THE CULTURE OF ALBINO MAIZE

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(WITH TWO FIGURES)

Introduction

A number of attempts have been made to grow albino plants by means of artificial nutrition, but so far as I am aware, in none of these have plants been grown to maturity or with any material gain in dry weight. KNUDSON and LINDSTROM (**6**) succeeded in keeping albino maize plants alive when supplied with sugar, and noted the formation of five to seven leaves, while the check plants had only two to three leaves. But the albino plants failed to make a sustained growth or to show a marked increase in weight. By the use of a sterile culture method RISCHKOW and BULANOWA (**12**) were able to maintain albino seedlings of *Artemisia vulgaris* alive for three months with the formation of three to four leaves. The seedlings were grown in test tubes containing mineral nutrient and glucose.

In the attempts just cited the experiments were so arranged that dependence was placed upon the capacity of the roots to absorb sufficient sugar for the development of the plants. However, this method in principle offers little promise of success, for it is known from earlier experiments that organic matter supplied to the roots cannot compensate for the lack of photosynthetic activity of the leaves of higher plants [CERBIAN DE BESTEIRO and MICHEL-DURAND (**1**)]. The roots of plants appear to be ill adapted for the absorption of carbohydrates. At least for the practical purpose of culturing larger quantities of plants the method of organic nutrition through the roots involves an inordinate amount of labor if the culture solutions are to be kept free of infection.

That albino leaves show some characteristic differences as compared with green leaves has been shown by the chemical analyses of CHURCH (**2**) and of GRANDSIRE (**4**). These analyses were made primarily on variegated leaves and albino shoots. Albino leaves seem to be characterized by a relatively high water content and high ash. The ash contains a remarkably high percentage of potassium and a striking deficiency of calcium; there appear to be no significant differences in iron. The older analyses by CHURCH of nitrogen compounds may be open to some doubt, but both GRANDSIRE (**4**) and SCHUMACHER (**14**) reported albinos as showing a relatively higher content of soluble nitrogen compounds and a deficiency of protein nitrogen. Similarly, albinos are low in organic matter, in carbohydrates and in organic acids. SCHUMACHER (**14**) concluded that the relative deficiency of protein was a secondary effect, because by feeding carbohydrates to these leaves a decided increase in protein content was observed. It is rather remarkable that the dry albino leaves yield more material extractable with absolute ether than the corresponding green leaves. Little is known, however, regarding the nature of the organic material in albinos.

Methods of culture

The investigations here reported were carried out with albino maize seedlings.[1] Only the pure white seedlings were used in both water and sand cultures. Of the hundreds of seedlings which were grown in the course of three years under a variety of conditions of light, temperature, and mineral nutrients, no tendency of the pure white seedlings to form chlorophyll was ever observed. There was, however, a considerable variability in the vigor of individual albino plants. This manifested itself in that some plants could be kept alive through artificial nutrition for 3 to 4 months, and during this time produced both types of inflorescence, whereas other plants, raised from the same lot of seed and under identical conditions, languished and died after a few weeks or produced only one inflorescence. Such variation among individuals in inbred strains is well known to geneticists. In order to bring some plants to maturity it was therefore necessary to start with a considerable number of seedlings.

For the water culture experiments the seeds were first sterilized. Several methods were tried: calcium hypochlorite, chlorine water, ultraviolet light, and "Semesan." The seeds were sprouted on sterilized filter paper. When it became apparent which seedlings were albino they were transferred to 0.5- or 1-liter wide-mouth Erlenmeyer flasks provided with rubber stoppers. The seedlings were packed by means of cotton in a hole of the stopper with the roots immersed in mineral nutrient solution. Although a number of seedlings started in this manner finally grew to maturity, in general the water culture method did not prove to be entirely satisfactory because, in spite of various methods of sterilizing the seeds, a large number of infections developed in the endosperms and often spread to the root system.

