KINETIC INVESTIGATION OF THE PHOTODESTRUCTION OF PIGMENTS IN NORMAL AND ALBINO MAIZE LEAVES

by

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Introduction

The albinism of green plants is a hereditary abnormality of their photosynthetizing apparatus. The saturation level of photosynthesis is lower in such mutants than in normal strains so that, exposed to light intensities above this level, their photosynthetizing apparatus is reversibly or irreversibly damaged (20). The deterioration of this apparatus, as induced by high light intensity, has chiefly been studied on alga mutants and photosynthetizing bacteria (8, 41). Reports on the physiological basis of albinism in higher plants are summarized in the Table 1. (pp. 70—75.)

It is evident from the table that the extreme photosensitivity of albino plants is attributed to various factors, and that its true mechanism is still not fully cleared up. The elucidation of the processes influencing light tolerance requires a detailed study of the kinetics of pigmental decomposition.

The present paper presents the results of studies concerning the point of attack of light and of investigations into the mechanism of photodestruction.

Material and method

The generation descending from individuals of *Zea mays* L., heterozygous with respect to albino mutation, was studied in the present experiments. We propagated the strain by repeated inbreeding. The strain has the characteristic feature that the colour of the endosperm enables us to distinguish between the homozygous recessive individuals of the albino phenotype on the one hand, and the heterozygous and/or homozygous dominant individuals of the normal phenotype on the other hand. The endosperm of the homozygous recessive albino individuals has a lighter colour. The seeds were germinated in the dark, in a 30 °C thermostat. After removing the coleoptyles from the shoots of 6 day-old seedlings, they were transferred to a phtalate buffer of 0,005 M which contained 1% sacroz (pH = 4,8). We employed a low-pressure xenon lamp of 500 watts as light source because its composition of wavelengths is nearest to that of the sun. The applied light intensities of 5, 100, 2500 and 10 000 lux were produced by means of filters, and uniform temperature was ensured by ventilation. The treatments lasted 2, 6 and 12 hours respectively, after which the buffer was absorbed from the shoots. The latter were then rinsed. We extracted the leaf pigments with K o s k i's technique (31). The leaves were homogenized with sand and acetone in the presence of $MgCO_3$. We extracted the pigments by adding peroxide-free aether. After the removal of the acetone by repeated elutions, the aether extract was filled up to a given volume.

Table 1.

Plant	Brief summary of the works	Hypothesis regarding the factor responsible for the low light-tolerance of chloroplasts	Authors
Arabidopsis thaliana	In variegated leaves the grana of the photolabile sectors appear vacuolized	Lack of stable orientation in the submicroscopic structure of the grana	Röbbelen (41)
Aspidistra elatior	The saturation level of photosynthesis in plants with a preference for shade is lower by several orders of magnitude than that in plants with a preference for light. The saturation level for shade-preferring plants is lower in bluish-green than in yellowish-red light; bluish-green light promotes O_2-uptake very considerably	The oxidation level of cellular metabolism is rapidly increased in plants with a preference for shade	Voskresenskaya and Zak (52)
	Increased O_2-uptake under the effect of blue light is principally due to increased cytochrome-oxidase activity	The degree to which the level of oxidation is increased depends on the amount of flavoprotein and carotenoid content in the leaves	Voskresenskaya (51)
	Exposed to light, albino leaves produce rather proteins than carbohydrates, while higher light intensities promote the formation of carbohydrates in green leaves	–	Andreyeva, Bondarenko et al. (3)
Bougainvillea glabra	The ratio P/Fe is twice, the ratio K/Ca six times as high in albino as in normal leaves	–	DeKock and Hall (13)
	Albino leaves show a higher level of free amino acids, and the concentration of arginine is four times as high as in normal ones	–	DeKock and Morrison (14)
	The level of organic acids is lower, and the ratio citric acid: malic acid is higher in the albinos	–	DeKock and Morrison (15)

