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EFFECT OF LIGHT ON THE FORMATION OF A PIGMENT IN THE TOMATO FRUIT CUTICLE[1]

A. A. PIRINGER AND P. H. HEINZE
HORTICULTURAL CROPS RESEARCH BRANCH AND BIOLOGICAL SCIENCES BRANCH,
AGRICULTURAL MARKETING SERVICE, U. S. DEPARTMENT OF AGRICULTURE,
PLANT INDUSTRY STATION, BELTSVILLE, MARYLAND

Geneticists and plant breeders have for many years recognized differences in the color of the skins of fruit of certain tomato varieties and have classified the skins as yellow or clear. Duggar (3) reported in the walls of the epidermal cells an unidentified pigment whose presence or absence made the skins either yellow or transparent. When combined with lycopene, the red pigment in the flesh, the superimposed yellow skin gave the fruit an orange-red appearance, while with red flesh and a transparent epidermal wall the fruit appeared pink.

Duggar mentioned further that young fruits placed at high temperatures failed to develop the red pigment in the flesh and appeared light yellow. He stated: "In such cases color seems to be due in the main to a deposition of pigment in the cuticular layer or cuticle and this unidentified pigment is with great difficulty extracted. . . ." Smith (6) noted that light during the ripening period had considerable effect on the carotenoid content of the skins of tomato fruits and also influenced the color of the outer wall of the epidermal cells.

In a preliminary note Heinze and Borthwick (4) reported that harvested mature-green tomato fruits exposed to short daily periods of light from an incandescent-filament lamp ripened to an orange-red color in contrast to the pink color observed in fruits ripened in total darkness. Microscopic examination of the tomato skin showed that the pigment was in the cuticular layer of the epidermal cell walls. When small portions of the skin were removed from fruits of each of these lots and leached with acetone and petroleum ether, the carotenoids in the adhering cells were removed and the skin from the light-ripened fruit was bright yellow, while that from the dark-ripened fruit was clear or colorless. The difference in appearance of the cuticle in the fruits ripened in light or total darkness was even more noticeable when the ripening occurred at temperatures at which no lycopene developed (32° to 35° C). Data from these preliminary experiments indicated that the threshold value for the light requirement to produce the yellow cuticle pigment was equivalent to that supplied by an incandescent-filament lamp somewhere between 0.0005 and 0.005 fc for one hour, or 0.03 or 0.3 fc for one minute per day during the ripening period.

After this approximation of the amount of white light needed to produce the pigment had been obtained the relative effectiveness of the different regions of the spectrum was investigated. The results of this and subsequent experiments on the influence of the energy and wave length of light on the cuticle-pigment development of ripening tomatoes are reported herein.

MATERIALS AND METHODS

Field-grown tomatoes of the Rutgers variety were used in all experiments. They were harvested as mature-green fruits with no yellow or pink coloration at the time of harvest and graded for uniformity of maturity. The tomatoes were handled in the same manner for all studies. Four fruits were randomly selected and packed firmly, with cheek exposed, in a quart strawberry box. Usually they were ripened in total darkness at 21° or 26.7° C except for the brief periods of treatment with light. In general, small samples per treatment were necessary because of the bulkiness of the plant material.

Except in one experiment in which spectrograph

[1] Received April 19, 1954.

equipment was used, the source of red radiation for all treatments was a group of 4500 Å white fluorescent lamps with a red cellophane filter which transmitted wave lengths longer than 5800 Å. Since fluorescent lamps emit little or no far-red radiation, this filtered source provided reasonably pure red radiation. Far-red radiation was obtained from a sunlight source and a combination blue and red cellophane filter which transmitted wave lengths beyond 6950 Å.

At the desired stage of ripeness the tomatoes were removed from the dark and circular sections of the skin, 2.5 cm in diameter, were removed with a sharp cork borer from the exposed cheek of the fruit. Each section was immersed in boiling water for one minute and then cooled immediately by immersion in cold water. With a scalpel, adhering tissue was scraped from each skin section and the section was placed in acetone.

After being leached for several days the sections were placed in small vials of clear acetone for visual comparison with a standard to determine the degree of effectiveness of treatment. A subjective method of color evaluation was necessitated by the extreme difficulty for complete extraction of the pigment from the cuticle as well as the difficulty of preparation and handling of the cuticle sections required for precise objective methods of measurement. The standard consisted of a series of treated sections prepared as previously described and selected to present a range of possible color intensities from the minimum, which was colorless, to the maximum, which was orange. Effectiveness of treatment was expressed as numerical designations for the range of color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to the maximum, 9 (orange).