More satisfactory results were obtained with sand cultures which for the present purposes were much simpler to start and to maintain. The seeds, without being sterilized, were sprouted in clean sand, and as soon as it was apparent which were albino seedlings these were transplanted in sand in 4- or 6-inch pots. The pots were placed on glazed saucers and the mineral nutrient solution (or water) was added to these saucers so that the top of the sand in the pots was always dry. These cultures showed the best growth and there were no evidences of disturbing effects due to infection.

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[1] The original lot of seed for these experiments was obtained through the kindness of Maize Genetics Coöperation of Cornell University, for which I wish to express my sincere appreciation.

Stock solutions of mineral nutrients were prepared as follows, each separately in 1000 ml. of distilled water: 5 gm. KCl; 5 gm. KNO_3; 28.75 gm. $Ca(NO_3)_2 \cdot 4H_2O$; 10.25 gm. $MgSO_4 \cdot 7H_2O$; 2.5 gm. K_2HPO_4 plus 2.5 gm. KH_2PO_4 adjusted to a pH of 6.6 to 6.7. Of these five stock solutions 200 ml. of each were added to four liters of distilled water and the following additions were made to make up the mineral nutrient solutions used: 10 ml. of a solution of 16.65 gm. $FeCl_3 \cdot 6H_2O$ in 1 liter of water; 1 ml. of a solution of 0.157 gm. $MnCl_2 \cdot 4H_2O$ in 1 liter of water; and 0.1 ml. of a solution containing 2.86 gm. H_3BO_3, 1.81 gm. $MnCl_2 \cdot 4H_2O$, 0.22 gm. $ZnSO_4 \cdot 7H_2O$, 0.08 gm. $CuSO_4 \cdot 5H_2O$, 0.072 gm. MoO_3 in 1 liter of water. In the nutrient solution prepared in this manner green seedlings made good growth in the light in water cultures as well as in sand cultures.

A second mineral nutrient solution was tried in which the potassium phosphate mixture in the solution just described was replaced with an ammonium phosphate mixture of pH 6.7. It was thought that the ammonium mixture might be more favorable for protein synthesis and consequently for the general development of albino plants. This, however, was found not to be the case.

After many efforts to achieve satisfactory growth of the albino seedlings by the method of supplying them with sugar added to the mineral nutrient solution, this method was abandoned as unsuitable. Recourse was taken to what would appear to be a more natural method, that of supplying the plants with organic nutrients through the leaves. The tip of the leaf was cut off and the portion attached to the plant was immersed in a sucrose solution contained in a glass vial, usually 1 cm. in diameter; this was then stoppered with a wad of cotton. See figure 1. The vials were held in coils of wire attached to supports which could be adjusted in every direction. Various sugars and mixtures of different sugars were tried. The experiments here described were carried out entirely with sucrose, which yielded the best results. By empirical methods a concentration of 0.3 molar sucrose was determined as giving the best growth effects. The method is of course, not a strictly sterile one, but precautions were taken to use sterilized scissors, and the vials, after being carefully washed, were kept in an oven at 100° C., and the sucrose solution was sterilized before use. Every other day, or every day during warm weather, the sucrose solutions were replaced by removing the vial, cutting off about 0.5 cm. from the end of the leaf and immersing it in a fresh solution of sucrose in a clean vial.

In an effort to attain as rapid and as great a growth as possible of the albinos, it was thought that this might be aided by the addition of some of the accessory factors which have been found to stimulate growth. Experiments were carried out in which some of the following, singly or combined, were added to the sucrose solution: ascorbic acid, vitamin B_1, vitamin B_6, adenine, and indolylacetic acid. No significant differences were noted in plants thus fed as compared with the controls which were fed sucrose only.