	Albinos are more sensitive to CN^- and CO inhibition	Disorder of respiratory system due to lack of ferrous oxidases	McDonald and DeKock (38)
Bromus sp.	It is impossible to isolate, by means of centrifugation a homogeneous protein fraction from albino leaves which characterizes photosynthetizing tissues. The fraction contains RDP-carboxylase	–	Lyttleton (37)
Daucus carota	$^{14}CO_2$, incorporated into albino leaves, appears mostly in the organic and the amino acids, while sugars show less activity	Apart from the deficiency of photosynthesis, metabolism is normal	Roux and Tendille (40)
Helianthus annuus	Catalase activity is normal in darkness; in light, it decreases to one third of the normal value	–	Weinstein and Robbins (55)
	The protein content of albino plants grafted upon normal individuals diminishes owing to the irondeficient nutrition of the latter. The grafts do not respond to high doses of Mn. If, however, a normal one, high doses of Mn elicit signs of Fe-deficiency in the grafts	–	Weinstein and Robbins (56)
	The amount of pigments is still normal in the cotyledon, while only traces can be found in the first pair of leaves	–	Lyastchenko (35)
	It can be observed in differently photosensitive albino races that the hypocotyl remains green long after the leaves have bleached	–	Lyastchenko (36)

Hordeum vulgare	Deficiency of carotenoids prevents the esterification of chlorophyll in albino leaves	Phytol synthesis is weak	Euler, Hellström et al. (16)
	Carbonic anhydrase activity is lower	–	Waygood and Clendenning (53)
	Only chlorophyll-*a* is formed in the albinos, resulting in the death of the plants	–	Highin (27)
	The ratio of chlorophyll *a* and chlorophyll *b* is below normal in albino and xantha mutants, and above normal in viridescent plants	–	Holm (28)
	Ribulose-di-PO_4-carboxylase activity is lost, glycerin-3-PO_4-ase activity preserved. The incorporation of $^{14}CO_2$ is much below normal and almost entirely taken up by malic acid	–	Fuller and Gibbs (24)
Lycopersicum esculentum	Owing to insufficient N-supply and abundant K-supply, the venose mutants are bleached	Abnormal protein synthesis	Sagromsky (42, 43)
	Owing to insufficient mineral nutrients, smaller but green leaves are formed. Already developed chloroplasts do not degenerate even in spite of intensive food uptake; nutrients rich in minerals destroy the chloroplasts	An osmotically sensitive phase occurs in the course of chloroplast differentiation	Sagromsky (44)
Oenothera hybrids	O_2-atmosphere accelerates the destruction of pigments; it occurs after a longer time in N_2-atmosphere	From the fact that albinos do not take up glucose in N_2-atmosphere, it is concluded that they have no photophosphorylative activity	Kandler and Schötz (29)
Pandanus veitchii	Albino leaves contain less plastoquinone; coenzyme Q_{10}-content is normal	–	Crane (9)
Tradescantia sp.	The carbonic anhydrase activity of albinos is considerably below that of normal plants	–	Waygood and Clendenning (54)

Zea mays	The uptake of O_2 is weaker in albino leaves owing to the absence of reducing sugars	Utilization of foodstuffs from the endosperm is reduced	Lebedieff (33)
	Albinos contain more nitrogenous, soluble matter and less carbohydrates; the intensity of respiration is normal	Abnormal protein synthesis	Groner (26)
	Absence of carbohydrate synthesis destroys albinos; they survive if sugar is administered through the leaves	–	Spoehr (47)
	Chloroplasts, isolated form albino leaves grown in darkness, exhibit considerable Hill activity which disappears in light. Normal leaves are inactive in the dark, and their production of O_2 in light is inferior to that of albinos kept in darkness	–	Clendenning (7)
	The catalase activity of albinos germinated in the dark exceeds that of normal plants, and diminishes on being illuminated. Light of low intensity provokes a slight increase in activity	–	Eyster (17)
	Exposed to light, some albino strains with normal protochlorophyll contents show increased chlorophyllase activity, while the chlorophyll-absorption maxima are shifted in others. Generally, they contain less carotenoid, but there are exceptions (xantha)	Destruction of chlorophyll may be due to lack of phytol, irregular chlorophyll synthesis, irregular carotenoid synthesis	Smith, Durham et al. (46)
	Albinos contain more aconitic acid, but less malic and succinic acid than green plants	–	Le Roux (34)
	The synthesis of carotenoid pigments is blocked in the mutant white-3. Its synthesis of chlorophylls and chloroplasts is normal. They are, however, decomposed at high light intensities in the presence of oxygen. Decomposition of chlorophyll does not occur under anaerobic conditions	Carotenoid pigments protect chlorophylls from photodestruction	Anderson and Robertson (1)