Results

Early experiments using Corning glass filters indicated a difference in the effectiveness of the red and blue regions of the spectrum to promote yellow-pigment formation in the cuticle. The spectrograph equipment described by Parker et al (5) for determining action spectra was used to obtain more precise data on a number of regions of the spectrum. Twice replicated lots of two fruits each were irradiated once daily for 14 days at various regions in the spectrum. The nature of the equipment permitted exposure of only two fruits per treatment at a given station along the spectrum. The time of exposure at each station was selected from consideration of a previous experiment (4). An action-spectrum curve was obtained by plotting the data of table I. The points indicated in figure 1 are for color intensity values at a given wave length (station) and for a given energy. That is, a given tomato fruit was irradiated at a particular wave length and energy and the result was expressed as a color intensity value at that point. The curve was drawn through points of a similar color intensity of the value 5. A greater effectiveness was found for the red region than for other regions of the spectrum (table I, fig 1). It was also found that only a few minutes of red radiation daily was sufficient to promote the yellow pigmentation in tomato cuticle. Additional studies were made to consider the effects on pigment formation of such factors as number of treatments with red radiation, the stage of fruit maturity, the time of treatment during the ripening period, the temperature during ripening, and the localization of the response. In all experiments where red radiation was applied the exposure period was 2 minutes.

Results of early experiments indicated a disturb-

Table I

Color Intensity* in Tomato Fruit Cuticles as Influenced by Wave Length of Light and Period of Exposure

Station	Wave length (Å) at center of station	Irradiance ergs cm^2 sec	Color intensity** after indicated exposure				
			½ min	1 min	3 min	9 min	27 min
1	7700	7,450	..	..	..	..	3.2
2	7250	6,950	..	..	..	..	5.6
3	6770	6,000	6.2	5.3	5.6	..	..
4	6440	5,700	5.0	5.0	6.0	..	..
5	6180	5,350	2.7	5.5	6.8	..	..
6	5900	4,950	3.5	5.5	6.7	..	..
7	5700	4,600	2.5	3.2	3.7	5.0	..
8	5480	4,200	1.5	3.2	4.2	4.7	..
9	5320	3,850	..	..	4.0	4.0	3.5
10	5170	3,400	..	..	1.2	2.7	4.5
11	5030	3,000	..	..	2.2	3.0	3.5
12	4930	2,700	..	..	2.2	3.0	3.5
13	4810	2,250	..	..	..	..	3.2
14	4710	2,000	..	..	..	..	2.5
15	4620	1,700	..	..	..	..	2.7
16	4540	1,450	..	..	..	..	2.7

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).

** Mean of four readings.

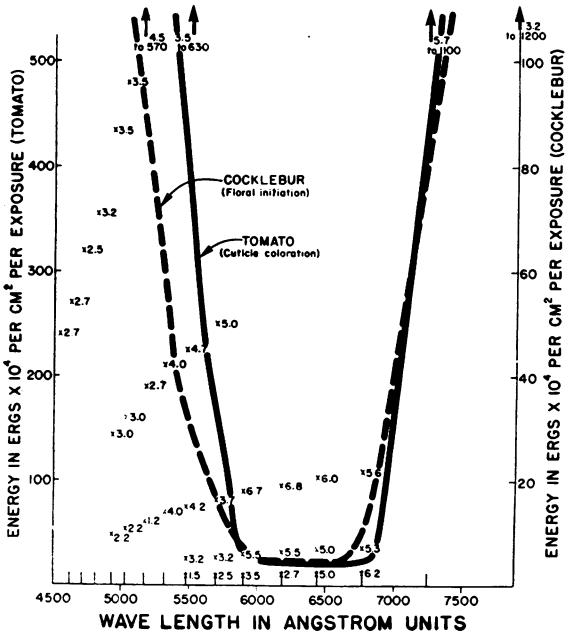

FIG. 1. Action-spectrum curves for cuticle coloration in tomato fruits and floral initiation in cocklebur.