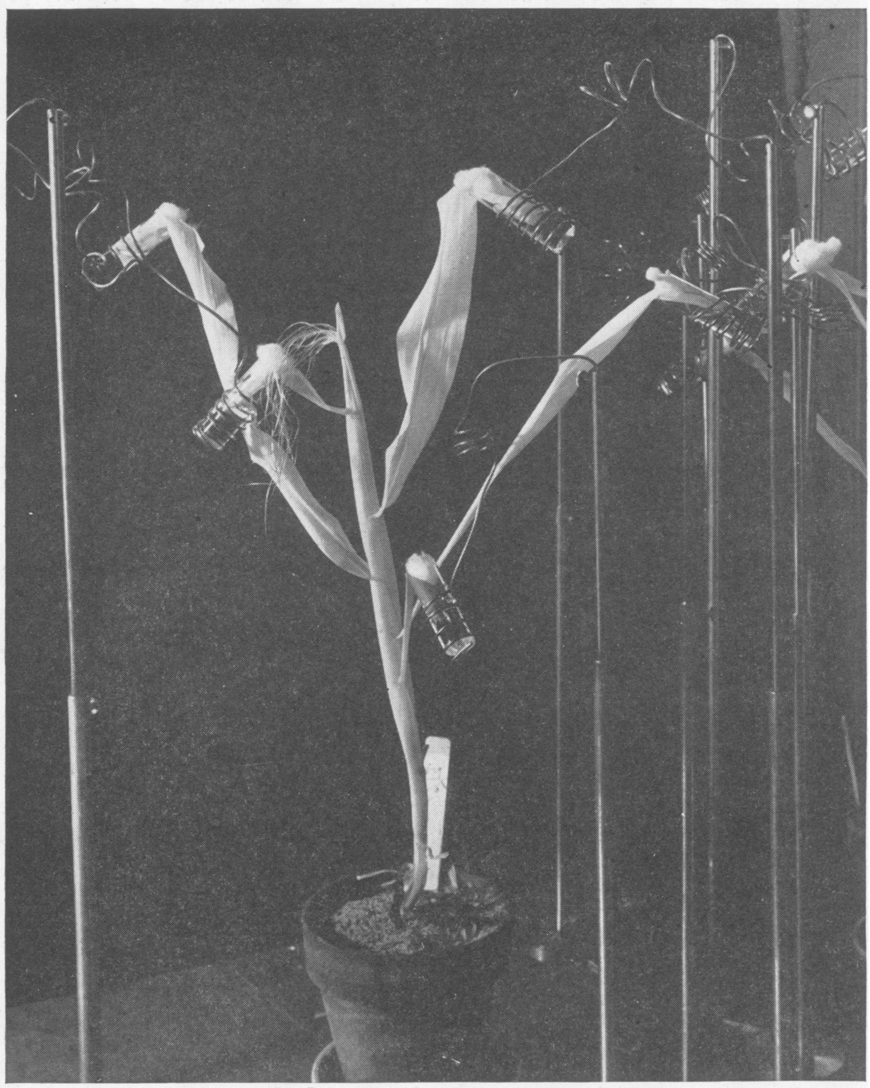

FIG. 1. Albino maize plant, in sand culture, grown with 0.3 molar sucrose solution as only organic nutrient, in 4-inch pot.

It is probably important in this connection to give consideration to the great variability in the albino stock itself, so that it could probably be expected that significant differences could be noted only in experiments with large

