hibitory antimetabolites of folic acid. Folic acid, adenine, guanine, thymine, and uracil reversed these inhibitions. The implications of some of these findings are discussed.

We wish to thank the Lederle Laboratory for generously supplying the anti-folic compounds.

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CHLOROPHYLL AND CAROTENOID DESTRUCTION IN THE ABSENCE OF LIGHT IN SEEDLINGS OF ZEA MAYS L.[1,2]

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Seedlings require light not only for the initial formation of chlorophyll, but apparently also for its continued maintenance, for a seedling containing chlorophyll will, when placed in the dark, lose its green pigmentation (1). This suggests that, to maintain a high chlorophyll level in the living plant, light-dependent synthetic reactions must keep pace with, or exceed the light-independent destructive processes that occur concomitantly and continuously. These "dark" destructive processes must occur in addition to the photochemical oxidations of the chlorophyll molecule extensively described in the literature (2, 3).

Carotenoid pigments can be synthesized by dark-grown seedlings, but under certain conditions light will accelerate the synthesis of these yellow plastid pigments (4, 5, 6, 7, 8). The destructive reactions of the carotenoids have also been studied in detail, and are considered to be both enzymatic and photochemical in nature (9).

Thus, it is evident that the amount of chlorophyll and carotenoids present in a plant grown in the light is the resultant of at least the following reactions:

1) "light" formation of chlorophyll,
2) "light" destruction of chlorophyll,
3) "dark" destruction of chlorophyll;

and for carotenoids,

1) "dark" formation,
2) "light" formation,
3) "dark" destruction,
4) "light" destruction.

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The present investigation was undertaken to elucidate those destructive reactions of chlorophyll and carotenoids that occur exclusively in the absence of light. In this way, it is hoped that the complex network of reactions involving these pigments will begin to be unraveled.

Materials and Methods

Materials: Seedlings of *Zea mays* L. of a hybrid stock named Cornell M-4 were used in this investigation.[4] Seeds were soaked for 24 hours in distilled water, and after soaking, about 25 seeds placed around a rim of a 600-ml beaker, between the glass surface and a layer of moistened filter paper. Distilled water (350 ml) was placed in each beaker to insure a high relative humidity. The beakers were placed in a constant temperature chamber at 27° C in the complete absence of light, and the seedlings allowed to develop until they were one week old. At the end of this time, a sample of plants was extracted to determine the concentration of carotenoid pigments that had developed during this period, some seedlings were left in the dark chamber to serve as controls, and the remaining seedlings were exposed to various conditions of light. After the exposure period, samples of the light-exposed seedlings were killed, extracted and analyzed for pigment content (chlorophyll and carotenoid), and the remaining light-treated plants in this series of exposure times were then returned to the dark 27° C temperature chamber. Seedlings were periodically sampled, after various times in the dark, and extracts made to follow the changes in chlorophyll and carotenoid content occurring during the dark period. At the same time, control plants were analyzed, that is, plants which were comparable in age, but which had received no light treatment.

Extraction Procedure: The seedlings were killed by placing them in boiling water for one minute, this treatment also serving to minimize the oxidative destruction of carotenoids (10). The sheath was dissected away, and the leaf tissue weighed on a torsion balance and immediately extracted. Four seedlings were used for each extract. The wet weights of the leaf tissue averaged from 100 to 800 mgs. The tissue was ground in a mortar containing Berkshire sand and 20 ml C.P. methyl alcohol. The grinding of the plant tissues was carefully timed and kept standardized. At the end of the grinding period, the extract was filtered with suction and the filtered tissue examined to see that it was colorless. The filtrate was then centrifuged for ½ hour, and the clear greenish-yellow methyl alcohol solution brought up to constant volume (25 ml) before measuring the pigment content spectrophotometrically.