ing variation within lots suspected of being due to differences in initial fruit maturity despite careful selection. An experiment was therefore conducted in which mature-green fruits were carefully reclassified in two groups of apparent but very slight differences in maturity and placed in total darkness for ripening. Fruits in each of these groups were given one to ten consecutive daily treatments with red radiation for 2 minutes beginning the first day, after which each lot was ripened in the dark until 1 day after the last lot was treated, i.e., an 11-day ripening period. The ripening temperature was 26.7° C. The

TABLE II

COLOR INTENSITY * IN TOMATO FRUIT CUTICLES AS INFLUENCED BY THE NUMBER OF DAILY TREATMENTS WITH RED RADIATION AND THE DEGREE OF INITIAL FRUIT MATURITY

NUMBER OF TREATMENTS	COLOR INTENSITY **	
	MATURITY STAGE 1 †	MATURITY STAGE 2
0	0, 0, 0, 0	0, 0, 0, 0
1	0, 0, 0, 1	0, 0, 0, 0
2	0, 0, 0, 0	0, 0, 0, 0
3	0, 0, 0, 3	0, 0, 0, 0
4	0, 0, 4, 6	0, 0, 0, 4
5	4, 6, 6, 7	0, 0, 0, 4
6	4, 6, 6, 6	4, 5, 6, 6
7	0, 6, 6, 6	0, 0, 6, 8
8	5, 6, 6, 6	0, 5, 6, 6
9	6, 6, 6, 7	1, 2, 6, 6
10	6, 6, 6, 6	4, 5, 6, 6

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).
** Each value represents an individual fruit.
† Maturity stage 1 indicates the more mature group.

results indicated a definite effect of maturity in that the more mature fruits exhibited the phenomenon earlier with respect to treatment and also that more than six daily treatments were superfluous (table II). The occasional fruit without yellow pigment after seven or eight treatments showed that the selection of fruit of initial uniform maturity continued to be a problem.

TABLE III

COLOR INTENSITY * IN TOMATO FRUIT CUTICLES AS INFLUENCED BY THE NUMBER AND DISTRIBUTION OF DAILY TREATMENTS OF RED RADIATION DURING A 12 DAY RIPENING PERIOD

NUMBER OF DAILY TREATMENTS	DAYS OF TREATMENT DURING RIPENING IN TOTAL DARKNESS	COLOR INTENSITY **
0 †	...	0, 0, 0, 0
1	1st	0, 0, 0, 2
	2nd	0, 0, 0, 1
	3rd	0, 1, 3, 3
	4th	0, 0, 1, 2
	5th	0, 0, 0, 4
	6th	0, 0, 0, 0
	7th	0, 0, 0, 0
2	1st, 2nd	0, 0, 0, 0
	2nd, 3rd	0, 2, 3, 4
	3rd, 4th	0, 0, 3, 4
	4th, 5th	2, 4, 5, 5
	5th, 6th	0, 0, 3, 6
	6th, 7th	0, 0, 0, 4
	7th, 8th	0, 0, 0, 0
3	1st –3rd	0, 1, 2, 5
	2nd–4th	0, 0, 3, 5
	3rd –5th	1, 3, 4, 6
	4th –6th	0, 3, 4, 6
	5th –7th	0, 0, 2, 3
	6th –8th	0, 0, 0, 6
	7th –9th	0, 0, 0, 0
4	1st –4th	1, 2, 5, 6
	2nd–5th	0, 5, 6, 6
	3rd –6th	1, 2, 4, 4
	4th –7th	0, 1, 5, 5
	5th –8th	0, 0, 0, 0
	6th –9th	0, 0, 0, 0
5	1st –5th	0, 1, 2, 5
	2nd–6th	3, 4, 4, 5
	3rd –7th	3, 5, 5, 6
	4th –8th	0, 1, 3, 4
	5th –9th	0, 0, 0, 0

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).
** Each value represents an individual fruit.
† Dark control.

Although the data presented in table II indicated that six daily light treatments early in the ripening period were sufficient to cause the development of the cuticle pigment, an experiment was performed to determine the effectiveness of one or more daily applications of red radiation later in the ripening period on fruits kept in the dark prior to such treatment. Lots of four fruits each given various numbers of treatments with red radiation (one to five) were ripened for various periods at 21° C. in total darkness

before and after treatment, as outlined in table III. The total ripening period for all fruits was 12 days. It was apparent from the data in table III that several daily treatments, preferably five, must be applied early during the ripening period. Treatments started after the fruits had ripened in total darkness for more than 5 days were ineffective in causing the formation of the yellow cuticle pigment.