Zea mays	The oxygen uptake of albino plants is 20 to 30 per cent higher; the 0_2-uptake of albino leaves, bleached by intensive illumination, cannot be inhibited by cyanide; 2,4-dinitrophenol promotes 0_2-uptake less in albinos and more in green plants. NaN_3 and CO inhibit respiration to a lesser extent in albinos, while the respiratory effect of NaF and malonic acid is equal in normal and albino plants. Blue light is the most efficient for the production of bleaching and for that of differences in the respiratory system. Albinos contain a greater amount of soluble nitrogenous substances and amide-N, due in the first place to the difference in asparagin concentration	An enzyme, activated by blue light, is involved in the destruction of pigments. Flavoprotein may be the cyanid-resistant terminal oxidase in albino plants. There occur irregular protein synthesis, and protein hydrolysis connected with necrosis	Seltman (45)
	The leaves of etiolated plants contain more ketonic-acid, pyruvic acid and pyruvic-acid-derivatives than normal individuals. With equal uptake of O_2 by both varieties, malonic acid reduces the keto-acid level of albinos very considerably and has no such effect on normal plants	The respiratory system of albinos is abnormal even in darkness.	Faludi and Dániel (18) Dániel (11)
	Albino leaves contain more than normally saturated fatty acids. The concentration of 18-C atomic trienes in albinos is one third of the normal	–	Crombie (10)
	Albinos contain only colourless carotenoids, phytoene and phytofluene. They survive for a long time in weak light	The lack of dimming effect of carotenoids	Anderson and Robertson (2)
	Compared with normal plants, the incorporation of P^{32} is less pronounced, the specific activity of the acid-soluble fraction weaker, that of the alkali-soluble fraction stronger in the leaves of albino seedlings. These differences manifest themselves in isolated plastids as well	Disorder of protein synthesis	Faludi, Gyurján et al. (22)

A colored and two colourless carotenoids are found in albinos. The curves of optimum light intensities, necessary for the formation of the various pigments, differ from the normal. Destruction of pigments is promoted by O_2 and retarded by N_2 and DIECA	The activity of Cu-containing oxidase is increased owing to abnormal light regime caused by irregular carotenoid synthesis	Faludi, Dániel et al (21) Dániel and Kelemen (12)
The incorporation of $^{14}CO_2$ into albino plants in darkness, in weak light is stronger than into normal plants. It is in intensive light that normal individuals bind CO_2 stronger than albinos. The latter shows a conspicuously high concentration of labelled malic acid irrespective of light intensity. Exposed to strong illumination, normal plants produce a great amount of sucrose and alanine	Whether the assimilation of CO_2 occurs predominantly through ribulose-diphosphate or chiefly through phospho-enolpyruvic acid, depends also on light tolerance and light intensity	Faludi, Gyurján and Dániel (20)
The rate of carotenoid synthesis is more rapid in less intensive, that of chlorophylls in intensive light. Strong illumination provokes a rapid decomposition of pigments in albinos, and retards the synthesis of pigments even in normal plants	Partial saturation of carotenoids	Faludi, Dániel and Gyurján (19)
In respect of the change from protochlorophyll to chlorophyll, blue light is twice as efficient for albinos than normal plants; prolonged illumination causes decomposition of chlorophyll	Chloroplasts are exposed to stronger blue light owing to lack of carotene	Koski, French and Smith (32)
The composition of carotenoids is normal but its amount very low in the endosperm and the leaves	Synthesis of the supposed common precursor of chlorophylls and carotenoids is inhibited	Tulpule (49)

Beckmann's spectrophotometer served to determine the absorption spectrum of the pigment solution. Earlier investigations proved the composition of normal carotenoids to be different from that of albino carotenoids. Their highest common absorption occurs at 415 m μ so that we have expressed the carotenoid contents of both green and albino leaves by their extinction values at this wave-length as referred to a gramme of the examined material. The amounts of protochlorophyll, chlorophyll *a* and chlorophyll *b* were computed from their extinction values at 624, 644 and 663 m μ with the method of Withrow (57). The results, as here given, represent the means of four series of experiments.

Results

The difference spectra of the leaves of normal seedlings illuminated for 6 hours at different light intensities (i. e. spectra characterizing the effect of light) are shown in Fig. 1.