Estimation of Pigment Content: The solutions were analyzed in a Beckman spectrophotometer Model DU. The photometric density at 660 mμ was taken as a measure of chlorophyll concentration, and the density at 440 mμ was used to estimate the total carotenoid concentration. In these seedlings, the chlorophyll concentration was always low relative to the carotenoid concentration, so the following method of estimating carotenoids was adopted: chlorophyll a has two peaks of absorption of almost equal height, one at 440 mμ, one at 660 mμ; the optical density of the solution at 660 mμ was subtracted from its optical density at 440 mμ, the remainder being considered a measure of the carotenoid concentration. The presence of chlorophyll b would introduce an error in this method of estimating carotenoid content, since the relative height of its absorption peak at 440 mμ compared with 660 mμ is 2.87. No evaluation of chlorophyll b concentration was made, but it can be estimated that its presence might cause at most a 10 % error in the carotenoid determination. (In the experiments reported here, the optical density of the extracts at 660 mμ was never more than $\frac{1}{3}$ the optical density at 440 mμ, and at most only $\frac{1}{3}$ of the density value at 660 mμ would be due to the presence of chlorophyll b.)

In all tables and figures, pigment concentration is expressed as density per mg wet weight of leaf tissue. However, the raw data were obtained by analyzing the pigment content in the leaves of 4 seedlings, whose fresh weights were known. Thus, the change in total pigment content in each seedling with time in the dark could also be followed. Light-treated plants invariably had higher fresh weights than dark-grown plants of comparable age, and it was felt that this increased growth might also involve increased pigment synthesis. In an effort to balance out this effect, the fresh weight basis for expressing pigment concentration was decided upon, rather than a per plant basis. However, pigment changes expressed on a per plant basis were essentially of the same order as those expressed on a per mg fresh weight basis. That is, the percentage of pigment loss with time in the dark was parallel in both cases. This is true in spite of the fact that plants returned to the dark showed increases in wet weight. A dilution of pigment concentration would be expected as a result. Evidently, this dilution effect was constant over the range studied here, since in spite of its presence the time course of pigment destruction was not different from that of pigment loss within a single seedling.

Light Exposure: The seedlings were exposed to white light for varying durations (from 4 to 12 hours) at a constant light intensity of 90 fc. The light source was a 300-watt projection bulb operating through a voltage regulator on 115 volts AC; the intensity of the light was measured using a Macbeth illuminometer. When the seedlings were about to be exposed to light, they were taken from the beakers and transferred between two glass surfaces to orient them uniformly to the light source. The exposure took place in a specially constructed light-tight box, the only light falling on the plants coming from the projection

[4] These seeds were made available for experimentation by the generosity of the Department of Plant Breeding, Cornell University Agricultural Experiment Station, Ithaca, N. Y. and are gratefully acknowledged.

bulb. At all other times, the plants were handled in the dark, with the aid of a dim green Christmas tree bulb as safe light.

Results and Discussion

Table I shows the effect of 4 different light exposures on the amount of chlorophyll and carotenoid pigment in the leaf tissue of one-week-old corn seedlings. The figures give an idea of the type of variability encountered.

In tables II and III and figure 1, the time course of the light-independent destruction of the two pigments is shown. Each figure in the table and point on the curve is an average of at least 5 determinations. Regardless of the initial pigment concentration in the seedling at the time of return to the dark, the rate of the pigment destruction is the same. After 120 hours in the dark at 27° C, virtually all the chlorophyll initially present is destroyed (upper curve, fig 1). The time course of chlorophyll destruction was followed in a few cases, not shown in table II

Table I

Effect of Different Durations of Exposure to White Light on the Chlorophyll and Carotenoid Content of 1-Week-Old Etiolated Corn Seedlings

Time of exposure in hrs	Pigment conc *	
	Chlorophyll ($\times 10^{-5}$)	Carotenoids ($\times 10^{-4}$)
4	19.0	5.2
	22.7	6.7
	14.7	4.2
	8.7	2.3
	averages	
	15.4	4.4
6	29.0	3.5
	27.1	5.3
	22.3	3.8
	32.5	6.2
	13.8	4.3
	17.9	4.7
	21.1	5.3
	averages	
	23.4	4.7
8	33.8	6.1
	28.0	5.6
	30.4	4.9
	30.9	4.8
	averages	
	30.8	5.4
12	43.4	5.2
	27.9	4.4
	31.6	4.3
	43.3	4.9
	29.6	4.5
	averages	
	35.2	4.5

* Pigment concentration is expressed as the optical density of the extracts/mg wet wt of leaf tissue, the density at 660 mμ measuring the chlorophyll conc, and the density at 440 mμ, the carotenoid conc.