In the experiments just discussed development of lycopene pigment in the flesh of the fruit occurred regardless of the light conditions under which the fruits were ripened. This indicated a separate control for formation of lycopene and the cuticle pigment. Further proof of this was given by another experiment in which lycopene formation was prevented. This was accomplished by ripening the fruit at a high temperature at which it was known that lycopene would not develop. Two lots of eight fruits each were held at 32° C during a 10-day ripening period. One lot was wrapped in black cloth and ripened in total darkness and the other lot was exposed 2 minutes daily to incandescent light for 10 days. No lycopene developed in either lot. The cuticles of all fruits ripened in the dark were colorless; those of fruits ripened in the light were colored, the color ranging in intensity from a yellow tint to orange.

Early experiments had suggested that the pigmentation was restricted to the surface of the tomato exposed directly to the light and that the cuticle from the underside of the fruit was frequently colorless. This non-systemic nature of the light stimulus was demonstrated by an experiment in which several tomato fruits were individually wrapped with aluminum foil either completely or except for small exposed areas 3.5, 12.5, or 15.0 mm in diameter. Other fruits were not wrapped. The fruits were ripened at 26.7° C and the exposed areas were irradiated 2 minutes daily for 10 days. Circular sections of 2.5 cm diameter were processed as in the other experiments. As would be expected, the cuticles of the non-wrapped fruits were bright yellow and those of the completely wrapped fruits were colorless. Sections from the 3.5 mm area exposed to light had a localized yellow area about 1 cm in diameter. Those with larger exposure areas had an intense coloration in the center of the section with a yellow shading of the whole section toward the periphery. Although the effect does extend somewhat from the immediate area of the light exposure, it is still localized in that area.

Experiments were also performed to determine whether the phenomenon of the reversal of the red effect by far-red radiation, as reported by Borthwick et al (1, 2) for lettuce seed germination and for photoperiodic control of flowering in Xanthium was present also for the yellow cuticle pigmentation. The first of this series of experiments involved two groups of fruits exposed to red radiation for 0 or 10 minutes. Lots of four fruits each from these two groups were then exposed to far-red radiation from a Corning molded red purple ultra filter of 8 mm thickness with a sunlight source of light for 0, 4, 16, or 64 minutes, respectively. The fruits were ripened at 21° C and radiation treatments with red and far-red were made on 11 successive days. Ten minutes of red radiation with no far-red treatment induced the yellow pigment formation to a relatively high degree (table IV). Far-red given after similar red treatments resulted in markedly less pigment formation but more than in the dark control. The data also showed that far-red radiation alone had a slight promotive effect on pigment formation.

TABLE IV

COLOR INTENSITY * IN TOMATO FRUIT CUTICLES AS INFLUENCED BY THE DURATION OF DAILY TREATMENT WITH RED AND FAR-RED RADIATION

MINUTES OF RED RADIATION	COLOR INTENSITY ** AFTER FAR-RED RADIATION			
	0 MIN	4 MIN	16 MIN	64 MIN
0	0, 0, 0, 4 †	1, 2, 3, 3	2, 2, 2, 3	2, 3, 4, 4
10	5, 6, 6, 7 ‡	3, 4, 4, 4	3, 3, 3, 4	2, 3, 3, 4

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).
** Each value represents an individual fruit.
† Dark control.
‡ Red control.

Another experiment followed to determine whether multiple reversal was possible and whether the pigment response depended upon the last in a sequence of exposures to red and far-red, as was shown to be true for lettuce seed germination by Borthwick et al (1). Light treatments were made daily for 10 days on lots of four fruits each. These fruits were ripened at 26.7° C. The results of this experiment in which a sequence of up to four reversals was made in-

TABLE V

COLOR INTENSITY * IN TOMATO FRUIT CUTICLES AS INFLUENCED BY THE SEQUENCE OF RED AND FAR-RED RADIATION

TREATMENT **		COLOR INTENSITY †
SEQUENCE	FINAL	
Dark control	..	0, 0, 0, 0
R	R	2, 2, 5, 5
R–F	F	0, 0, 0, 0
R–F–R	R	4, 4, 5, 5
R–F–R–F	F	0, 0, 0, 1
R–F–R–F–R	R	2, 4, 5, 5
R–F–R–F–R–F	F	0, 0, 0, 1
R–F–R–F–R–F–R	R	0, 1, 5, 5
R–F–R–F–R–F–R–F	F	0, 0, 1, 1

