is measured in the course of 24 hours, namely August the 10th, 1939. To make this determination we must know (1) the course of the intensity of light during the day, (2) the leaf area per ha. of the stock, and (3) the light assimilation curve of the stock. The course of the intensity of light on the 10th of August, 1939, is given in Table 4, 2nd column.[1] By means of the curve in fig. 4, giving the real assimilation for the stock per 50 sq.cm. ground area (compare fig. 2, curve *c*)[2], the assimilation value corresponding to each of the above-mentioned intensities of light is found. The latter values are stated

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[1] The average daily course of the intensity of light during the individual months of 1937—38 is given in figs. 3*a* and 3*b*.

[2] The curve in fig. 4 differs from that in fig. 2*c* by being displaced parallelly to the ordinate axis, so that it commences in the intersecting point of the axes; by this displacement the quantity of carbon dioxide given off by respiration is added to the quantity apparently taken up. The curve in fig. 4 thus renders the influence of light on the gross production, the so-called real assimilation. The leaf area in the experiment was only 1.6 times that of the ground area. Such a leaf area is not sufficiently large to utilize the full light intensity. Already at a light intensity of 30.000 BJ-Lux the curve will be almost parallel to the axis of abscissae.

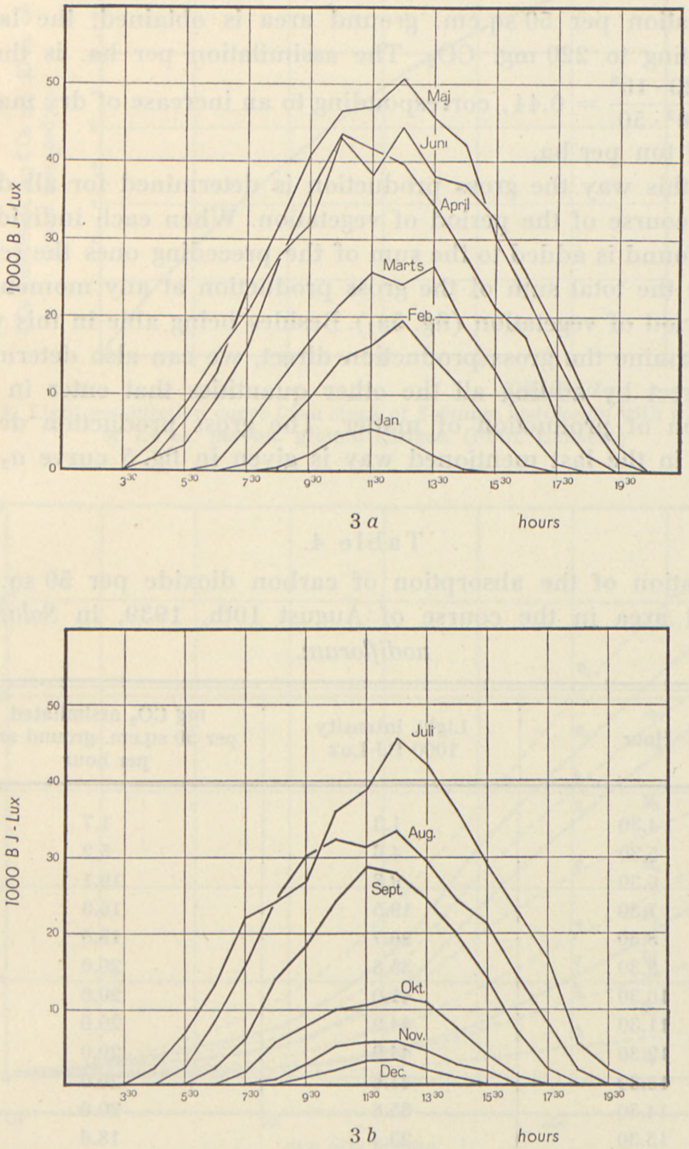

Fig. 3*a* and 3*b*. The curves represent the daily course of the light intensity during the months from July 1937 to June 1938 in Copenhagen. The light intensity, given in BJ-Lux, was measured with a photo-electric cell connected to a self-registering ampèremeter (Romose 1940).

in Table 4, 3rd column. By adding the said values, the total assimilation per 50 sq.cm. ground area is obtained, the latter amounting to 220 mg. CO_2. The assimilation per ha. is therefore $\frac{220 \cdot 10^8}{10^9 \cdot 50} = 0.44$, corresponding to an increase of dry matter of 0.27 ton per ha.