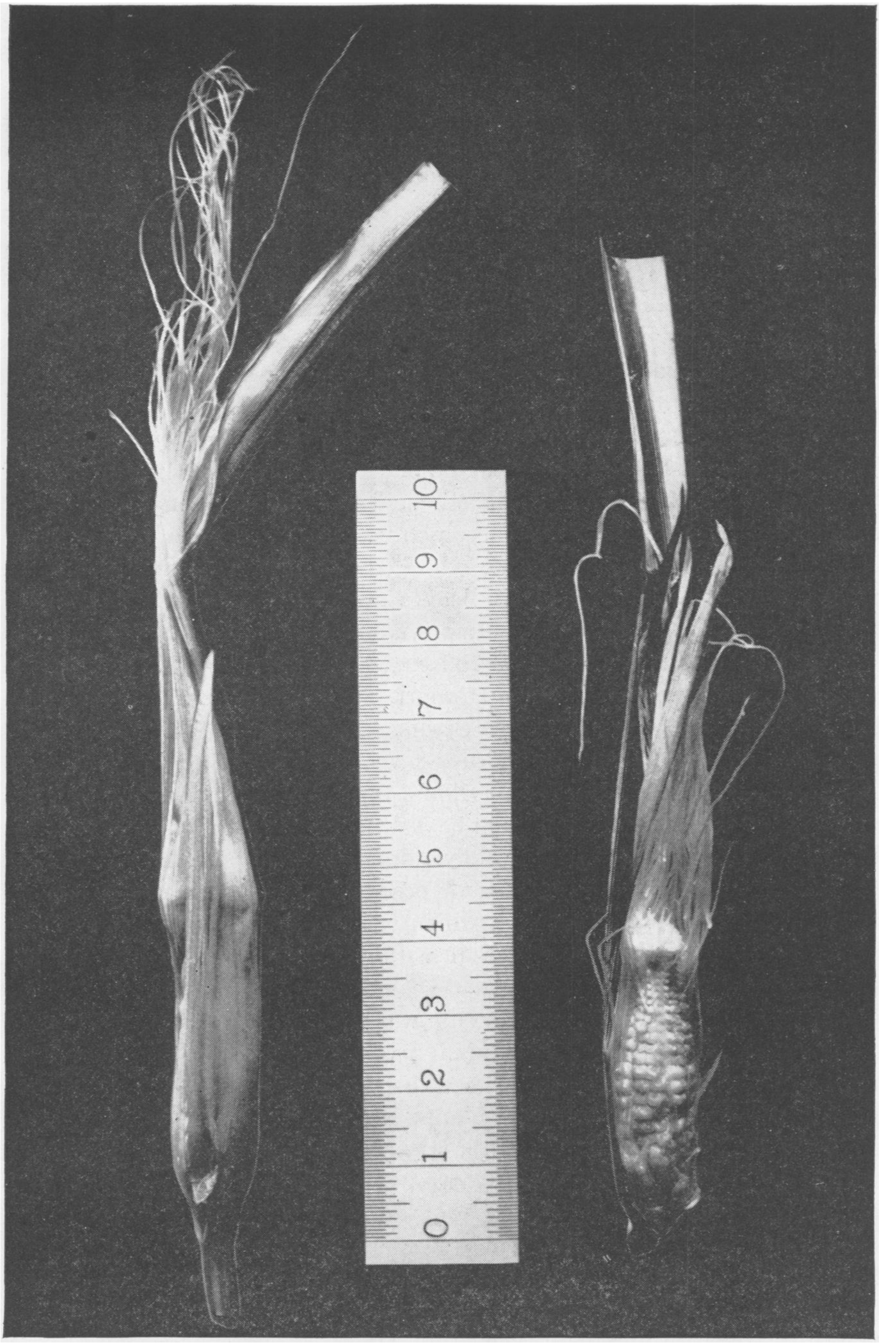

FIG. 2. Ears of albino maize plant grown with 0.3 molar sucrose as only organic nutrient, 10-cm. scale.

numbers of plants. It is also possible that there were other, unrecognized factors which were more limiting for the growth of the plants than the growth-promoting materials which were added to the sucrose solution.

In the endeavor to determine the most favorable conditions for the culture of albino plants through artificial organic nutrition, it was found that the form and rate of growth of these plants are strikingly affected by light. Albino plants were grown under three sets of light conditions: in the greenhouse, in diffuse north light, and in the dark. The temperature in all of these ranged from 18 to 25° C. Of necessity the dark series was exposed to some light, because about one-half hour of illumination with a 25-watt lamp was required every day to replace the organic nutrient solutions. This was not sufficient to maintain or produce chlorophyll in normal etiolated maize plants. The plants grown in the greenhouse in the spring and summer months were quite dwarfed and attained a height of not over six inches. They produced 10 to 15 leaves and none of these was over six inches in length. The addition of indolylacetic acid to the organic nutrient solution did not improve the growth of these plants.