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).
** R designates 2 minutes of red radiation from a 4500 Å white fluorescent source with a red cellophane filter which transmitted wave lengths beyond 5800 Å; F designates 2 minutes of far-red radiation from a sunlight source and a combination blue and red cellophane filter which transmitted wave lengths beyond 6950 Å.
† Each value represents an individual fruit.

dicated that the formation of the yellow cuticular pigment in tomato fruits was dependent upon the last of the sequence of exposures (table V).

The importance of applying far-red radiation soon after the red radiation in order to show the reversal phenomenon has been demonstrated in other plant material.[2] To determine whether this time relationship between applications of red and far-red radiation was true also for cuticle pigment formation, lots of four fruits each were subjected to seven daily light treatments and ripened at 26.7° C. for an additional 7 days. Various periods, 0 to 120 minutes, between the red and the far-red radiations were tried. An outline of the treatments, as well as the results, is given in table VI. As the period between applications of the red and the far-red was increased there was a progressive loss of ability of the far-red radiation to reverse the effect of the red.

In an attempt to identify the yellow pigment formed in the tomato skin, the pigment was obtained from cuticles of fruits ripened in the light and analyzed as described below. Cuticles from which the carotenoids had been removed by leaching with acetone and petroleum ether were used. When the cuticle was dissolved in alcoholic potassium hydroxide and the solution was neutralized with strong acid, the pigment was easily extracted from the aqueous layer with ethyl ether. Treatment of the ether solution with a sodium carbonate solution caused the pigment to be concentrated in the aqueous phase again. After neutralization of the sodium carbonate the pigment was re-extracted with ethyl ether. Evaporation of the ether solution left a residue soluble in acetone, ethyl acetate, and isopropyl alcohol; sparingly soluble in chloroform and dichloromethane; and insoluble in petroleum ether and water. Alkali intensified the yellow color. Basic lead acetate produced a yellow precipitate in an acetone solution and ferric chloride gave a brown coloration. The pigment gave the boric acid color reaction described by Wilson (7) for flavone derivatives, but the pigment could not be reduced to give the cyanadin test.

An equal volume of petroleum ether added to the ethyl ether solution of the pigment caused it to precipitate. The precipitate was dissolved in ethyl acetate, spotted on chromatographic paper and developed with ethyl acetate saturated with water. An Rf value of approximately .92 was obtained. With 60 % isopropyl alcohol as the developer, Rf values of .68 to .71 were obtained. There was no evidence of more than one compound in the colored zone on the chromatographic sheet, but the spots were not distinct, indicating that other colorless impurities were interfering to some extent. Present evidence indicates the pigment is of a flavonoid type.

[2] R. J. Downs, Plant Industry Station, Beltsville, has found a critical time period within which the far-red had to be applied to be effective in reversing the effect of the red on leaf expansion of dark-grown seedlings and flowering in cocklebur and in Biloxi soybean.

TABLE VI

COLOR INTENSITY * IN TOMATO FRUIT CUTICLES AS INFLUENCED BY TIME LAPSE BETWEEN APPLICATIONS OF RED AND FAR-RED RADIATION

MINUTES OF TREATMENT			COLOR INTENSITY **
RED	TIME LAPSE	FAR-RED	
0 †	0	0	0, 0, 0, 1
0 ‡	0	2	1, 1, 1, 2
2 ▪	0	0	4, 4, 4, 6
2	0	2	0, 1, 1, 1
2	5	2	1, 1, 1, 2
2	10	2	1, 1, 1, 1
2	20	2	1, 1, 1, 2
2	40	2	1, 1, 2, 3
2	60	2	2, 2, 2, 2
2	80	2	2, 3, 3, 3
2	100	2	2, 3, 4, 4
2	120	2	1, 2, 3, 4

* Numerical values represent color intensities as follows: 0 (colorless) through 3 (yellow tint) through 6 (bright yellow) to 9 (orange).
** Each value represents an individual fruit.
† Dark control.
‡ Far-red control.
▪ Red control.

