SMITHSONIAN MISCELLANEOUS COLLECTIONS
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THE FUNCTIONS OF RADIATION IN THE PHYSIOLOGY OF PLANTS

II. SOME EFFECTS OF NEAR INFRA-RED RADIATION ON PLANTS

(With Four Plates)

BY
EARL S. JOHNSTON
Division of Radiation and Organisms, Smithsonian Institution

(Publication 3180)

CITY OF WASHINGTON
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Experimental results bearing on the influence of near infra-red radiation on plant growth and coloration are presented and discussed in this paper. Plants were grown under two different radiation distributions of equal visual intensity, one limited entirely to visible radiation, the other including a large amount of energy in the near infra-red. These preliminary experiments are a part of the program being undertaken by the Smithsonian Institution bearing upon the functions of radiation in various plant processes. A description of the special equipment (see pl. 1) that has been developed for the study of the effects of radiation upon plants grown under controlled conditions has been given in another publication (5).[1]

CULTURAL METHODS

The tomato plant was selected for these experiments because considerable work (12, 13, 14) had already been done with it in water culture and many of its growth characteristics are known. Furthermore, it has been used as an indicator plant (10) for determining the deficiency of certain fertilizer elements in the soil, and it responds very quickly to unfavorable atmospheric conditions. Because of its quick response to slight environmental changes its behavior is an excellent criterion of those conditions.

Tomato seeds of the Marglobe variety were germinated between layers of moist filter paper in a covered glass dish at a temperature of 25° C. When the roots had grown to a length of 2 to 10 mm the young plants were transferred to a germination net. This net was made by stretching two pieces of paraffined cotton fly-netting over a circular glass dish 19 cm in diameter by 10 cm deep. The

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[1] Numbers in parentheses refer to the list of literature cited, found at the end of this paper.

two pieces of netting were separated by a piece of glass rod 0.5 cm thick, bent to fit inside the dish. As the roots grew through the mesh the two layers served to hold the plants in an upright position. Flowing tap water was passed through the dish in a manner to keep the upper layer of netting afloat. The plants were illuminated by a 200-watt Mazda lamp placed 30 cm above the netting. Lateral light was cut off by surrounding the germination net and plants with black cardboard tacked to a light wooden frame. This frame was raised above the table level and was large enough to provide ample air circulation around the plants. When the seedlings were approximately 3 cm in length they were transferred to the culture solutions. Each culture consisted of a single plant supported by means of cotton in a small hole in a paraffined flat cork stopper which fitted into a 2-quart Mason jar containing the nutrient solution. Four of these jars were then screwed to the under side of the bottom plate of each growth chamber; the young plants extended through the holes into the chamber.

The nutrient solution was made up of the following salts with the corresponding partial volume-molecular concentrations:

$Ca(NO_3)_2$	0.005
$Mg\,SO_4$	0.002
$K\,H_2PO_4$	0.002
$Mn\,SO_4$	0.0000178
H_3BO_3	0.00005

The approximate calculated concentrations of the nutrient ions in this solution expressed as parts per million and milliequivalents are:

	Ppm.	Milliequivalents [a]
Ca	200	10.0
Mg	49	4.0
K	78	2.0
NO_3	620	10.0
SO_4	194	4.0
PO_4	190	6.0
Mn	1	0.0364
B	0.55	0.15

[a] Calculations based on milliequivalent per liter $= \frac{\text{valence}}{\text{at. wt.}} \times$ ppm.

To this nutrient solution was added humic acid[2] containing 2.4 mg iron per cc at the rate of 0.5 cc per liter of nutrient solution. The

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[2] The humic acid used in these experiments was supplied by Dr. Dean Burk of the Fixed Nitrogen Research Laboratory, United States Department of Agriculture.

method of making this iron compound has been described and discussed by Burk, Lineweaver, and Horner (6). This compound promises to be a very useful source of iron for nutrient solution experiments. Unlike most of the other iron compounds used in this type of work, the solution contains very little if any precipitate, even at high pH values. Hence it is not necessary to add this form of iron every day or two during the early stages of growth as must be done with ferric tartrate and some other iron compounds. One application of iron humate is sufficient to keep the plants green under good growing conditions for at least two weeks.