It can be seen from the curve that high (100 lux) and medium (2500 lux) light intensities increased the carotenoid and chlorophyll contents of normal leaves, while stronger illumination (10 000 lux) did no longer stimulate the accumulation of carotenoid and markedly reduced the amount of chlorophyll.

The difference spectra of the leaves of albino seedlings, likewise illuminated for 6 hours at different light intensities, are presented in Fig. 2.

It can be seen in Fig. 2. that light of 100 lux diminished the amount of carotenoids, while it increased that of chlorophills to a lesser extent than in normal leaves. Moderate illumination (2500 lux) induced a considerable destruction of pigments in albino leaves; strong illumination (10 000 lux) was followed by their almost complete destruction. The curve of the difference spectrum at a light intensity of 100 lux shows that decrease in absorption began at 426 m μ.

We studied the changes in carotenoid contents by comparing the effects of 2, 6 and 12 hour treatments. The behaviour of extinction at 415 m μ is illustrated in Fig. 3.

The figure 3. shows that, if normal leaves are illuminated for 2 hours, the extinction values remain at the same level or go slightly down. Illumination of 100 lux for 6 hours was followed by a further decrease of extinction values. The amount of pigments in normal leaves was considerably increased under the effect of medium (2500 lux) and high (10 000 lux) light intensities. A treatment with low or medium illumination during 12 hours increased the amount of pigments, while extinction at 415 m μ in strong light showed a diminishing tendency. The 100-lux curve of albino leaves is strikingly similar to the 10 000-lux extinction curve of normal leaves. High light intensities seemed to induce a prompt and sweeping destruction of pigments in albino leaves, a process which continued at 6 and 12 hours also.

These observations lead to the conclusion that the optimum light for pigment synthesis in normal leaves is around 2500 lux, while that for the production of pigments in albinos is in the next lower range of intensities.