In this way the gross production is determined for all days in the course of the period of vegetation. When each individual value found is added to the sum of the preceding ones the result will be the total sum of the gross production at any moment in the period of vegetation (fig. $5a_1$). Besides being able in this way to determine the gross production direct, we can also determine it indirect by adding all the other quantities that enter in the equation of production of matter. The gross production determined in the last mentioned way is given in fig. 5 curve a_2.

Table 4.

Calculation of the absorption of carbon dioxide per 50 sq.cm. ground area in the course of August 10th, 1939, in *Solanum nodiflorum*.

Hour	Light intensity 1000 BJ-Lux	mg CO_2 assimilated per 50 sq.cm. ground area per hour
4.30	1.3	1.7
5.30	4.6	5.2
6.30	9.8	10.1
7.30	19.5	16.9
8.30	26.7	19.5
9.30	35.8	20.0
10.30	41.0	20.0
11.30	44.9	20.0
12.30	44.9	20.0
13.30	41.6	20.0
14.30	35.8	20.0
15.30	23.4	18.6
16.30	12.4	12.3
17.30	5.9	6.5
18.30	7.8	8.2
19.30	0.7	0.9

Total... 219.9 mg CO_2

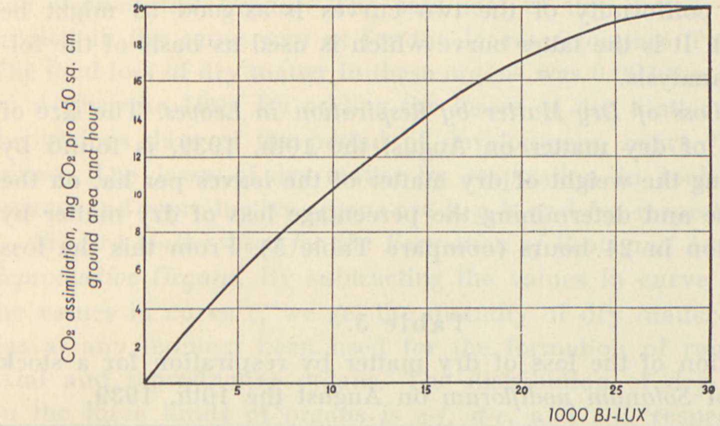

Fig. 4. Light-assimilation curve for a stock of *Solanum nodiflorum* with a leaf area of 1.6 ha. per ha. ground surface. (POUL LARSEN.)

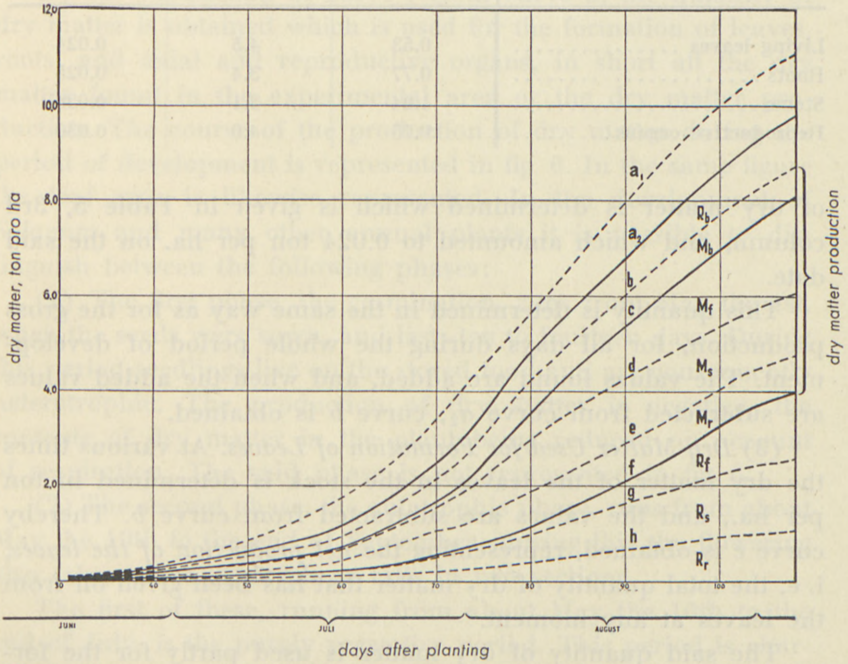

Fig. 5. The course of the individual quantities determining the production of matter in a stock of *Solanum nodiflorum*. All quantities expressed in ton dry matter per ha. M_b, M_f, M_s, and M_r represent the amount of leaves, reproductive organs, stems, and roots; R_b, R_f, R_s, and R_r represent the loss of dry matter by respiration in the same organs. For further particulars see text (according to POUL LARSEN).

