3. It was concluded that the photosynthetic pigments of the studied bacterium are likely to be attached to lamellae.

Thanks are due to Dr. J. A. Niemeyer for placing the magnetostriction oscillator at our disposal, and to Mr. C. Bril for preparation and purification of the bacterial extract.

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FORMATION AND BLEACHING OF CHLOROPHYLL IN ALBINO CORN SEEDLINGS [1]

JAMES H. C. SMITH, LOIS J. DURHAM and CHARLES F. WURSTER
Carnegie Institution of Washington, Department of Plant Biology, Stanford, California

In 1951 Koski and Smith (5) found that albino seedlings of corn formed protochlorophyll and chlorophyll equally as well as normal plants. These albinos lacked the ability to accumulate chlorophyll, however, because the chlorophyll was bleached by continued illumination. Several factors were suspected of causing the instability of the chlorophyll, and this paper presents an examination of these factors.

Granick (3) observed that a Chlorella mutant which formed only protochlorophyllide (i.e., phytyl-free protochlorophyll) bleached in the light. He suggested that the loss of pigment was caused by the lack of the phytyl group. Loeffler (6, 11) and Wolff and Price (15) discovered independently that normal seedlings grown in the dark formed both protochlorophyll and protochlorophyllide, which they transformed to chlorophyll a and chlorophyllide a in the light and subsequently esterified the chlorophyllide a to chlorophyll a. If, in accordance with Granick's suggestion, the albino plants contained protochlorophyllide and were unable to completely esterify (phytylate) the chlorophyllide formed therefrom, this might be a cause of albinism. For this reason a number of albino plants were examined for their esterifying ability.

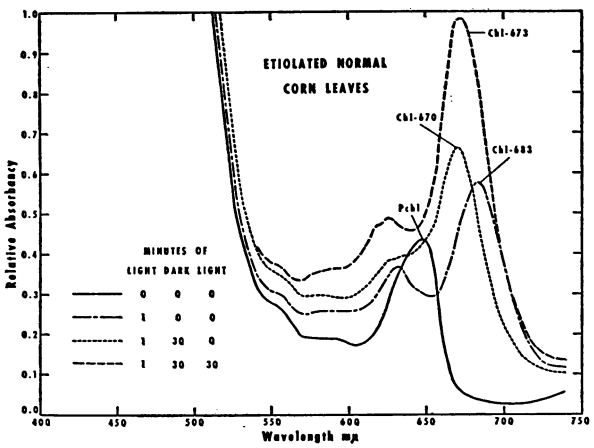
Another suspected cause of bleaching was that albino plants did not stabilize the chlorophyll after it was formed. Shibata (8) discovered that in normal plants the chlorophyll first formed from transformation of protochlorophyll had an absorption maximum at about 684 mμ. When the plants were allowed to stand in the dark the absorption maximum of this chlorophyll changed to about 670 mμ. Since the chlorophylls extracted from these two forms showed the same absorption spectrum in ether the difference between them was attributed to the variation in the relation of pigment to carrier rather than to the pigment molecules themselves. It was surmised that this change in chlorophyll absorption might signify the stabilization of the newly formed chlorophyll. A number of albinos have been examined in respect to this post-illuminative spectrum shift to determine whether it can be correlated with chlorophyll bleaching.

A third factor examined was the relation of carotenoid content to bleaching. Willstätter and Stoll (14) suggested that the function of the yellow pigments in leaves was to protect the chlorophyll from bleaching. Cohen-Bazire and Stanier (1) have recently suggested "that the carotenoid pigments characteristically associated with the photosynthetic apparatus perform an essential physiological function, by protecting the cell from the deleterious effects of chlorophyll-catalysed photo-oxidations." Koski (cf. 13) found, however, that one chlorophyll-deficient mutant of corn, Golden 1, contained a large quantity of yellow pigment and yet bleached. It seemed worthwhile, therefore, to examine other corn mutants to determine whether the yellow pigments afford any protection against chlorophyll bleaching.

[1] Received April 1, 1959.