Table II

Effect on the Chlorophyll Content of 1-Week-Old Corn Seedlings When Placed in the Dark at 27° C after Previous Light Exposure of Different Durations

Light exposure in hrs	Chlorophyll conc * ($\times 10^{-5}$)	Hrs in dark after light treatment	Chlorophyll conc * ($\times 10^{-5}$)	% Loss of pigment
4	15.4	24	8.3	47
		48	4.7	69
		72	4.2	72
		96	3.6	76
6	23.4	24	16.3	31
		48	10.2	56
		72	3.8	83
		96	5.2	77
		120	4.0	83
		144	2.2	90
8	30.8	24	20.7	33
		48	11.2	64
		72	6.7	78
		96	6.5	79
		120	5.0	84
		144	2.5	92
12	35.2	24	28.5	19
		48	13.4	61
		72	7.4	78
		96	4.7	86
		120	5.6	84
		144	3.9	88

* Chlorophyll conc is expressed as the optical density of the extracts at 660 mμ/mg wet wt of leaf tisue.

or figure 1, where the initial concentration of chlorophyll present in light-treated seedlings prior to return to the dark was 5 to 150 times greater than the lowest value in table II. Here too, the destruction of pigment proceeded in these seedlings at the same rate as in the other plants. Thus, the time required for the destruction of a given percentage of pigment is independent of the initial concentration, even though the initial concentration may vary 150-fold. Such a kinetic picture suggests that the destruction of chlorophyll proceeds as a first-order reaction where the rate at which the molecular species disappears is proportional at each instant to the amount of that species.

Unlike the chlorophyll destruction curve, the carotenoid destruction curve (lower curve, fig 1) does not approach 100 % loss of pigment but seems to level off at 40 % of the initial pigment concentration. A possible interpretation of this curve is suggested by an examination of table IV.

Table IV shows the light-independent destruction of carotenoids in seedlings previously light-treated compared with control seedlings of the same age, grown throughout their history in the dark. It is clear that carotenoids are destroyed with time in the dark in both the light-treated seedlings and in the dark-grown controls. From an examination of the rate of carotenoid destruction in the dark-grown control plants, it can be seen that this rate is slower than the dark destruction of chlorophyll. After 120 hours, about 50 % of the carotenoids have disappeared, while

TABLE III

EFFECT ON THE CAROTENOID CONTENT OF 1-WEEK-OLD CORN SEEDLINGS WHEN PLACED IN THE DARK AT 27° C AFTER PREVIOUS LIGHT EXPOSURE OF DIFFERENT DURATIONS

LIGHT EXPOSURE IN HRS	CAROTENOID CONC * ($\times 10^{-4}$)	HRS IN DARK AFTER LIGHT TREATMENT	CAROTENOID CONC * ($\times 10^{-4}$)	% LOSS OF PIGMENT
4	4.4	24	4.5	0
		48	3.6	18
		72	2.8	36
		96	2.4	41
6	4.7	24	4.5	4
		48	3.8	19
		72	2.3	51
		96	2.8	41
		120	2.7	43
		144	2.0	57
8	5.4	24	4.9	9
		48	3.4	37
		72	2.8	48
		96	2.5	53
		120	3.1	45
		144	2.1	61
12	4.7	24	4.8	0
		48	3.5	25
		72	2.8	40
		96	2.7	40
		120	2.5	46

* Carotenoid conc is expressed as the optical density of the extracts at 440 mμ/mg wet wt of leaf tissue.

table II indicates that for this time interval, well over 80 % of the chlorophyll has disappeared.

Column 3 of table IV shows the difference in amount of pigment in the "light" and "dark" plants at different times in the dark. This increment decreases very rapidly with time, and the difference all but disappears after 96 hours in the dark. Thus, actually, the "light-formed" carotenoids disappear completely after 96 hours, and the lower curve in figure 1 is deceptive. While it is true that the total carotenoid concentration is never completely depleted in the dark, as shown by this curve, an examination of column 3 of table IV shows that in reality the carotenoids formed by light are completely destroyed during the time interval of these experiments.