The conformity of the two curves is as good as might be expected. It is the latter curve which is used as basis of the following analysis.

(2) *Loss of Dry Matter by Respiration in Leaves.* The size of the loss of dry matter on August the 10th, 1939, is found by measuring the weight of dry matter of the leaves per ha. on the said date and determining the percentage loss of dry matter by respiration in 24 hours (compare Table 5). From this the loss of dry matter is determined which is given in Table 5, 3rd column, and which amounted to 0.024 ton per ha. on the said date.

Table 5.

Calculation of the loss of dry matter by respiration for a stock of *Solanum nodiflorum* on August the 10th, 1939.

	Average weight of dry matter of the organs, ton per ha.	Percentage loss of dry matter during 24 hours at 19°	Loss of dry matter Aug. 10th, 1939, ton per ha. 19°
Living leaves	0.53	4.5	0.024
Roots	0.77	3.4	0.025
Stems	1.24	3.1	0.038
Reproductive organs	0.75	4.0	0.030

This quantity is determined in the same way as for the gross production, for all days during the whole period of development. The values found are added, and when the added values are subtracted from curve a_2, curve b is obtained.

(3) *Dry Matter Used for Formation of Leaves.* At various times the dry matter of the leaves in the stock is determined in ton per ha., and the values are subtracted from curve b. Thereby curve c is obtained, representing the *net production of the leaves,* i. e. the total quantity of dry matter that has been given off from the leaves at any moment.

The said quantity of dry matter is used partly for the formation of axial organs and roots, as well as reproductive organs, partly for covering the loss of dry matter by respiration in these organs. The latter quantity is determined first.

(4) *Loss of Dry Matter by Respiration in Axial Organs, Roots,*

and Reproductive Organs. The said loss of dry matter is calculated in the same way as for the leaves (compare Table 5). The total loss of dry matter in these organs was 0.093 ton per ha. on August the 10th. By adding the losses of dry matter during the various days of the period of development, curve *f* is obtained. The losses of dry matter by respiration in roots, axial organs, and reproductive organs are *h*, *g-h*, and *f-g*, respectively[1].

(5) *Dry Matter Used for the Formation of Roots and Axial and Reproductive Organs.* By subtracting the values in curve *f* from the values in curve *c*, we get the quantity of dry matter which has at any moment been used for the formation of roots and axial and reproductive organs. The distribution of dry matter on the three kinds of organs is *e-f*, *d-e*, and *c-d*, respectively. It is seen that the formation of reproductive organs does not get an impetus till the latter half of July.

By the subtraction of curve *f* from curve *b*, the quantity of dry matter is obtained which is used for the formation of leaves, roots, and axial and reproductive organs, in short all the dry matter found in the experimental area or the dry matter production. The course of the production of dry matter during the period of development is represented in fig. 6. In the same figure the leaf area is likewise represented. In the development of *Solanum* and many other annual plants it is possible to distinguish between the following phases:

(1) The first phase, the germination, runs from May the 1st, when the seeds were sown, and lasts ten to fourteen days. During this period seedlings live on the stored food and are consequently heterotrophic. The production of dry matter is negative, the contents of dry matter in the plant being reduced on account of respiration. The said phase is not represented in fig. 6.

(2) The second phase, the autotrophic phase, runs from about May the 10th to the end of September; during this the flowering also takes place. This phase falls in two sections.

The first of these, running from about May the 10th to the end of July, is the purely vegetative period. This period is characterized by the development of the assimilatory system, partly

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[1] Besides in the leaves, chlorophyl is likewise found in herbaceous stems, immature fruits a. s. o. In the latter a recovering assimilation will therefore be able to take place, by which part of the carbon dioxide produced by the respiration will again be built up, if light is present.

roots and axial organs, partly leaves. At first the plants are sparse, a coherent leaf area is developed only gradually. As the development of the leaf area is progressive, the net production of the leaves and the quantity of dry matter will also increase progressively according to a curve which is convex against the axis of abscissae.