The albinos grown in the dark exhibited the elongation typical of etiolation, with long, slender, delicate leaves and narrow, weak stems. These plants were kept alive over four months and produced rudimentary ears. They attained a height of 80 to 100 cm., but because of their long, weak internodes they were difficult to support. Here also the addition of indolylacetic acid produced no visible effects. Alongside of these albinos some chlorophyllous seedlings were also grown by artificial organic nutrition. The latter soon lost their chlorophyll and the new leaves were free of chlorophyll, so that these plants could not be distinguished from the albinos. After having been in the dark for 125 days, during which period they produced 10 to 14 leaves, all the plants were exposed to the light of 250-watt Mazda lamps for 12 hours. The plants which originally had been green, formed perceptible amounts of chlorophyll within two hours, while the albinos showed no change in color.

The objective of these experiments was to determine the most favorable conditions for culturing albino plants, which could then be subjected to chemical analysis. For this purpose the best results were obtained under conditions of diffuse light. The plants grown under these conditions were sturdier, had broader leaves with a strong midrib, and more of the plants survived. They grew to 40 to 70 cm. in height in 120 days. Some of them produced both pistillate and staminate inflorescences, the latter with considerable pollen; other plants produced only pistillate inflorescences and from these the silk grew 10 to 20 cm. long. Finally, some plants produced no inflorescences at all, and about one-half of the seedlings for no apparent reason died before they had reached an age of 90 days.

Results

The experiments have demonstrated that it is posible to maintain cultures of albino maize plants by means of artificial organic nutrition and that under favorable conditions the dry weight of these plants is considerably higher than that of the seeds. Beyond this fact the data probably have little quantitative significance.

The gain in dry weight

To illustrate the magnitude of this gain in organic matter by the artificially nourished albino plants the following experimental results are presented. One hundred maize seeds, dried *in vacuo* over calcium chloride, showed a mean weight for each seed of 0.20003 grams with a standard deviation of 0.04097 grams and a standard error of 0.004097 grams. While the calculations of the percentage gain in dry weight of the nourished plants over the seeds (table I) is based upon this mean weight, it must be remembered that the artificial nutrition of the plant does not start from this stage. During the germination of the seeds and the growth of the seedlings to a stage where they can be artificially nourished through the leaves, material contained in the endosperm is being consumed. Thus, thirteen sturdy albino seedlings, 12 days after sowing, were dried at 97° C. for 30 minutes and then *in vacuo* over calcium chloride. They had a mean dry weight of 0.15904 grams, representing a loss of the original dry weight of the seeds of about

TABLE I

Gain in dry weight of artificially nourished albino maize plants calculated on the basis of the mean dry weight of the seed. Plants grown in sand culture at 22 to 26° C. in diffuse light

Growing period	Days	Fresh weight	Dry weight	Percentage dry weight	Calculated percentage gain in dry weight
		gm.	*gm.*	%	%
May 29 to Sept. 29	123	8.80	1.10	12.5	450
" " " " "	123	4.70	0.72	15.3	265
" " " " "	123	3.51	0.70	19.9	250
May 29 to Oct. 3	127	12.00	1.90	15.8	855
" " " " "	127	4.50	0.50	11.1	150
" " " " "	127	12.00	1.53	12.7	665
" " " " "	127	17.01	1.62	9.5	710
" " " " "	127	12.20	1.54	12.6	670
May 29 to Oct. 16	140	....	2.92	....	1365
" " " " "	140	....	0.56	....	180
" " " " "	140	....	1.20	....	500
" " " " "	140	....	1.89	....	845
" " " " "	140	....	1.39	....	595
" " " " "	140	....	1.30	....	550

20 per cent. The standard deviation in the dry weights of the albino seedlings was 0.05337 grams and the standard error 0.014802 grams.