Materials and Methods

Esterification Experiments: The seedlings, both normal and albino, were grown in complete darkness except for the weak green or blue light used during the watering, picking and handling of the leaves [cf. Koski (5)]. After being harvested, 3 equal portions, weighing from 2.5 to 3.5 g, were taken from each lot of leaves and stored in a dark cold-room until they were used. One portion of leaves was extracted without being illuminated, another was illuminated and then immediately extracted, and the 3rd was illuminated and stored over night in the dark cold-room before being extracted. Illumination consisted in exposing the leaves for 20 minutes to light of 17 ft-c intensity from a fluorescent lamp. Each lot of leaves was cut into about 5-mm lengths and extracted in a Waring blendor successively with 25, 20, and 20 ml of 80 % acetone. The pigments were quantitatively transferred to ether [cf. Mackinney (7)] and the solution brought to 25.0 ml with ether (solution 1, total pigment) and the spectrum automatically recorded with a Beckman DK-2 spectrophotometer. Solution 1 was then extracted with 10, 8, and 7 ml portions of 0.1 M sodium bicarbonate in 25 % acetone and then with 10 ml of dilute sodium chloride solution. The ether solution was brought to 25.0 ml with ether (solution 2, neutral fraction). The alkaline extracts and salt solution were combined and extracted with 15 ml of ether while being treated with 18 to 25 ml of 0.1 M tartaric acid, added in 8 to 10 portions and shaken gently after each addition. The ether layer was removed quantitatively and the aqueous layer extracted with 10 ml of ether. The ether extracts were combined and diluted to 25.0 ml with ether (solution 3, acidic fraction). The absorption spectrum of each solution was recorded and the percentage of the total pigment recovered in the neutral, "N," and acidic fractions, "A," of tables I and II calculated. The columns headed "μg/2.5 g" mean that the weight of pigment in micrograms is in reference to 2.5 g fresh weight of leaves.



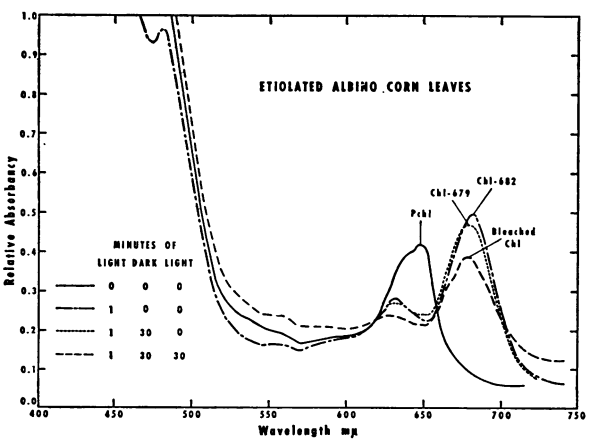


Fig. 1 (*top*). Changes produced in the absorption spectrum of a live etiolated normal corn leaf by the different light-dark treatments shown.

Fig. 2 (*bottom*). Changes produced in the absorption spectrum of a live etiolated albino corn leaf by the different light-dark treatments shown.

Post-illuminative Spectral Shift: The leaves were grown in the dark as has already been described. The albino leaves were harvested in blue light so as to be visibly distinguishable from their normal sibs. They were cut into 1- or 2-cm lengths, placed in the opal-glass apparatus of Smith, Shibata and Hart (12), and their absorption spectra recorded with the Beckman DK-2 spectrophotometer. The sequence of dark and light treatments used in handling the leaves is shown in figures 1 and 2. The leaves were illuminated with light of about 200 ft-c intensity from an ordinary frosted-bulb incandescent lamp while remaining in the holder and without being removed from the cell compartment of the Beckman instrument. This technique was adopted to avoid variation in absorption due to change in position of the leaves. The wave lengths and heights of the absorption maxima resulting from each treatment were measured and are reported in table III, column k.

Carotenoid Content: The absorption maxima of the carotenoid pigments, in the spectrophotometric recordings just described, lie close to 480 mμ. The absorbancies at this wave length were measured and are tabulated in table III. For comparative purposes, this value is divided by the height of the maximum near 647 mμ due to protochlorophyll. This quotient is given in table IV, column h'.

Results and Discussion

The results of the esterification experiments are shown in tables I and II. The age is the number of days from planting to harvest. The recovery, R, is the sum of N and A. The percentages of transformation, T, of the protochlorophyll-like pigments to chlorophyll-like pigments were obtained from the absorption spectra of the total converted pigments

(Solutions no. 1) according to the method of Koski (4). [cf. Smith and Benitez (10)].