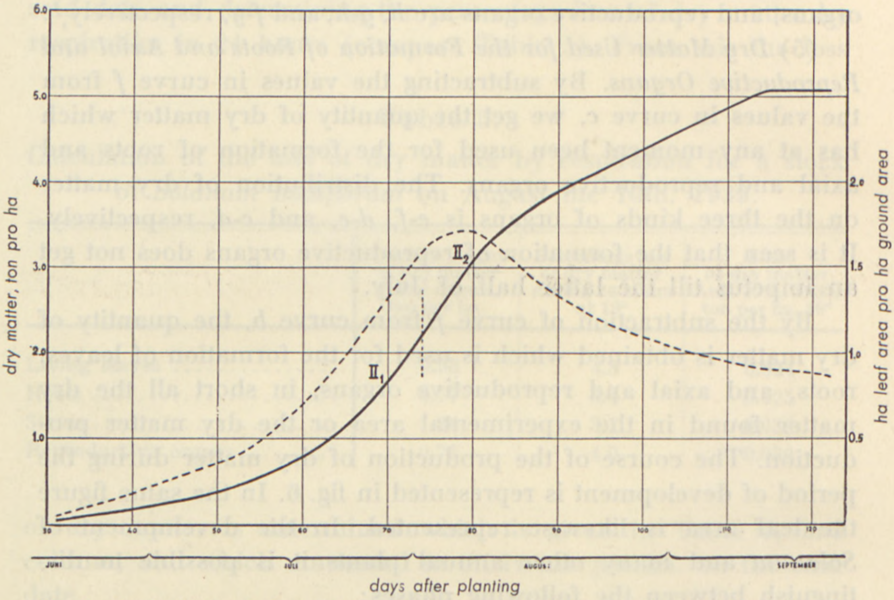

Fig. 6. Production of dry matter in *Solanum nodiflorum*. The numbers for the inked-in curve denote dry matter per ha.; for the stippled curve the leaf area in ha. per ha. on the various times after the planting out. II$_1$ and II$_2$ are the two sections within the autotrophic phase (Poul Larsen).

The second section of the autotrophic phase runs from the end of July to the end of September; it is characterized by the fact that the development of leaves, roots, and axial organs ceases, and that the assimilation products, besides being used to cover the respiratory loss, are also used for the formation of reproductive organs. The leaf area is at most 1.7 times as large as the ground area and is slowly decreasing as part of the leaves wither and die. So the daily net production of the leaves is also slightly decreasing; as the loss of dry matter by respiration in roots and axial and reproductive organs is simultaneously increasing, the curve for the production of dry matter will be concave against the axis of abscissae during this period.

The curve for the production of dry matter during the autotrophic phase is consequently S-shaped.

When the leaves have withered completely, the production of dry matter ceases; the curve for the production of dry matter will then run parallel to the axis of abscissae, at last it falls off slightly.

(β) Water deficiency. When a period of water deficiency sets in, the stomata are closed, the intake of carbon dioxide, and consequently the production of matter will then stop almost completely, so that the part of the period of development when the supply of water is insufficient is lost for the production of matter.

The effect of such a period of drought is very different on one hand in plants with purely vegetative development (e. g. beets) and on the other in plants in which the development of leaves is limited by the formation of flowers.

In the first case the carbon dioxide assimilation and consequently the production of matter ceases during the period of drought, but if the latter does not to any further degree damage the plants, the production of matter will continue, when rain comes again, so that the only effect of the period of drought is that the said period is lost to the production of matter.

In cereals, e. g., the effect of a period of drought may on the other hand be more complicated, as besides stopping the production of matter, it may also restrain the development of leaves and accelerate the development of the ear. When the said change from purely vegetative development to formation of flowers has occurred, it cannot recede any more. Besides its direct stopping effect on the production of matter, the drought may, therefore, also have an indirect effect on such plants, namely by preventing the assimilatory system from reaching a sufficient development, and thus reducing the production of matter.

The large fluctuations in the harvest yield seen from one year to another in Denmark may, especially as far as the summer crops are concerned, be traced back to fluctuations in the supply of water during the period of vegetation.

(γ) The significance of mineral nutrients. In plants suffering from want of nitrogen or potassium or phosphate, the maximum rate of assimilation may go down to half the normal value and even further, even if the stomata are open, and the content of chlorophyl has no limiting effect on the carbon dioxide assimilation.

The decrease in the rate of assimilation is only one of the causes of the restraining effect of nitrogen and phosphate deficiency on the production of matter; another, more indirect, effect consists in the fact that the formation of stems and roots is furthered at the expense of the leaves, and such an unfavourable distribution of matter will contribute further to diminish the production of matter (D. MÜLLER 1932).

In potassium deficient plants the relation stem + root : leaf area is, on the other hand, normal (D. MÜLLER and P. LARSEN 1935).

2. The Distribution of Matter.

Annual and biennial plants are characterized by the fact that besides the vegetative organs—leaves, stems, and roots—storage organs are likewise produced, such as seeds or tubers, containing relatively little cellulose, but much starch, sucrose or fat and protein. The distribution of the matter produced through the carbon dioxide assimilation over the different organs takes place in a way which is specific to each plant species.