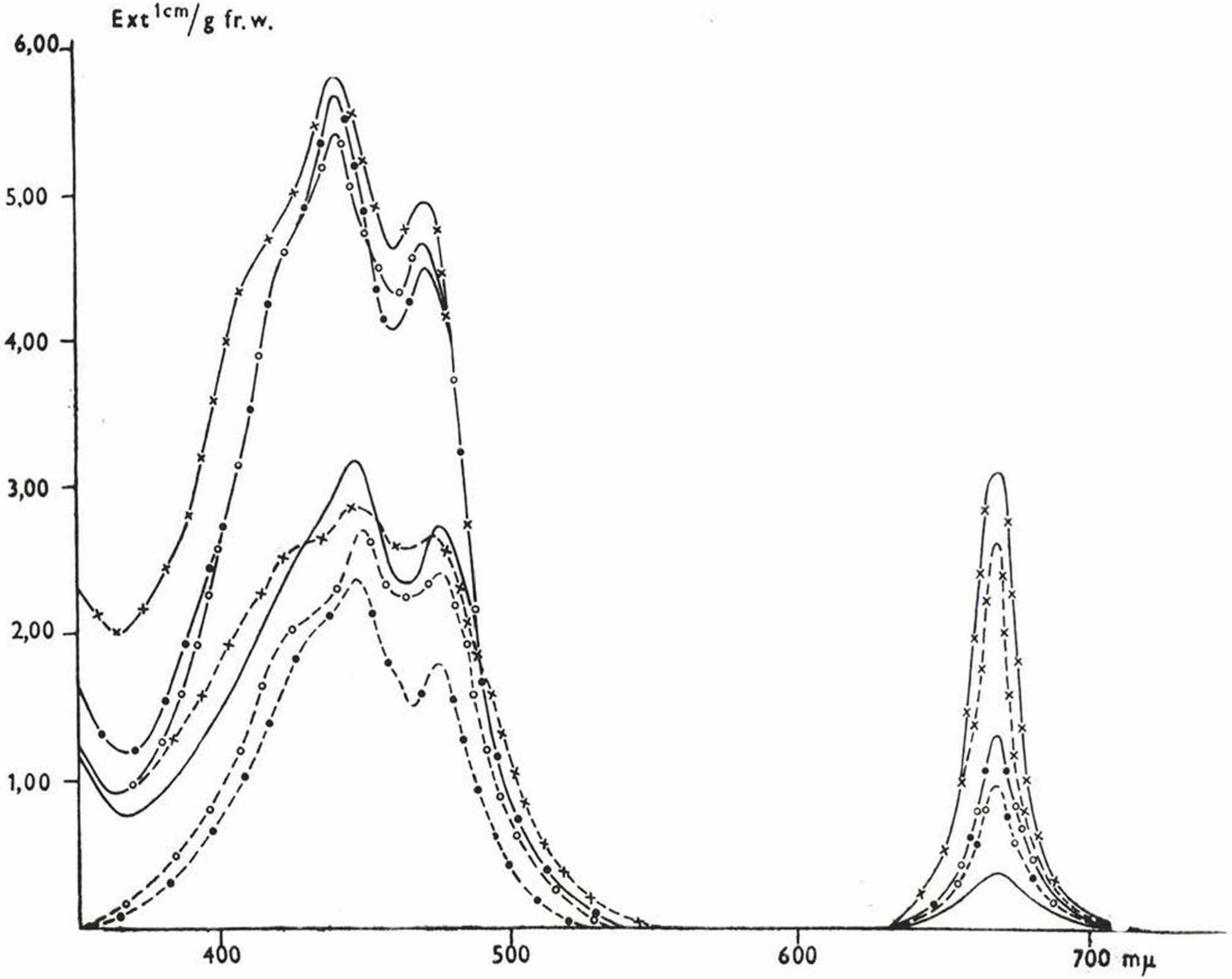

Fig. 1. Effect of 6-hour illumination of different intensities on the pigment extract of normal leaves as shown by difference spectrum