In table II, "Mutant designation" refers to the code number of mutant assigned by donors of the seed. The headings "Not illuminated," "Illuminated-no standing," and "Illuminated-with standing" refer to the results obtained under the 3 light-dark sequences described under Esterification Experiments. For convenience in comparing results, the recovery was arbitrarily brought to 100 % and the percentages of neutral and acidic components adjusted accordingly (last line of table I).

The results in table I indicate that through photoconversion more acidic and less neutral pigment was obtained than existed in the leaf before illumination, an indication that hydrolysis occurs during the photochemical transformation. During an overnight sojourn in the dark the neutral pigment increased, which finding agrees with the observations of Loeffler, and of Wolff and Price, already referred to.

Comparison of these results with those obtained with albinos (table II) shows that initially most of the albinos have nearly the same percentages of neutral and acidic forms of the pigment as normal leaves. One exception is W-alb-7752 which has only a little of the acidic form. The albinos, as well as normal plants, hydrolyze the neutral esterified pigment during transformation. Most of the albinos fail, however, to esterify the acidic form on standing in the dark subsequent to being illuminated. Mutant Vp_5 is an exception to this and, significantly, it contains no appreciable amount of carotenoid. This implies that no connection exists between the carotenoids and esterification with a phytyl group, presumably derived from carotenoid [cf. Smith (9); Frank (2)]. The lack of phytyl cannot be the sole cause of albinism since one mutant, Vp_5 (and possibly W-alb-8852), esterfies its chlorophyllide and yet bleaches in the light.

In figures 1 and 2 are depicted the effects of illumination on the spectra of live etiolated normal and albino leaves. Both contain protochlorophyll-like pigments (continuous line) which they convert to chlorophyll-like pigments having an absorption peak near 683 mμ (dash-dot line). On standing in the dark at room temperature for 30 minutes the position of the chlorophyll absorption changes in the normal

TABLE I

NORMAL ETIOLATED CORN LEAVES: THE CONTENT OF NEUTRAL AND ACIDIC PROTOCHLOROPHYLL- AND CHLOROPHYLL-LIKE PIGMENTS IN ILLUMINATED AND UNILLUMINATED SAMPLES

	NOT ILLUMINATED				ILLUMINATED—NO STANDING					ILLUMINATED—WITH STANDING				
AGE DAYS	WT μG/2.5G	R %	N %	A %	WT μG/2.5 G	R %	N %	A %	T %	WT μG/2.5 G	R %	N %	A %	T %
16										8.2	97	86	11	80
										7.9	91	78	13	68
16—	14.3	94	62	32	11.9	78	41	37	81	10.3	99	87	12	79
18										11.9	94	85	9	82
15	18.5	83	71	12	13.6	90	80	10	90					
13	15.2	94	81	13	11.8	82	57	25	81					
14	17.0	80	69	11	13.9	79	61	18	79					
17					13.0	89	68	21	80	11.9	95	90	5	78
18										9.7	94	89	5	78
Average		88	71	17		84	61	22	82		95	86	9	78
Mean dev from mean		±3.7	±3.9	± 5		±2.5	±6.4	±6.1	±4		±1.3	±1.7	±1.4	±4
Adjusted		100	81	19		100	73	26			100	91	9	

TABLE II

ALBINO ETIOLATED CORN LEAVES: THE COMPARISON OF VARIOUS ALBINO CORN MUTANTS WITH RESPECT TO THEIR CONTENT OF NEUTRAL AND ACIDIC PROTOCHLOROPHYLL- AND CHLOROPHYLL-LIKE PIGMENTS IN ILLUMINATED AND UNILLUMINATED SAMPLES