In the experiment with *Solanum nodiflorum* mentioned above, the production of dry matter per ha. (i. e. the quantity of dry matter found in the field at the end of the period of vegetation) was 4.77 ton. Of the said amount the leaves made up 0.66 ton (14 per cent.), the roots 0.79 ton (16 per cent.), the stems 1.32 tons (28 per cent.), and the reproductive organs 2.00 tons (42 per cent.).

In an experiment with *Sinapis* (HORNBERGER 1885) the production of dry matter per ha. was 9.4 ton, distributed over the different organs in the following way: leaves 0.9 ton (10 per cent.), stems 5.9 ton (63 per cent.), roots 0.3 ton (3 per cent.), and siliques 2.3 ton (24 per cent.).

Of a crop of wheat about 30 per cent. becomes grain, 50 per cent. straw, and the rest, 20 per cent., is left in the field in the shape of stubble and roots.

The distribution over the various organs of the matter produced may be altered somewhat under the influence of external factors. As mentioned above, deficiency of mineral nutrients may further the development of stems and roots at the expense of the leaves. In many plants the length of day also determines the time in which the flowering will occur and consequently the distribution of matter. (GARNER and ALLARD, see MAXIMOV 1929.)

In long-day plants, e. g. barley, the long day favours the formation of grains, the short day the formation of vegetative organs, in short-day plants, e. g. millet, it is vice-versa. The effect of the length of day on the distribution of matter in the plants mentioned appears from Table 6. It should, however, be emphasized that such extreme conditions as those in the table will not normally appear in nature, because the plants growing or being cultivated in a given locality will generally be adapted to the day length of the latter.

Table 6.

Influence of the length of day on the distribution of matter in short- and long-day plants (RASUMOV).

	Length of day in hours	Weight; per cent. of total weight			
		Leaves	Roots	Stems	Ears
Barley (long-day plant)	18	12	11	55	22
	12	30	32	37	1
Millet (*Panicum*, short-day plant)	12	19	10	26	45
	18	25	17	40	18

IV. Increase of the Production of Matter and its Limitation.

Of the large number of plants found in nature only a rather small number is especially valuable as food for man and domestic animals. The aim of agriculture is, therefore, to replace the natural vegetation by cultures of such valuable utilitarian plants.

Now in order to get as large a production of matter of these as possible, two different ways may be followed. We may try to utilize the given conditions of vegetation as well as possible and further try to improve them still more, or we may try to improve the plants proper by breeding.

1. Utilization and Improvement of the Conditions of Vegetation.

(α) Utilization of the Period of Vegetation. It will be seen from the above, partly that there is a *period of vegetation* limited by external factors, temperature or rainfall, partly that many cultural plants, e. g. cereals, have a definite *period of development*, by which is understood the time from germination to ripening. Hence, it is a question of selecting plants, whose period of development is such that they are able to utilize the period of vegetation as well as possible. Possibly several crops may be cultivated after each other.

Among the plants cultivated in Denmark the period of vegetation is rather badly utilized by the cereals. The assimilation is finished as early as July, so that the large quantities of light in August-September are lost to the plant production in the fields of cereals. The period of vegetation is utilized far better by grass and beet crops, which continue assimilation into the month of October. The annual production of dry matter is therefore also considerably larger in a beet crop than in a cereal crop, and the introduction of beets into the agriculture of Denmark has therefore involved an increase in the annual yield. Cereals are, however, the most important food for man, and also play a great part as fodder for the domestic animals; so they can be only partly replaced by beets, and there is a limit how far we may go in replacing cereal crops by grass- and beet-crops.

(β) Alteration of the Edaphic Factors. These factors may be altered by the farmer to an extreme degree, especially the necessary mineral nutrients may be added, and the hydrogen ion concentration may be regulated, so that it reaches its optimum.

The products harvested in the fields are preferably storage organs, containing relatively large quantities of mineral nutrients. With a potato crop 90 kilos N, 18 kilos P, and 130 kilos K are removed. It is evident that the condition for an intensive plant culture over prolonged periods is the restoration to the soil of at least part of the mineral nutrients removed from it. As regards most of the essential elements it is unnecessary to supply them by fertilizing, because the quantities absorbed by the plant are small as compared to the quantities present in the soil. The most important fertilizers are N-, P-, and K-compounds.