An alternative interpretation to these data, however, is that we are dealing with chlorophyll b disappearance rather than the destruction of light-synthesized carotenoids. The difference between the carotenoid destruction in the dark-grown and light-treated plants is of sufficiently small magnitude to make this alternative plausible.

EFFECT OF SUCROSE ON PIGMENT DESTRUCTION: A seedling growing in the light enjoys the benefits of continuous sugar production, whereas the seedlings in these experiments were returned to the dark with little food reserves, their source of energy being the small amount of sugar produced during the short light exposures and whatever may remain of food in the endosperm. The following question thus arises. Can

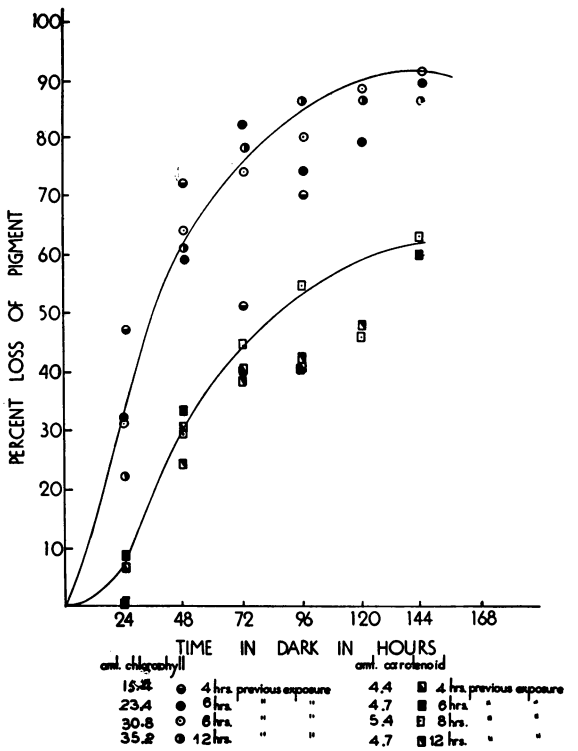

FIG. 1. The time course of the light-independent destruction of chlorophyll (*upper curve*) and carotenoids (*lower curve*). Numbers at the bottom show the concentration of chlorophyll and carotenoid initially present in seedlings at the time of return to the dark.

exogenous sucrose protect the "light-independent" destruction?

Tables V and VI and figure 2 show the effect of adding sucrose to the seedlings during their "dark" period following light exposure. In table V and figure 2, the effect of various concentrations of sucrose was determined for seedlings previously exposed to 12 hours of light and returned to the dark for 48 hours.

TABLE IV

LIGHT-INDEPENDENT DESTRUCTION OF CAROTENOIDS IN PREVIOUSLY LIGHT-TREATED CORN SEEDLINGS (12 HRS LIGHT EXPOSURE) AS COMPARED WITH DARK-GROWN CONTROLS OF THE SAME AGE

HRS IN DARK	CAROTENOID CONC * ($\times 10^{-4}$)		DIFFERENCE BETWEEN LIGHT-TREATED AND DARK CONTROLS
	PREVIOUSLY LIGHT-TREATED	DARK CONTROLS	
0	5.7	4.6	1.1
28	4.6	4.2	0.4
48	4.4	4.1	0.3
72	2.9	2.7	0.2
96	2.4	2.5	−0.1
120	2.3	2.2	0.1

* Carotenoid conc is expressed as the optical density of the extracts at 440 mμ/mg wet wt of leaf tissue.

TABLE V

EFFECT OF VARIOUS SUCROSE SOLUTIONS ON THE LIGHT-INDEPENDENT DESTRUCTION OF CHLOROPHYLL AND CAROTENOIDS

TREATMENT *	SUCROSE CONC %	CAROTENOID CONC ** ($\times 10^{-4}$)	% LOSS OF CAROTENOIDS	CHLOROPHYLL CONC ** ($\times 10^{-5}$)	% LOSS OF CHLOROPHYLL
12 Hrs light	0	4.5	..	29.6	..
12 Hrs light +48 hrs dark	0	2.8	37	8.2	72
	1	3.3	27	13.2	55
	2	3.95	11	16.7	43
	3	4.5	0	18.3	38
	4	4.7	0	19.5	34
	5	4.2	0	21.0	29

* One-week-old corn seedlings were previously exposed to 12 hrs white light and returned to the dark for 48 hrs.