DISCUSSION

Photoperiodic control of flowering in *Xanthium saccharatum* and the light regulation of germination of seed of *Lactuca sativa* var. Grand Rapids have identical action spectra (2). These action spectra have two very striking features; one is a region in the red that inhibits flowering of Xanthium and promotes germination of Lactuca seed, and the other is a region in the far-red that has the opposite effect, promoting flowering of Xanthium and inhibiting the germination of Lactuca seed.

The fact that the light-controlled yellow pigment in tomato cuticles and the photoperiodic control of flowering in Xanthium are phenomena controlled by the same photoreaction is indicated by the similarity in action spectra (fig 1). That the production of light-induced yellow cuticle pigment could be reversed by far-red radiation is especially striking in view of the fact that far-red radiation similarly reversed the effect of red radiation in the photoperiodic control of Xanthium flowering and Lactuca seed germination. Moreover, the pigment formation was repeatedly reversible as had been shown to be true for Lactuca seed germination (1). With tomato cuticles, however, it was found that far-red radiation alone would induce a slight yellowish tint and it is noteworthy that the bright-yellow-pigment formation induced by red radiation was never reversed completely to a colorless condition but rather to one of a slight tint characteristic of the effect of far-red radiation alone.

There is little doubt that the same photoreaction regulates these seemingly unrelated phenomena — the photoperiodic control of flowering in Xanthium, the light controlled germination of Lactuca seed, and the yellow pigment formation in the fruit cuticles of some tomato varieties.

The pigment involved in the tomato cuticle seemed to be a flavonoid and it probably appeared as an end product rather than as the active receptor of the light stimulus. When the light treatment was restricted to a small area on the surface of the fruit the response was highly localized in the treated area. Whatever the action of the light, the response apparently occurred in living tissue adjacent to the cuticle and in the immediate area of the reception of the stimulus. The possibilities that suggest themselves as to the action of the light in relation to the appearance of the pigment in the cuticle are (1) an effect of light on some form of the flavonoid pigment in adjacent tissue followed by diffusion of the pigment into the cuticle; (2) an effect of light on the transport of the preformed pigment to the cuticle; or (3) a combination of these two processes. The occurrence of some decreasing pigment intensity away from the point of treatment in the localization study was more probably caused by diffusion of the pigment itself into the surrounding area rather than due to light diffusion from the point of treatment. Some of these processes can perhaps be elucidated when additional studies on the response of the pigment in tissues adjacent to the cuticle and analyses of the pigment are made. Although at present the origin of the yellow pigment in the tomato fruit and its precise chemical nature are unknown, a complete identification of the pigment may be helpful in identifying the precursor or in explaining the possible mechanism of the action of light in the formation of the pigment.

The presence of the yellow cuticle pigment is known to be genetically controlled. The fact that the response is absent in certain tomato varieties does not necessarily indicate that the photoreaction controlling the phenomenon is absent, but possibly that some link in the chain between the receptor and the resulting flavonoid pigment is missing and it is this link that is genetically controlled.

The tomato has long had the reputation for being a photoperiodically indeterminate plant. It is noteworthy that a response is now found in one of its organs that, though not photoperiodic per se, is identical in action spectrum with the photoperiodic responses of other plant materials.

Summary

1. The light-controlled production of a yellow pigment in the cuticle of fruits of the tomato variety Rutgers was studied.

2. The yellow pigment was present in cuticles of fruits ripened in light but absent in those of fruits ripened in dark.

3. Formation of the pigment in dark-ripened fruits can be induced by brief daily irradiations with light of very low energies early during the period of ripening.

4. The effect of red radiation of longer than 5800 Å was the production of the yellow pigment. The effect of the red radiation was cancelled by subsequent treatment with far-red radiation beyond 6950 Å, leaving the apparent effect of uninterrupted darkness.

5. When fruits were immediately given additional cycles of red and far-red, the pigment response depended upon the last of the sequence of exposures to red and far-red. The action of the far-red to reverse the effect of the red tended to be lost if its application following the red was delayed too long.

6. The action of the red and far-red light that controls the production of pigment in the cuticles of tomato fruit is identical with that regulating flowering of *Xanthium saccharatum* and for the seed germination of *Lactuca sativa* var. Grand Rapids.

7. The response, production of yellow pigment, was restricted to the general area of the light treatment.

8. The yellow pigment involved in the cuticle phenomenon appears to be a flavonoid.

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