Though on the whole the mineral requirements of the plants are known, it is not possible to develop a completely rational theory of fertilization. The basis of such a theory must be the fact that it is the substances present in minimum quantities which chiefly limit the size of the production of matter, and which must therefore preferably be added; it must consequently be the endeavour to see that all fertilizers are present in an optimum quantity. This optimum quantity of fertilizers is, however, very difficult to determine, partly because we are only able to determine the available salts in the soil very roughly, partly because the requirement of the plants vary very much and finally because the optimum quantity of fertilizers is also dependent on other factors influencing growth, especially the rainfall, which is not known in advance. In practice, e. g. heavy fertilization with nitrogen in humid summers will be able to further the formation of lodging, whereby the production of matter is diminished.

Another edaphic factor which is of importance to the production of matter, is, as mentioned above, the hydrogen ion concentration. As far as the latter is concerned, we must likewise endeavour to obtain the optimal value for the plant in question; for the cereals it is near the neutral point. A displacement of pH in a basic direction is obtained by addition of marl or pure carbon of lime.

(γ) Supply of Water. When the edaphic factors are optimal the key to creating a large production of matter is above all to keep the stomata open during the period of development, and this is again dependent on a favourable supply of water. This factor can, however, as already mentioned, be regulated to a slight degree only. Excess of water may certainly be carried away by means of draining, which must not be so deep that too much water is drained away from the soil. Deficiency of water may generally be remedied with difficulty only; it must be the endeavour to utilize the water present as economically as possible; this may to a certain degree be effected by means of the planting of shelters, which diminish the promoting effect of the wind on transpiration.

Attempts at increasing the resistance of plants to drought were made by Henckel and Kolotova (1934) by alternatively dessicating and moistening the seeds before the sowing.

There is a possibility that the increase of the production of dry matter which according to certain authors (cf. Amlong und Naundorf 1938, and later papers by Amlong) is said to be obtained by treating seeds with growth substances (for instance β-indolyl-acetic acid) is due to a more vigorous development of the root system, so that the plants become able to absorb more water.

(δ) Tension of Carbon Dioxide. Some years ago much work was devoted to the problem of increasing the production of matter by means of an increase of the tension of carbon dioxide in the air, especially in green-house cultures, but also in agricultural crops. It must be considered probable that an increased tension of carbon dioxide involves an increased intensity of assimilation. It may not, however, be concluded that it will also involve an increase of the production of dry matter, because there is a possibility that the plants cannot transport away and utilize more assimilates than those formed at the normal tension of carbon dioxide. Experiments are published, according to which it should be possible to increase the production of matter in green-house cultures by 50—100 per cent. (cf. Bornemann 1920). The said experiments do not appear to have got any practical value hitherto.

(ε) Control of Weeds, Noxious Animals, and Plant Diseases. It would take us too far to approach these problems here, but they are of far-reaching importance to the production of matter.

(ζ) Distribution of Matter. It is not, however, sufficient to increase the production of matter; the point is also that the matter produced is distributed in the right way, that as large a percentage as possible is deposited in the organs which are the main object of the cultivation, and that means—at any rate as far as our cereals are concerned—in the grain. It must therefore be our endeavour to obtain the most favourable distribution of the matter produced. On the one hand there must be leaves enough to utilize the light, and on the other there must be a sufficient number of organs, e. g. in cereals ovules, in which the assimilates may be stored. The maximum yield of grain in the cereals is dependent upon the flowering commencing at the right time. This may be obtained by using species and varieties whose requirement as to the length of day is in accordance with that found in the place of cultivation. In certain cases the time of flowering may be promoted by external factors, especially by exposing seeds in a partially soaked state to low temperature. This treatment is generally called vernalization (Lysenko and others, Maximov 1934, Imper. Bur. Plant Genet. 1935).

(η) Summary. The factors of vegetation may be divided into two groups, viz. those which can be altered, and those which cannot be altered. To the first belong the climatic factors, light, temperature, to the second the edaphic factors, mineral nutrients, and, in part, the supply of water.

When the influence of a factor of the latter group, e. g. the concentration of phosphate, on the production of matter is examined, it will be seen that the yield is first increased by an increasing supply of phosphate, until it has reached a certain size. A further increase of the concentration of phosphate will cause no further increase of the yield and the curve will run parallel to the axis of abscissae (fig. 7). This law holds good not only of phosphate, but of all the other edaphic factors alike. When they are optimal, an increase of them will not involve an increase in yield. It will then be the climatic factors which cannot be altered that will limit the size of the yield.