** Pigment conc is expressed as the optical density of the extracts/mg wet wt of leaf tissue, the density at 660 mμ measuring chlorophyll conc, and the density at 440 mμ, the carotenoid conc.

The destruction of both chlorophyll and carotenoids was affected by the added sucrose. The carotenoids were completely protected by 3, 4, and 5 % sucrose solution (lower curve, fig 2), while the chlorophyll values showed approximately a 30 % drop for these sugar concentrations, as compared with 72 % loss of pigment when no sugar was added.

In table VI chlorophyll destruction in seedlings was followed for different times in the dark in the presence and absence of 2 % sucrose. The seedlings had been previously exposed to 12-hours light before their return to the dark. The added sucrose affected the destruction of chlorophyll, but the effect seems to be to delay the onset of the destruction rather than to prevent it. Chlorophyll is destroyed with time in the dark in both the sucrose and non-sucrose treated seedlings. However, the last column in the table

TABLE VI

EFFECT OF ADDING 2 % SUCROSE SOLUTIONS ON THE COURSE OF THE LIGHT-INDEPENDENT DESTRUCTION OF CHLOROPHYLL

HRS IN DARK AFTER PREVIOUS LIGHT TREATMENT	CHLOROPHYLL CONC *		% PIGMENT DESTRUCTION		DIFF IN DESTRUCTIVE RATES
	NO SUCROSE	2 % SUCROSE	NO SUCROSE	2 % SUCROSE	
0	36.5	...	..	..	..
48	21.9	25.2	40	31	9
72	7.5	11.9	79	67	12
96	4.7	8.9	87	75	12
120	5.6	10.0	84	72	12
144	3.9	3.1	89	91	-2

One-week-old corn seedlings, previously exposed to 12 hrs white light were returned to the dark at 27° C for various times.

* Chlorophyll conc is expressed as the optical density of the extracts at 660 mμ/mg wet wt of leaf tissue.

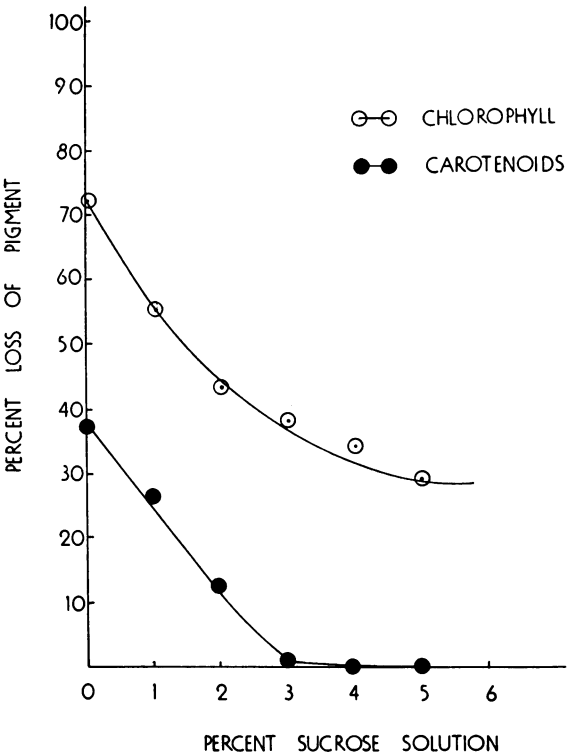

FIG. 2. The effect of adding sucrose solutions to seedlings previously light-treated for 12 hrs and returned to the dark for 48 hrs. *Upper curve.* The effect of sucrose solutions on the light-independent destruction of chlorophyll. *Lower curve.* The same for carotenoids.

shows the difference in destruction rates of the two groups. This difference is relatively constant for 120 hours in the dark, suggesting that the added sucrose has merely shifted in time by a constant amount the inevitable destruction of chlorophyll. Beyond the 120-hour period, the sucrose failed to affect the pigment destruction.