EXPERIMENTAL PROCEDURE

In the experiments herein described, only the overhead illumination was used. The light period for each 24 hours extended from 9 a. m. to 12 midnight. This period of illumination (15 hours) falls within the optimum range for tomato plants. Two wave-length ranges for two different light intensities were used. One wave-length range included all radiation transmitted by a water cell 1.5 cm thick with pyrex cover glasses, and the other was further limited by a heat-absorbing filter. Two chambers of each pair had the same visual intensity. It is realized, of course, that the radiant energy required in plant reactions is not exactly limited to the visible region, nor is it at all likely that their requirements are at all proportional to the visibility. It would be preferable to compare the effect of radiation in the range absorbed by chlorophyll with radiation including the near infra-red as well. Practical considerations make it necessary to use a heat-absorbing filter which cuts off not sharply at the limit of chlorophyll absorption, but gradually from 6,000 to 8,000 A. The method to be described for equalizing the visual intensities is simply a convenient means of attaining approximate equality of intensities in the visible range common to both types of radiation.

The light intensities were equalized at the beginning of the experiment by means of a Weston photronic cell provided with a special heat-absorbing filter (Corning heat-resisting, heat-absorbing, dark shade filter 2.82 mm thick). At the conclusion of the experiment of two weeks' duration the light intensities gave the values indicated in Table 1. This combination yielded a sensitivity curve shown as a continuous line in Figure 1. Sensitivity is plotted as ordinates in arbitrary units with 100 as maximum against wave lengths in Angstrom units. The visibility curve shown as the dash line is included in this figure for the sake of comparison.

The two distributions of energy, adjusted for equality for visible radiation measured as indicated, are shown in Figure 2. In order to determine the distribution of energy in the chambers with and without the heat-absorbing filters, a curve of relative emission per unit wave length of radiation for a tungsten filament at the absolute temperature of 2,980° K. was constructed. This tungsten radiation curve was then corrected for energy absorbed by the pyrex filters and 1.5 cm of water. Another curve was obtained by further correcting for energy absorbed by the heat-resisting, heat-absorbing light shade filter (8 mm thick) and 1.5 cm of water. From each of these two distribution curves corresponding response curves were drawn by applying the factors obtained from the sensitivity curve of the photronic cell with its special heat-absorbing filter. The ratio of the areas under the two response curves then gave a factor which was applied to one of the distribution curves in order to adjust their relative values so as to yield equality of total response, that is, equality of visible radiation as determined by the photronic cell with its filter. These two adjusted curves are the ones presented in Figure 2. A comparison of the areas of these curves shows that the total energy applied to the plants receiving no near infra-red radiation was 22 per cent of that applied to the plants receiving radiation including the near infra-red.

Table 1

Light sources and intensities

Chamber	Mazda lamp (watts)	Glass [a] of water filter	Illumination measured by Weston photronic cell with filter [b]	
			Microamps	Estimate of foot-candles
1	500	p and p	100	339
2	500	h and p	106	359
3	1500	h and p	580	1966
4	1000	p and p	580	1966

[a] p, pyrex; h, Corning heat-resisting, heat-absorbing, light shade filter, 8 mm thick.

[b] For these measurements a circular piece of Corning heat-resisting, heat-absorbing, dark shade filter, 2.82 mm thick was placed over the Weston photronic cell.

Thermometers were hung in the chambers in such a manner that their bulbs were shaded from the direct rays of the lamps but were