Ext1 cm/g in 5 ml of aether

—— absorbtion spectra

- - - - difference spectra

—— = 5 lux

● = 100 lux

× = 2 500 lux

○ = 10 000 lux

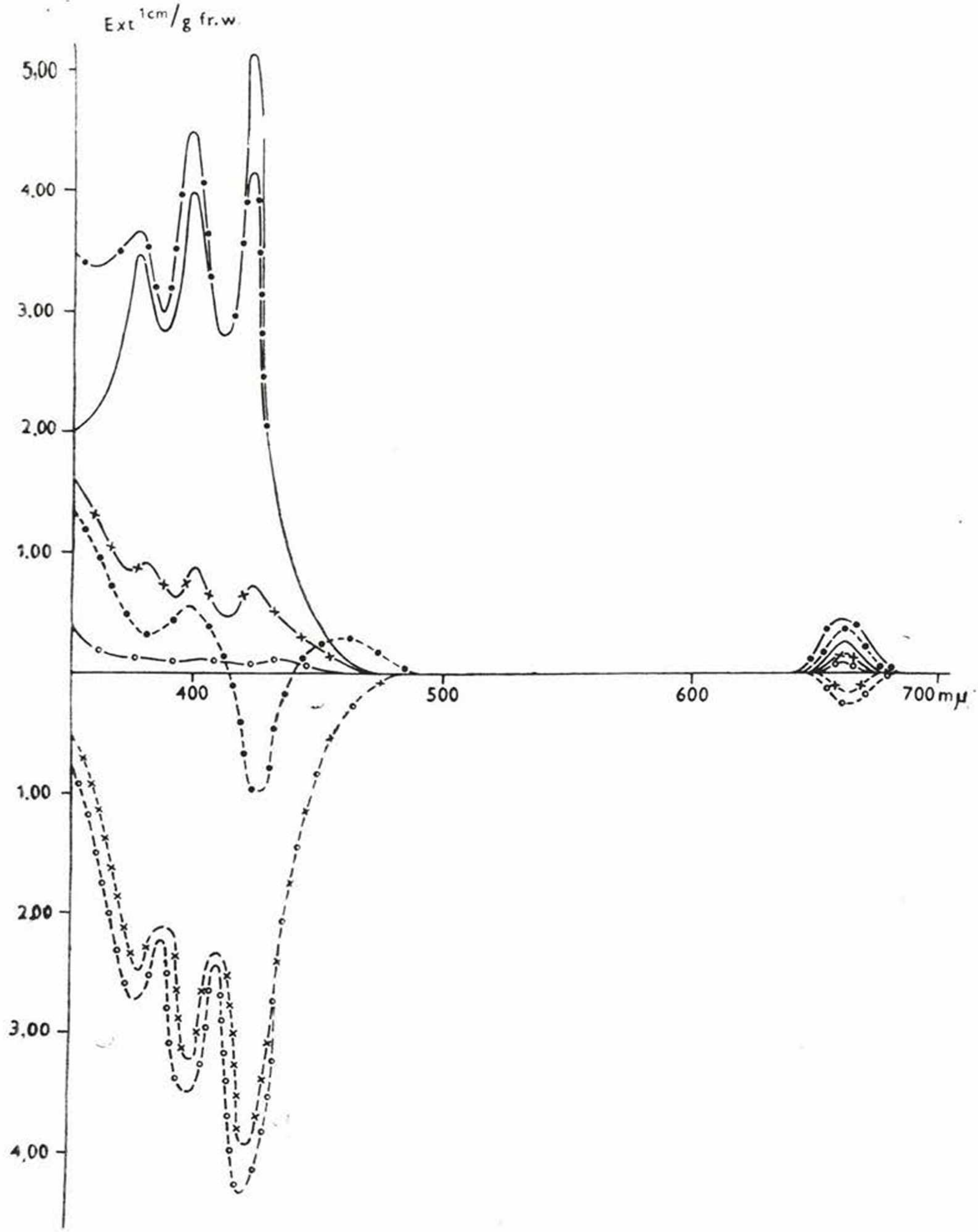

Fig. 2. Effect of 6-hour illumination of different intensities on the pigment extract of albino leaves as shown by difference spectrum

Ext1 cm/g in 5 ml of aether

———————— absorbtion spectra

- - - - - - - - difference spectra

— = 5 lux

● = 100 lux

× = 2.500 lux

○ = 10 000 lux

A quantitative statement regarding the amount of the components of the pigment extract is given in Table 2.

It can be seen in Table 2. that normal and albino leaves have more or less the same pigment composition in the dark (5 lux), the only notable difference being a higher chlorophyll-*a* content in normal leaves. Illuminated by a light of 100 lux, the carotenoid contents of normal leaves are doubled, whereas they are lessened in albino leaves. The concentration of chlorophylls becomes

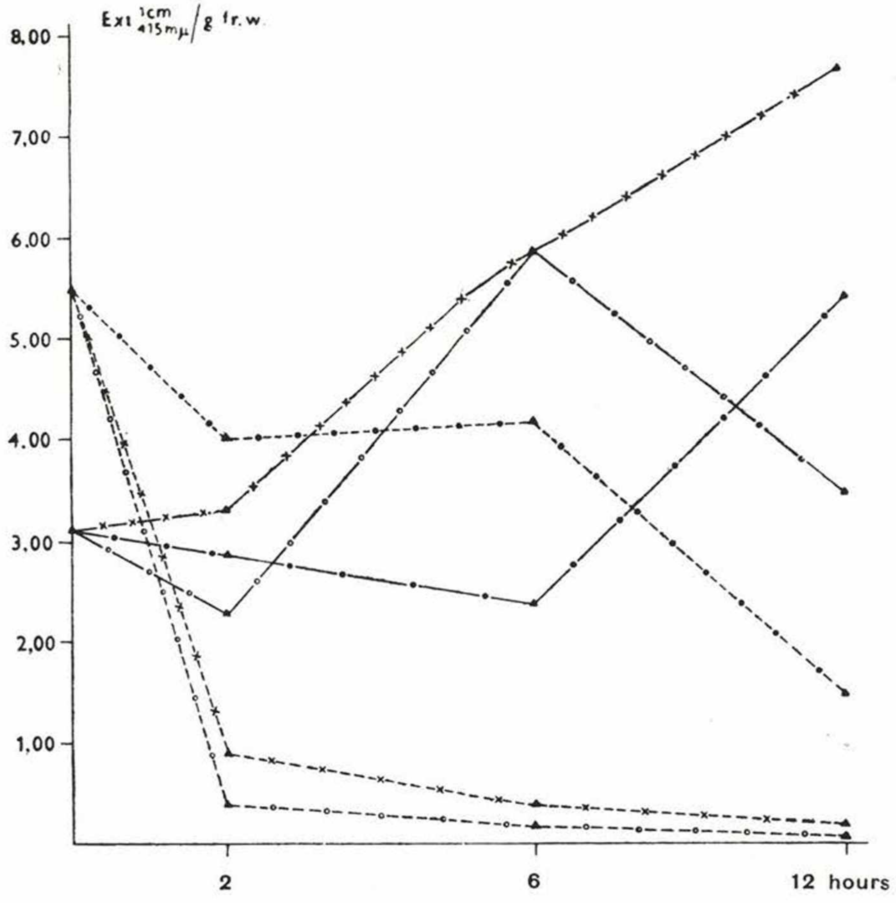

Fig. 3. Changes produced by illuminations of different intensities in the carotenoid contents of normal and albino leaves