		NOT ILLUMINATED				ILLUMINATED—NO STANDING					ILLUMINATED—WITH STANDING				
MUTANT DESIGNATION	AGE DAYS	WT μG/2.5 G	R %	N %	A %	WT μG/2.5 G	R %	N %	A %	T %	WT μG/2.5 G	R %	N %	A %	T %
W-alb-6474	10	26.8	92	64	28	20.5	84	58	26	74	20.6	91	64	29	81
W-alb-7748	13	32.9	92	70	22	22.8	81	52	29	72	21.2	72	38	34	69
W-alb-7752	11	25.1	94	87	7	19.1	85	65	20	76	13.7	90	72	18	79
Vp_5						14.0	82	69	13	79	15.9	93	90	4	78
lw_3 lw_4	10	27.0	89	69	20	19.2	86	55	29	79	20.6	88	57	31	79
											16.5	83	44	39	87

TABLE III

SPECTRAL PROPERTIES OF ETIOLATED NORMAL AND ALBINO CORN SEEDLINGS BEFORE AND AFTER VARIOUS EXPOSURES TO LIGHT

	MUTANT	PROTOCHLOROPHYLL 0-0-0 [2]		CHLOROPHYLL 1-0-0 [2]		CHLOROPHYLL 1-30-0 [2]		CHLOROPHYLL 1-30-30 [2]		CAROTENOID
NO.	REF. NO. [3]	λ MAX	A	λ MAX	A	λ MAX	A	λ MAX	A	A λ 480
		$M\mu$		$M\mu$		$M\mu$		$M\mu$		
a	b	c	d	e	f	g	h	i	j	k
1	1a	647	0.222	680*	0.305	680	0.300	676	0.085	0.770
2	1b	647	0.172	679	0.238	677	0.230	677	0.132‡	0.580
3	"	646	0.263	680	0.324	679	0.315	680	0.170	>0.920
4	1c	648	0.240	678*	0.300	677	0.310	677	0.210	0.630
5	2	646	0.275	679*	0.320	671	0.325	672	... [1]	> 1
6	3a	646	0.325	678	0.388	678	0.402	678	0.160	0.615
7	3b	645	0.175	680*	0.210	666	0.240	668	0.350	> 1
8	4a	640**	0.405	677	0.480	677	0.490	678	0.388	0.600
9	4b	644	0.498	678	0.630	678	0.640	682	0.380	0.720
10	4c	646	0.435	680	0.560	678	0.600	681	0.298	0.730
11	5†	647	0.036	682	0.040	668	0.042	665	0.009	0.130
12	6	648	0.220	677*	0.265	667	0.272	667	0.170	0.200
13	"	645	0.215	676	0.195	669	0.195	669	0.125	0.288
14	7	648	0.165	679	0.228	668	0.250	667	0.183	0.340
15	8	646	0.360	682	0.445	678	0.415	678	0.330	0.980
16	9	644	0.265	680	0.370	676	0.370	677	0.180	0.630
17	10	647	0.420	683	0.565	670	0.645	671	0.980	> 2

* 30 seconds of illumination rather than 60 seconds.

** Broad maximum the exact position difficult to assess.

† Sample very thin; accuracy poor.

‡ 15 minutes of illumination.

[1] Abnormal behavior on long illumination.

[2] Light-dark sequence used cf. figures 1 and 2.

[3] Mutant reference numbers refer to the designations given the various mutants: 1a, W-alb-6474 : 54-6506-33xn; 1b, W-alb-6474 : 54-6506-34xn; 1c, W-alb-6474 : 54-6506-102x; 2, W-alb-7716 : 54-6501-91xn; 3a, W-alb-7752 : 54-6538-1xn; 3b, normal plants from 3a seeds; 4a, W-alb-7748 : 54-6622-9xn; 4b, W-alb-7748 : 54-6622-10xn; 4c, 7748 : 54-6622-3x; 5, Vp_5 : 53-5171-14x; 6, Vp_5 : 53-5168-5/5189-2; 7, Vp_9 : 54-6670-59x; 8, lw_3lw_4 : 54-6588-1xn; 9, lw_3lw_4 : 54-6589-3xn; 10, normal yellow dent corn.

leaf to about 670 mμ whereas only a slight shift occurs in the albino leaf (dotted line). On continued illumination the chlorophyll peak of the normal leaf is enhanced but that of the albino leaf is depressed (dashed line). On 1 curve, the dot-dash line of figure 2, the carotenoid maximum at 480 mμ is evident.