A similar type of study was made to test the effect of 2 % sucrose on carotenoid destruction. The results showed considerable variation, so they are not published here. In general, however, the sucrose effect seemed to be similar; that is, the carotenoids are destroyed in the presence and absence of sucrose, and there has been a shift in time of onset of this destruction in the sucrose-treated seedlings.

Just how the sucrose accomplishes this delay in the onset of pigment destruction can only be a matter of speculation. Perhaps sugar helps to maintain some plastid structure that temporarily binds the pigments in a stable structure.

It is clear, however, that depriving a plant of light and thus adequate sugar supply affects pigment maintenance in a way that is separate and distinct from the role of light and sugar in pigment synthesis. A young etiolated seedling, when exposed to light, forms chlorophyll from protochlorophyll. Protochlorophyll can be synthesized by the plant in the absence of

light, the light acting as the agent only in the ultimate step in chlorophyll formation. Sugar and other organic and inorganic compounds are presumably needed for the initial and continuous formation of protochlorophyll. A short time after chlorophyll has been formed, the plant becomes capable of photosynthesis and new sugars are thus supplied for further pigment synthesis. When such a seedling is deprived of light, chlorophyll formation is halted by the direct removal of the agent in the protochlorophyll-chlorophyll transformation; secondarily, sugar production ceases, and this affects the plant's ability to synthesize protochlorophyll, and other simpler precursors of the chlorophyll molecule.

We have seen here, however, that removing the plant from the light not only halts further pigment synthesis but affects the plant's ability to maintain the pigments it already has.

The seedling returned to the dark fails to maintain both chlorophyll and carotenoids. In earlier work with oat seedlings (6) we had shown that when chlorophyll was formed, the carotenoids fall in concentration, suggesting that the carotenoid molecule might be involved in the synthesis of the chlorophyll molecule, perhaps by supplying the phytol group. In the light-independent destruction of the chlorophyll molecule, if the backward reaction followed the same course as the forward reaction in reverse, one might expect to get an accumulation of carotenoids as the chlorophyll content decreased. However, the study reported here shows clearly that when chlorophyll is destroyed, carotenoids are also destroyed. So no reciprocal relationship exists between the two pigments with respect to their light-independent destruction.

Summary

One-week-old corn seedlings containing known amounts of chlorophyll and carotenoids were placed in the dark, and the time course of the destruction of the pigments followed. Both chlorophyll and carotenoids were destroyed rather rapidly at 27° C in the dark. All the chlorophyll disappeared completely after 120 hours in the dark, while the carotenoids fell to 40 % of their original value.

It was found that, even though the initial pigment concentration varied as much as 150-fold, the time required for the destruction of a given percentage of pigment was independent of the initial concentration. This suggests that the light-independent pigment destruction follows the kinetics of a first-order reaction.

Adding sucrose to the environment of the seedlings when placed in the dark effectively protected for a time against depletion of both chlorophyll and carotenoids. Concentrations of 3 % sucrose protected the carotenoids completely from destruction in the dark, whereas the chlorophyll concentration decreased 30 % in 3 % sucrose as compared with 72 % destruction in the absence of sucrose.

The protective effect of exogenous sucrose on pigment destruction seemed to be to delay the onset of destruction rather than to prevent it from occurring.

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RESPIRATION AND SALT ABSORPTION BY EXCISED BARLEY ROOTS[1,2]

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The fact that absorption of salt by plant tissue is usually accompanied by stimulation of respiration has been recognized for some twenty years.

Salt effects upon respiration have been studied in various types of plant tissue: wheat roots (8 to 10), carrot slices (15 to 20), beet slices (18), potato discs (23 to 25) and barley roots (11) among others. The phenomenon may then reasonably be believed to be of general occurrence.

In the early thirties Lundegårdh and Burström began a series of researches which culminated in an ingenious theory to account for the simultaneous absorption of salt and increase in the respiratory rate. The point of view of Lundegårdh and Burström has

[1] Received March 15, 1955.

[2] This paper is based on work performed under contract No. AT-(11-1)-34, project 5, with the Atomic Energy Commission.