2. Plant Breeding.

Plant breeding may have various aims. It may be the endeavour to extend the area of cultivation of a plant, for instance a cereal. Through the production of races with a shorter period of development it has been possible to displace the limit of the cultivation of cereals northwards. In other cases the same aim has been achieved by producing types which are especially winterproof, or the temperature acquirement of which is lower during the period of development. Yet the object of plant breeding will often be to produce varieties with a larger yield than those formerly known. The said aim may be gained by the production of types, which by a vigorous development of roots are especially

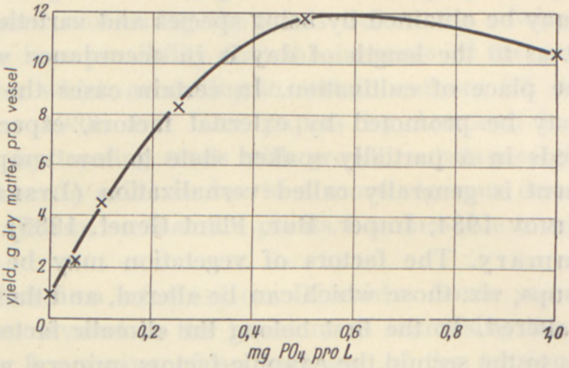

Fig. 7. Influence of phosphate concentration on the yield in maize. (Parker.)

resistant to drought, or which show a better distribution of matter, for the cereals for instance because of their having more ovules and stiffer straw. It is, however, obvious that it is the gross production that determines how far we may reach with regard to an increase of the yielding capacity of the plants. As mentioned above the size of the gross production is determined by the climatic factors, especially the light, partly also the temperature—provided the edaphic factors and the water supply are optimal. The problem is, therefore, whether it is possible to produce races which are able to utilize the light better than those already existing. The utilization of the light is again determined by two factors, viz. the assimilatory capacity of the leaves, and the more or less adequate structure of the assimilatory system.

It might be thought that an improvement of the assimilatory capacity of the leaves could be reached in two different ways, either by producing types with a higher maximum assimilation, or with a steeper assimilation curve than the types hitherto known (cf. fig. 8). In the first case the gross production of the stock would increase, because a smaller leaf area per ground area would be required in order to utilize the daylight completely.

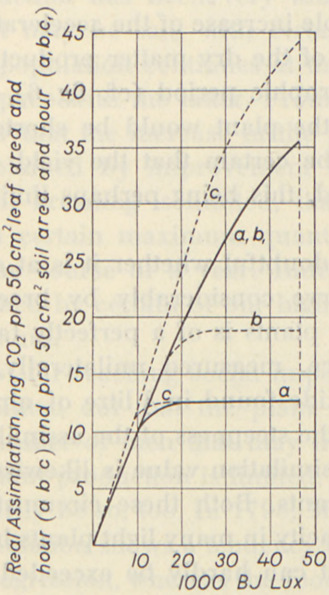

Fig. 8. Curve *a* represents the assimilation curve for a horizontal leaf and a_1 the corresponding curve for a stock of the same plant; a leaf area about 3 times the ground area is required in order to utilize the daylight fully. Curve *b* is a curve for a horizontal leaf, the maximum assimilation of which is larger than for the leaf in curve *a*; the corresponding assimilation curve for the stock b_1 is identical with a_1, but it demands a leaf area of only twice the ground area in order to utilize the daylight fully. Curve *c* is a curve for a horizontal leaf that has a steeper assimilation curve than the leaf in *a*; the corresponding assimilation curve for the stock is c_1; a leaf area of 4 times the ground area is required to utilize the daylight completely.

But it would be of greater importance still, if the steepness of the assimilation curve was increased. Not only would the maximum assimilation of the stock become considerably larger hereby, but in addition such a stock would be particularly able to utilize the smaller intensities of light to a higher degree; to be sure, a larger leaf area would also be required to utilize the full daylight, but that would be of no great importance. With regard to the increase of the net production of the leaves which might be reached by the alterations of the assimilation curves represented in fig. 8, it may be thought that the net assimilation in the course of 24 hours at intensities of light such as those stated in Table 4 would be increased by 5 per cent. in the case of curve *b* and by about 20 per cent. in the case of curve *c*. The said increase, however, means considerably more than it seems, as it would involve a considerable increase of the acceleration of the development of leaves and of the dry matter production during the first section of the autotrophic period (cf. fig. 6), so that the period of development of the plant would be shortened; on the other hand it might not be certain that the yield of grain in cereals would be augmented, this being perhaps limited by the number of ovules per ha.

Still it is rather doubtful whether it is at all possible to alter the assimilation curve considerably by breeding. The rate of assimilation in light plants is of a perfectly fantastic size, as per 1 sq.cm. leaf surface, measured unilaterally, during one hour all the carbon dioxide found in ½ litre of air can be taken up. As far as we know the steepness of the assimilation curve as well as the maximum assimilation value is likewise surprisingly alike in different light plants. Both these circumstances suggest that the assimilatory capacity in many light plants has already reached such a height that it can hardly be exceeded.