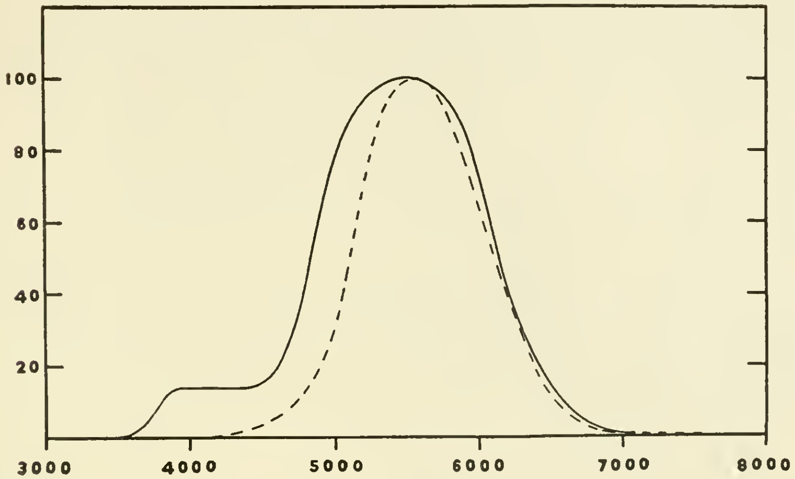

FIG. 1.—Sensitivity curve (continuous line) of a photronic cell provided with a special filter, and the visibility curve (dash line).

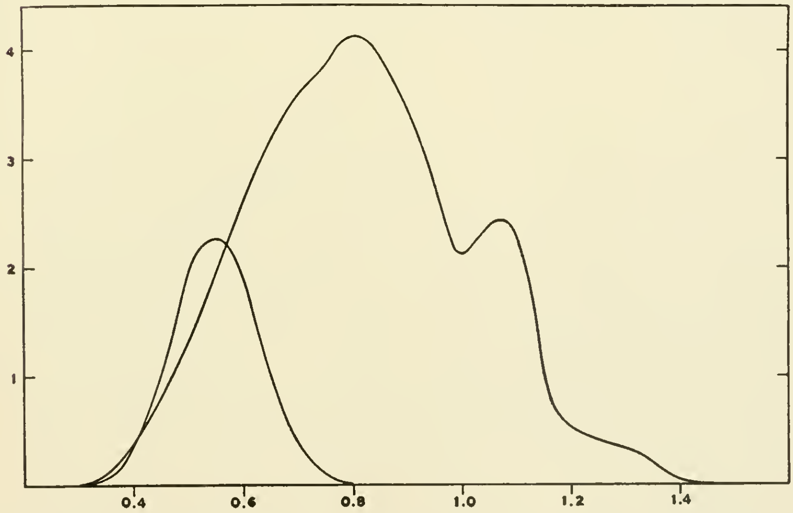

FIG. 2.—Curves showing the two types of energy distribution adjusted for equality of " visible " radiation as measured by the photronic cell with its special filter.

freely exposed to the air. Temperatures were usually read three times each day. During the light periods the temperatures were approximately 3.5° C. higher than during the dark periods. The average temperatures are shown in Table 2.

In this experiment no measurement was made of the rate at which air was recirculated through the chambers. Fresh air was injected into the system at the rate of 15 liters per minute. It should be emphasized that a sufficient rate of air movement in plant growth chambers is very essential. It is true, as has been discussed by Wallace (20), that some plants have been grown for several months in glass containers hermetically sealed. Few plants, however, are suited to such an existence and then only when there is a proper balance of mineral and gaseous elements, temperature, and light in their microcosm. In two previous experiments air was recirculated very slowly. Under these conditions the plants were very soon affected with oedema. Numerous frosty-white intumescences appeared on the midribs, petioles and stems. The leaves soon became twisted and contorted and finally gave the plant a wilted appearance as illustrated in Plate 2. Atkinson (4), Orton and McKinney (11), and others have described this disease as due to excess humidity, poor lighting, and overheating. With a low rate of air flow in the growth chambers the conditions are ideal for producing this disease. Further experimentation showed that with an air flow of 40 liters per minute per chamber all symptoms of oedema were entirely eliminated.

TABLE 2

Average air temperatures in the plant growth chambers

Growth chamber	1	2	3	4
Light period	24.4	24.5	25.3	25.9
Dark period	20.9	20.8	20.8	20.8

Marglobe tomato seeds were placed in the germinator on April 21, 1932, and the sprouted seeds removed to the germination net on April 26. Eight days later the young plants whose average height was 2.5 cm were set out in the culture jars and placed in the four growth chambers, four to a chamber. For comparison two groups of four plants each were grown under uncontrolled conditions in natural light, one group placed in a west window of a room in the Smithsonian tower, the other standing in the north window of the basement laboratory. At the end of two weeks the plants were photographed and measured. The plant data obtained from these measurements are presented in Table 3.