$Ext^{1\,cm}_{415\,m\mu}/g$ in 5 ml of aether

——————— normal

– – – – – – – albino

● = 100 lux

× = 2 500 lux

○ = 10 000 lux

Table 2.

Effect of different light intensities on the pigment contents of normal and albino leaves*

LUX	5		100		1000		10000	
Pigment	N	A	N	A	N	A	N	A
Carotenoid	0,8	0,7	1,5	0,6	1,9	0,3	0,9	–
Total chlorophyll	7,5	4,5	39,5	6,9	51,8	1,8	17,8	2,0
Protochlorophyll	2,0	2,1	13,2	4,0	15,3	0,9	5,3	0,4
Chlorophyll *a*	4,8	1,8	21,4	2,2	25,5	0,6	8,0	0,8
Chlorophyll *b*	0,7	0,6	4,9	0,7	11,0	0,3	4,5	0,8

N = normal; A = albino

* Carotenoid $Ext_{415\ m\mu}^{1\ cm}$/g fresh weight in 5 ml of aether

Chlorophylls: mg/g fresh weight

higher in such light both in green and albino leaves. This increase in concentration is more pronounced in normal plants.

Illumination of 2500 lux slightly increases the amount of carotenoids in normal and considerably decreases it in albino leaves. The same changes were observed in respect of chlorophylls. Exposure to 10 000 lux was found to reduce the pigment contents in green and albino leaves alike. This phenomenon was especially marked in the latter.

Table 3. shows the quantitative distribution of pigment components in normal and albino leaves.

Table 3.

Effect of different light intensities on the ratio of pigment components in normal and albino leaves

LUX		5	100	2500	10000
Chl / Car	N	9,4	6,2	28,2	19,8
	A	6,4	11,2	6,0	–
Chl *a* / Chl *b*	N	6,8	4,4	2,3	1,8
	A	3,0	3,1	2,0	1,0

Chl = chlorophyll; Car = carotenoid; N = normal; A = albino

It can be seen that the ratio chlorophyll – carotenoid increased up to the optimum light intensity, and decreased above this limit. The optimum intensity of light proved to be lower (by an order of magnitude) for albino leaves.

The ratio chlorophyll *a* chlorophyll *b* decreased with increasing light intensity, more in normal and less in albino leaves.

Discussion

The difference spectra, indicating changes in the pigment contents of normal leaves kept in darkness or illuminated with lights of various intensities, show different patterns. The illumination produces different effects on the different components of the light-absorbing carotenoid mixture in the shortwave zone of the spectrum.

A similar phenomenon was observed by Sapozhnikov (48) and Blass (4) who found that, with increasing light intensity, the amount of xantophyll rose, that of violaxanthine became less, and that of carotenoids remained unchanged.

Inspection of the red zone of the difference curves reveals that light of medium intensity is most favourable for chlorophyll synthesis.

The photodestruction of carotenoids which absorb light in the zone of shorter wave-lengths is well visible from the difference curves of albino leaves. This phenomenon is still negligible in a light of 100 lux; as far as can be judged from the course of the difference curve, light damages the molecular structure of albino carotenoid at a wave-length of 426 mμ, i. e. where their structural properties give rise to maximal absorption. Such change cannot be due to a disintegration of protochlorophylls or chlorophylls since their total amount is negligible in comparison with the observed decrease of absorption. A similar phenomenon has been observed in pale-green *Chlorella* and *Chlamydomonas* mutants (6). Decrease of extinction, as observed on the absorption curves of alga suspensions obtained from normal *Chlorella* strains, was found to be most pronounced at a maximum of 440 mμ (30), a phenomenon pointing to the destruction of carotenoids by illumination. The destruction of chloroplasts containing normal carotenoids requires much higher intensity of light than that of albino plants. Essentially, the difference between the carotenoids of normally and extremely photosensitive strains is that the latter contain one (21) or two (2) saturated double bonds. The mechanism of this abnormality has not yet been fully elucidated. Cohen-Bazire et al. (8) suggest that the normal submicroscopic structure of the photosynthetizing apparatus cannot develop in the presence of partly saturated carotenoids (50, 55). It is also possible that, in the absence of conjugated double bonds, carotenoids are incapable of transferring electrons required for the regeneration of chlorophylls (23).