By the method of culture of the albino plants here followed they were subject to further material losses which are also not included in the recorded percentage gain in dry weight. Each day a few millimeters to a centimeter was cut from the end of the leaves submerged in the nutrient sugar solution, so that eventually, especially in the older leaves, there was a loss of about 50 per cent. of the leaf weight. This is estimated to amount to about 10 per cent. of the entire weight of the plant. Consequently the calculated percentage gain in dry weight of the artificially nourished plants represents an underestimate of the total gain.

As has already been mentioned the albino seedlings show a considerable variation in vigor and this is reflected in the great range of the percentage gain in dry weight, varying from 150 to 1365 per cent. in the example cited. Needless to say these gains in dry weight are very much smaller than are those made by a normal plant which obtains its organic nutrition by means of photosynthesis. There are doubtless many improvements in the methods of culture which are still to be worked out. The factor of temperature alone may be cited as deserving of special study. In one series of cultures the temperature range was between 12° and 20° C. for 102 days and the plants appeared to be in good condition. But, although they had grown and put out new leaves, so far as the dry weight was concerned the plants just about held their own, because in all this time there was no appreciable gain in dry weight over that of the seeds.

Starch formation in albino leaves

Relatively little study has been given the organic nutrition of albino or chlorotic leaves. It has been known for a long time that, although the chromatophores of albino, chlorotic, and albescent leaves do not form starch in the light, starch is deposited in these organs when such leaves are floated on solutions of sucrose or glucose, as was demonstrated by Saposchinkoff (**13**) and Zimmermann (**18**). Winkler (**17**) also demonstrated that leaves of *Fagopyrum tataricum* and of *Zea mays,* which were white through withholding iron from the nutrient solutions, did not produce any starch in the light, but formed abundant starch when placed on solutions of glucose or sucrose. In our own experiments we have repeatedly been able to observe the formation of starch in albino maize leaves when these were fed sucrose.

In this connection an observation first made by Saposchnikoff (**13**) may be of significance. Normal green leaves are able to form starch in the dark not only from sugars such as glucose, fructose, galactose and sucrose, but also from such compounds as glycerine and mannitol which represent a slightly higher level of reduction than the sugars. Saposchnikoff found that the chlorophyll-free portions of variegated leaves do not form starch from glycerine and mannitol. We have also found that albino maize leaves do not form starch from glycerine or sorbitol. In table II the results are summarized of comparative experiments with green and albino maize leaves. The leaves were kept in the dark until they were free of starch. A number of leaves were then submerged in the solutions of sugars, glycerine, and sorbitol, and placed in a vacuum desiccator. By careful evacuation the air was removed from the leaves which thereby became infiltrated with the respective solutions of organic nutrients. This process required about 15 minutes. Air was admitted into the desiccator and the leaves removed to vials containing enough of each of the solutions so that the cut ends of the leaves were well submerged. The leaves were kept in the dark at 22 to 24° C. and tested for starch after 24 and 48 hours.

TABLE II

STARCH FORMATION BY GREEN AND ALBINO LEAVES OF *Zea mays* INFILTRATED WITH SOLUTIONS OF VARIOUS ORGANIC NUTRIENTS IN THE DARK

SOLUTIONS	*Zea mays*	
	GREEN	ALBINOS
0.3 M. sucrose	+	+
0.1 M. sucrose	+	+
0.3 M. d-glucose	+	+
0.1 M. d-glucose	+	+
0.3 M. glycerine	+	–
0.1 M. glycerine	+	–
0.3 M. d-sorbitol	+	–

This difference between albino and chlorophyllous leaves may be of more fundamental importance than has been realized. Starch formation from compounds such as glycerine and sorbitol indicates that normal leaves have the capacity to oxidize an alcohol group, probably forming a keto- or aldosugar. Albino leaves apparently lack this capacity. The formation of chlorophyll is also associated with oxidative reactions. Whether there is any connection between the lack of chlorophyll in albinos and their apparent incapacity to oxidize compounds such as glycerine remains to be established.