The adequate structure of the assimilatory system is obtained when a suitable leaf area is present in the stock, and the light is distributed as homogeneously as possible over the leaves. A suitable leaf area is obtained by a suitable number of plants, which is again determined by the quantity of seeds sown. The structure of the assimilatory system is determined by morphological properties in the plants and can hardly be altered; in the cereals with their long, slanting leaves it may be supposed that the distribution of light in the stock approaches the optimum.

V. Conclusion.

It may be considered certain that considerable improvements in the direction of increasing the yield may still be obtained by improving the growth conditions and by plant breeding. If we want to estimate the importance of such improvements, it will be most correct from a social point of view not to calculate their value in money, but to compare them with the increase of population. In Denmark, e. g. the population has almost doubled in 50 years, and the same applies to many other countries. Even if the plant production has been very much increased during the said period, it may be said with certainty that it will not, if the increase of population continues at the same rate, be able in future to keep pace with the latter. From what is said above, it will even appear that the increase in the production of matter which may be obtained by improvement of the conditions of growth or by plant breeding is limited, that it will be possible to produce only a certain maximum quantity of dry matter in a given area in the course of a year. Indeed we may suppose that the yield reached by certain of our high-bred cultural plants is near the maximum.

This result is of far-reaching social importance. In the introduction it was pointed out that the plant production is determinative of the number of men that may live on the surface of the earth. As the plant production is limited, the population of the earth must necessarily be so, too. In 1798, MALTHUS put forth the theory that the population shows a tendency to increase according to a geometrical progression, whereas the food increases according to an arithmetical progression only, and that if measures were not taken against this, this fact must lead to lack of food. As is well known, MALTHUS was not justified in his prediction in the first instance, but it is not out of the question that he will be in the next. There must necessarily exist a balance between plant production and population.

The reflections set forth preferably concern countries with a highly developed agriculture, but they will, if the increase of population continues, gradually make themselves felt everywhere.

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VI. References.

Amlong, H. U. und G. Naundorf, Die Wuchshormone in der gärtnerischen Praxis. Berlin 1938.

Avery, George S. and Elisabeth B. Johnson, Hormones and Horticulture. New York—London 1947.

Bornemann, F., Kohlensäure und Pflanzenwachstum. Berlin 1920.

Boysen Jensen, P., Die Stoffproduktion der Pflanzen. Jena 1932.

— Die Elemente der Pflanzenphysiologie. Jena 1939.

Gabrielsen, E. K., Einfluss der Lichtfaktoren auf die Kohlensäureassimilation der Laubblätter. Dansk botanisk Arkiv. Copenhagen 10, Nr. 1, 1940.

Henckel, P. A. and S. S. Kolotova, On Acquiring Drought-Resistance by Plants before Sowing under the Conditions of Vegetation Experiment. Bull. de l'Institut d. rech. biol. de Perm IX, 13, 1934.

Hornberger, R., Untersuchungen über Gehalt und Zunahmen von Sinapis alba an Trockensubstanz und chemischen Bestandteilen in 7-tägigen Vegetationsperioden. Landw. Versst. 31, 415, 1885.

Imperial Bureaux of Plant Genetics, Vernalization and Phasic Development of Plants. Aberystwith and Cambridge 1935.

Larsen, Poul, Vergleich der direct bestimmten und der aus Messungen der Assimilation und Atmung errechneten Stoffproduktion einjähriger Pflanzenbestände. Planta (Berl.) 32, 343, 1941.

Maximow, N. A., Experimentelle Änderungen der Länge der Vegetationsperiode bei den Pflanzen. Biol. Zentrbl. 49, 513, 1929.

— The Theoretical Significance of Vernalization. Herb. Publ. Ser. Bull. 16, 1934.

Müller, D., Analyse der verminderten Stoffproduktion bei Stickstoffmangel. Planta (Berl.) 16, 1, 1932.

Müller, D. und Poul Larsen, Analyse der Stoffproduktion bei Stickstoff- und Kalimangel. Planta. (Berl.) 23, 501, 1935.

Romose, V., Ökologische Untersuchungen über *Homalothecium sericeum*, seine Wachstumsperiode und seine Stoffproduktion. Dansk bot. Arkiv. Copenhagen, 10. Nr. 4, 1940.

Schroeder, Die jährliche Gesamtproduktion der grünen Pflanzendecke der Erde. Die Naturwissenschaften 1919, S. 8.

— Quantitatives über die Verwendung der solaren Energie auf Erden. Die Naturwissenschaften 1919, S. 976.

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