A third alternative is that because of the abnormal fluorescence of albino carotenoids, the transfer of energy from carotenoids to chlorophylls fails to take place. The maximum fluorescence of normal carotenoids, being of a reddish colour, is well accessible for chlorophylls, whereas partially saturated Θ or ζ carotenoids give a yellowish-green fluorescence which cannot be utilized by the chlorophylls.

Tables 2 and 3, which show changes in the ratio carotenoids total chlorophylls, make it evident that the chlorophylls are protected by carotenoids and that the photosensitivity of chlorophyll *a* is superior to that of chlorophyll *b*. The latter phenomenon may be due to that the chlorophyll *a* is directly responsible for the redox process of photosynthesis (39).

If one inspects the figure which illustrates changes in the UV-absorption of the pigment extract, as produced by illuminations at different intensities for 2, 6 and 12 hours, it is evident that illuminations of short duration reduce extinction values in both normal and albino leaves irrespective of light intensity. On the other hand, illuminations of longer duration give rise to increased extinction values in normal leaves and lead to a sharp decrease in albinos.

The general extinction-reducing effect of short illuminations is presumably due to that the normal chloroplastic structure is still undeveloped in such cases, and that carotenoids — situated outside the chloroplasts and formed in darkness — possess increased photosensitivity (25).

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Summary

The effect produced by illuminations of different durations and different intensities on the pigments of normal and albino maize leaves has been studied. Illumination of short duration decreases the amount of carotenoids and slightly increases that of chlorophylls in both varieties. If exposed to longer illumination, normal leaves show the highest pigment production at a light intensity of 2500 lux; the synthesis of chlorophylls becomes weaker in a light of 10 000 lux. Medium light intensity of 2500 lux has been found to be above the limit of optimum for albino leaves. The curves of the difference spectra of albino leaves indicate that light affects albino carotenoids in those of their molecular-structural properties which cause absorption at 426 mμ.

РЕЗЮМЕ

Изучалась кинетика изменения содержания пигментов в листьях нормальной и альбиносной кукурузы, полученной при разной интенсивности света.

Установлено, что поглощение пигментов нормальных и альбиносных листьев, измеренное при 415 мμ, в случае освещения разной длительности, показывает различные изменения (рис. 3.). У нормальных листьев поглощение под воздействием слабого освещения в начале уменьшаетcя, потом под влиянием более длительного освещения повышается. Для накопления пигментов освещение в 2500 люксов является самым оптимальным. При 10 000 люксах поглощение уже уменьшается. Для синтеза пигментов альбиносных листьев оптимальным является 100 люксовое освещение, а при более длительном освещении светом 2500 люксовой интенсивности уже появляется быстрая деструкция пигментов.

Исследовав соотношение компонентов пигментов у нормальных и альбиносных растений, оказалось что соотношение хлорофилла-харотиноида повышается до оптимума интенсивности света, а при более интенсивном свете уменьшается. У альбиносов максимум появляется при интенсивности света меньше на один порядок величин.

Из графика спектральных разцин, характеризующих действие света (рис. 1. и 2.) ясно, что свет слабой (в 100 люкс) или посредственной (в 2500 люкс) интенсивности света повышает содержание каротина, и хлорофилла нормальных листьев. При освещении в 10 000 люксов, получается сдвиг равновесия синтеза и распада пигментов в сторону распада. В

альбиносных листьях при 100 люксах освещения появляется увеличение хлорофилла и уменьшение каротиноидов. При более сильном освещении наблюдается резкий распад пигментов.

Самым выразительным является уменьшение поглощения при 426 мμ. Из этого можно делать вывод, что свет повреждает каротиноид альбиноса в его свойстве молекулярной структуры обусловливающей абсорбционный максимум при 426 мμ.

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