The measurements taken from the absorption curves of the normal and albino mutants are collected in table III. Columns c, e, g, and i give the wave lengths of the absorption maxima of the green pigments after each treatment, and columns d, f, h, and j the corresponding absorbancies (or optical densities defined by $\log_{10} \frac{Io}{I}$). Column k presents the absorbancies at 480 mμ representing carotenoid pigments.

The wave lengths of the protochlorophyll maxima, column c, are very consistent, 646.3 $\pm$ 1.1 mμ, among the different mutants, except 4a. This mutant had such a broad maximum that its exact position was difficult to assess and was not included in the averages. After from 0.5 to 1.0 minutes of illumination, the positions of the chlorophyll absorption maxima were consistent, 679.4 $\pm$ 1.4. After standing in the dark, however, the position was 674.2 $\pm$ 4.8 which showed a marked average deviation from the mean which correlates with the conspicuous variation of the post-illumination shift found for the different samples (table IV column e').

Table IV sets forth various ratios and differences derived from the experimental data of table III. In column c' the quotients of the absorbancies of chlorophyll newly formed (f, table III) to absorbance of the protochlorophyll, d, is in every case but one, line 13, greater than 1. Some of the mutants show values higher than the normals, lines 7 and 17. In column d' the ratio of the absorbancies after standing for 30 minutes in the dark to those existing immediately after illumination is close to 1.0 for all the albinos but no. 7 (line 14) and are all less than the values for normal leaves, lines 7 and 17. In general the shifts in absorption maxima, column e', are small for the albinos as compared to normal leaves (lines 7 and 17) but exceptions to this are apparent (lines 11, 12, and 14). The quotients of the absorbancies of the chlorophyll peaks

before and after illumination (column f') give a measure of the bleaching caused by continued illumination: the lower the quotient the greater the bleaching. In every case the albino mutants have a quotient less than 1.0 and the normal plants a quotient considerably greater than 1.0. Column g' shows the changes in the positions of the absorption maxima of chlorophyll caused by continued illumination. No consistent trend in these values is apparent.

Column h' gives the quotients of the absorbancies at 480 mμ divided by the absorbancies of the protochlorophyll maxima. These values provide some measure of the carotenoids present. They are higher for the normal than for the mutant plants. Some mutants have a relatively high carotenoid content, however, and bleach nevertheless.

In columns i', j', and k' are given the percentages of the esterified pigments components from normal and mutant plants—the N values from tables I and II. These values were determined on mixtures of mutants from a given category and are bracketed to signify to what plants they belong. There is no obvious relationship between these values and the differences and ratios just discussed except, perhaps a slight correlation between the post-illumination shifts in the absorption maxima (column e') and the esterification of the protochlorophyllide.

Conclusion and Summary

All the albino corn seedlings examined form protochlorophyll and protochlorophyllide during germination and growth in the dark. They convert these pigments to chlorophyll and chlorophyllide on exposure to light. Most of the mutants subsequently esterify their chlorophyllide to only a slight extent as compared to normals but 1 mutant is as effective as normal plants in this respect. Most of the mutants show only a slight, if any, post-illumination shift of the chlorophyll absorption maximum yet one mutant is equal to normals in this regard. All mutants have less carotenoid pigment than normals; however, some are quite rich in this pigment. All mutants bleach with continued illumination.

It may be concluded therefore that neither esterification ability, post-illumination shift in absorption spectra, nor carotenoid content is solely responsible for the stability or instability of chlorophyll in leaves.

Table IV

Comparison of Etiolated Normal and Albino Corn Seedlings in Respect to Different Factors Derived from Data in Table III

No.	Mutant ref. no.[3]	f/d	h/f	e–g Δλ max mμ	j/h	g–i Δλ max mμ	k/d	Esterified Pchl %	Esterified First chl %	Esterified Stored chl %
a'	b'	c'	d'	e'	f'	g'	h'	i'	j'	k'
1	1a	1.38	0.98	0	0.28	−4	3.48			
2	1b	1.39	0.97	2	0.57	0	3.37	64	58	64
3	"	1.23	0.97	1	0.54	+1	>3.50			
4	1c	1.25	1.03	1	0.68	0	2.62			
5	2	1.16	1.02	8	...[1]	+1	>3.64			
6	3a	1.19	1.04	0	0.40	0	1.89	87	65	72
7	3b	1.20	1.14	14	1.46	+2	5.70			
8	4a	1.19	1.02	0	0.79	+1	1.48			
9	4b	1.27	1.02	0	0.59	+4	1.45	70	52	38
10	4c	1.29	1.07	2	0.50	+3	1.63			
11	5†	1.11	1.05	14	0.21	−3	3.60			
12	6	1.20	1.03	10	0.63	0	0.91	...	69	90
13	"	0.91	1.00	7	0.64	0	1.32			
14	7	1.38	1.10	11	0.73	−1	2.06			
15	8	1.24	0.93	4	0.80	0	2.72			
16	9	1.40	1.00	4	0.49	+1	2.38	69	55	57
17	10	1.35	1.14	13	1.52	+1	> 5	71	61	86