In agreement with the results of GRONER (**5**) it was found that there is very little difference, if any, between the rates of respiration of albino and chlorophyllous leaves. In these experiments seedlings were used which drew upon the endosperm for their supply of carbohydrate. On the other hand, SMIRNOW (**15**) and SCHUMACHER (**14**) found that the white portions of variegated leaves had a lower rate of respiration than the portions containing chlorophyll, and SCHUMACHER was able to demonstrate that this lower rate was due to a deficient supply of carbohydrate. Beyond this, however, it appears to be quite well established from the investigations of SMIRNOW (**15**) and of SCHUMACHER (**14**) that the white and chlorophyllous portions of leaves differ in regard to the activity of certain enzymes which are presumed to be associated with oxidative processes of the cells. The chlorophyll-free tissue contains more peroxide and less catalase, and SCHUMACHER concludes that this is an indication of a lower or more sluggish rate of energy transfer. Until the rôle of these enzymes in the oxidative metabolism has been more clearly established there seems little prospect, however, of drawing definite conclusions from such data concerning the differences between the two types of tissue.

LEBEDEFF (**10**) made comparative studies of various functions of green and albino maize plants, including rate of phototropic response, rate of growth, swelling of the seeds, rate of respiration, and metabolism of nitrogen compounds. He concluded that the two forms of leaves did not differ in their assimilating mechanism but only in their capacity to utilize radiant energy.

Discussion

It has been generally assumed that in the photosynthetic process the carbon dioxide is reduced to the level of a carbohydrate. In any consideration of the chemical mechanism of this process it is obviously of importance to know whether carbohydrates are the only products formed, or whether simultaneously other products, such as hydroxyacids, fatty acids and hydrocarbons are also produced directly through photosynthesis. The concept that the carbon dioxide is reduced to the level of a carbohydrate rests essentially upon the results of chemical analysis and of measurements of the photosynthetic quotient.

It must be admitted that the enormous effort which has gone into determining the nature of the photosynthetic products of higher plants by means of chemical analysis, extending over fifty years, has not been very rewarding. No reliable information has been gained by this means as to intermediate products nor regarding the question whether there is a specific carbohydrate formed in the process. It is doubtful whether a solution of these problems can be gained without recourse to special means such as are afforded by the use of radioactive isotopes of carbon. It is primarily the question as to what percentage of the carbon dioxide absorbed in photosynthesis appears as carbohydrate. A definite answer to this question is still outstanding (**9**).

The observation that the photosynthetic quotient is very close to unity has been commonly assumed to mean that the carbon dioxide has been reduced to a carbohydrate (**16**). This interpretation is, however, open to some question. In the first place, a value of unity has usually been obtained only after the plant has been subjected to illumination for some time. During the first minutes of illumination the quotient is irregular and shows considerable deviation from unity (**5, 7, 11**). No entirely satisfactory explanation has as yet been offered for these fluctuations. Whether, for example, these deviations from unity in the value of the quotient signify the formation of intermediate products, which are subsequently further reduced, or whether it is an indication that during this period other products are predominantly formed, with a quotient higher or lower than unity, remains uncertain. Furthermore, the fact must be borne in mind, that in the measurement of the photosynthetic quotient the gas exchange of an over-all reaction is being determined. From these measurements alone there is nothing which precludes the concept that the value of the quotient represents the net result of the gas exchange of a number of reactions. Whether these reactions all proceed to the same end product is not known. But there is no evidence which precludes the possibility that the photosynthetic process consists of serial reactions, proceeding simultaneously and resulting in products of different nature, *i.e.*, of a different level of reduction. Each product would have a different individual photosynthetic quotient, and still the total or over-all quotient could be unity. For example, if in the photosynthetic process a mixture were formed consisting of a hydrocarbon with a quotient of less than one, a carbohydrate with a quotient of one, and a hydroxyacid with a quotient greater than one, the total gross reaction might still yield a photosynthetic quotient of unity.