† Sample very thin; accuracy poor.

[1] Abnormal behavior on long illumination.

[3] Mutant reference numbers refer to the designations given the various mutants: 1a, W-alb-6474 : 54-6506-33xn; 1b, W-alb-6474 : 54-6506-34xn; 1c, W-alb-6474 : 54-6506-102x; 2, W-alb-7716 : 54-6501-91xn; 3a, W-alb-7752 : 54-6538-1xn; 3b, normal plants from 3a seeds; 4a, W-alb-7748 : 54-6622-9xn; 4b, W-alb-7748 : 54-6622-10xn; 4c, 7748 : 54-6622-3x; 5, Vp_5 : 53-5171-14x; 6, Vp_5 : 53-5168-5/5189-2; 7, Vp_9 : 54-6670-59x; 8, lw_3lw_4 : 54-6588-1xn; 9, lw_3lw_4 : 54-6589-3xn; 10, normal yellow dent corn.

The authors wish to express their gratitude to Professor Ernest G. Anderson of the California Institute of Technology, and Dr. Donald Robertson of Iowa State College for supplying the seeds of mutants used in this investigation.

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ON THE MASS CULTURE OF ALGAE. II. YIELD AS A FUNCTION OF CELL CONCENTRATION UNDER CONTINUOUS SUNLIGHT IRRADIANCE [1]

JACK MYERS and JO-RUTH GRAHAM
Departments of Zoology and Botany, University of Texas, Austin, Texas

The considerable effort which has been directed toward the mass culture of algae under sunlight illumination (15) makes clear the critical problem of achieving maximum yields or maximum efficiency in use of available solar radiation. Measurements by Kok (4) and Oorschot (10) on total cell synthesis by Chlorella under low illuminance at 589 mμ may be interpreted as showing a 20 $\pm$ 2 % efficiency. Unpublished experiments of our laboratory, using entirely different techniques, show a maximum efficiency of 19 $\pm$ 1 % under similar illumination. In contrast, observed yields in outdoor mass cultures cited by Tamiya (15) allow estimates of only 3 to 7 % for efficiency of conversion of the visible or photosynthetically usable fraction of solar energy. A major fraction of the discrepancy has been attributed to the consequences of light saturation.

Estimate of performance of a dense algal culture under sunlight illumination may be visualized graphically from figure 1. Curve A is a characteristic irradiance curve for a very thin culture of Chlorella with rate measured in terms of apparent photosynthesis or specific growth rate. Its essential feature is that light saturation occurs at a low value, I_s, which is 1/20 to 1/10 of the irradiance of maximum sunlight. Curve B shows the expected decrease in irradiance within a dense culture. The abscissa is taken conveniently as Cl (cell concentration $\times$ depth) and a value of I_s on the ordinate is indicated at 1/20 of incident irradiance. Consider a cell at the upper surface of the culture (Cl = 0). It absorbs radiation at a rate proportional to $I_o = 100$ but works only at a rate proportional to $I_s = 5$. The argument may be repeated for all other values of Cl with the following result. Of the total light absorbed, measured by the area under curve B, only a fraction measured by the shaded area is used with maximum efficiency. The argument has been taken from a previous and more extensive treatment (6); it has been subjected to more elegant mathematical structure by Tamiya et al (16) for a hyperbolic irradiance curve and by Oorschot (10) for Blackman, hyperbolic, and logarithmic irradiance curves. The only essential difference between the 3 treatments lies in the shape assigned to the irradiance curve (fig 1, curve A).

[1] Received December 24, 1958.