If it were established that the photosynthetic process resulted directly in the synthesis of a variety of products of varying level of reduction instead of only carbohydrate, it would materially affect many theoretical concepts of the mechanism of the process. If carbohydrate were the only substance formed in the photosynthetic process, the commonly accepted opinion would hold, namely, that the great array of compounds found in plants arises from carbohydrate through biosynthetic reactions. On the other hand, if carbohydrate is not the only product of photosynthesis, even though the substances of higher and lower level of reduction are formed in relatively small amounts, our concepts of the mechanism of the photosynthetic reactions and of the organic nutrition of plants would have to be materially modified. Finally, it is conceivable that the photosynthetic and chemosynthetic reactions occurring in the plant are so inextricably intermeshed that the unravelling of this tangle and the elucidation of any one of these reactions may prove to be a far more complex problem than we now realize.

The theory that carbohydrate is the only product of photosynthesis and that the entire organic nutrition of the plant can ultimately be satisfied from this material can, in a measure at least, be subjected to experimental test. It has long been known that some of the lower plants, particularly the algae, can be kept alive for extended periods of time in the dark when cultured, in solutions of carbohydrates and other organic compounds. Similarly, the leaves of higher plants are known to form starch from a variety of carbohydrates. It appears that the higher plants are considerably more selective in respect to their artificial organic nutrition than are algae (**8**). By entirely excluding photosynthesis a test could be made to determine to what extent a higher plant can be brought to full development by means of artificial nutrition exclusively with a carbohydrate. Obviously two means are available for such an experiment: the culturing through artificial nutrition of normal, chlorophyllous plants in the dark, and the culturing by the same means of albino plants. Experience has demonstrated that the use of normal plants in the dark was considerably complicated by the "etiolation" effects produced by culturing the plants in the dark. On the other hand, albino plants can be grown in the light and all "etiolation" effects can be thus avoided; at the same time these plants are devoid of the capacity for photosynthesis.

It is, of course, difficult to establish criteria on which an unequivocal answer of this test can be based. As a beginning the simplest and most rational criterion has been the gross development of the plant, including the length of time it is kept alive, the number of leaves produced and the development of sex organs. This could then be supplemented with chemical analysis of the constituents of the artificially nourished plants as compared with normal ones. But for this latter purpose a sufficient amount of plant material must be available. Consequently, the chief effort for the present has been to determine the most favorable conditions for the culturing of albino plants by means of artificial nutrition.

The contrasting properties and the differences in their capacity to utilize compounds such as glycerine and sorbitol, exhibited by albino and chlorophyllous plants, emphasize the necessity of exercising caution in drawing conclusions regarding organic nutrition on the basis of the method which is here being considered. Associated with their lack of ability to form chlorophyll, other deficiencies may exist in albino plants which might make it impossible for them to carry on certain reactions occurring in chlorophyllous plants. It is conceivable, for example, that albinos lack not only the capacity to form chlorophyll, but that linked with this deficiency, are also other deficiencies affecting their metabolism.

Summary

It has been demonstrated that albino maize plants can be kept alive for several months by artificial organic nutrition with sucrose. These plants showed a definite increase in dry weight above that of the seeds from which they sprang. They produced the same number of leaves as normal green plants and also staminate and pistillate inflorescences. The albino leaves formed starch in the dark when infiltrated with solutions of sucrose and dex-

trose, but, in contradistinction to green leaves, not with solutions of glycerine or sorbitol. Some theoretical aspects of the use of cultures of albinos for elucidating certain phases of the photosynthetic problem are discussed.

It is a pleasure to acknowledge the assistance rendered by Miss NANCY CROSS in part of this investigation.

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