TABLE 3

Plant data at harvest, expressed as averages per plant

Radiation						
Intensity	Low		High		Daylight	
Distribution[a]	V and I	V	V and I	V		
Plant group	1	2	4	3	West window	North window
Dry weight (mg)						
Tops	126	16	426	199	162	16
Roots	14	3	40	31	30	3
Total	140	19	466	230	192	19
Water absorbed (cc)	45	15	88	93	85	18
Stem height (cm)						
Final	20.2	6.8	18.0	12.7	7.8	5.6
Increase	17.2	4.4	15.6	9.9	5.4	3.5
Number of leaves	5.0	4.3	5.8	5.8	5.4	3.5
Order of greenness	4	1	5	3	4	2
Water requirement	320	810	188	402	444	956
Ratio $\frac{\text{root}}{\text{top}}$ wt.	0.11	0.17	0.09	0.15	0.18	0.17
Internodal index Ratio $\frac{\text{stem ht.}}{\text{no. of leaves}}$	4.0	1.6	3.1	2.2	1.3	1.4
Stem elongation Ratio $\frac{\text{(final ht.}}{\text{original ht.)}}$	6.7	2.8	7.5	4.5	3.3	2.7

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[a] V and I, visible and near infra-red radiation; V visible radiation.

In an examination of the data of this table it should be remembered that the visible intensities in chambers 1 and 2 were approximately the same. Likewise those of 3 and 4 were alike. However, in the latter pair the light was much more intense. In chambers 2 and 3 the infra-red was removed. A comparison of the dry weights shows the greatest growth to have occurred in chamber 4 and the least in chamber 2. In a subsequent experiment, similar to this one except that the temperatures were higher, the same order of growth, as measured by dry weight, existed between the four chambers. That is, in order of plant dry weight the series in this and a subsequent experiment was 4, 3, 1, 2 (high visible plus infra-red, high visible only, low visible plus infra-red, low visible only). It is also rather interesting to note that the growth of plants in chamber 2 (low visible) was very similar to that in the north window of the laboratory. Also there was a good deal of similarity between the plants in chamber 3 (high visible) and those grown in the west window of the tower.

A greater amount of water was absorbed by the plants exposed to the greater light intensities—those in chambers 3 and 4. It should also be noted that in chambers 1 and 4, where the proportion of red and infra-red was greater, the plants elongated much faster than those in chambers 2 and 3. Although there was little difference found in the average number of leaves of plants in the four chambers, there is an indication that more leaves were produced in the more intense light.

Attention is directed to the order of greenness of the plants grown under these six conditions of illumination. Those grown in chambers 2 and 3, which received only visible radiation, and in the north window were greener than the others. The lower leaves of the plants in chamber 4, where the radiation was more intense and included infra-red, had turned yellow. Those in chamber 1, while not as yellow as those in 4, were far from a healthy green color.

In the lower part of the table several derived values are tabulated. Water requirement is here considered as the amount of water absorbed by the plant during the two weeks of growth per unit of total dry matter. Plants in chambers 1 and 4, where infra-red radiation was present, were more economical in their use of water than the others. The ratios of root to top dry weights indicate that somewhat heavier roots in proportion to tops occur without infra-red.

The internodal index was determined by dividing the height of the plant by the number of its leaves. It gives a relative index of the length of internodes. This index as well as the ratio of final to original height of the plants shows that much less elongation occurs without infra-red.

Plate 3 shows the general appearance of the six groups of plants after two weeks of growth under the conditions of light mentioned in this paper. With the exception of set 1 all the individuals of the various groups are very uniform, with but slight variations. For better comparison a representative culture from each group was selected and photographed. These are presented in Plate 4.

DISCUSSION

Growth of plants under different wave lengths of light has received considerable attention at the hands of plant investigators. Much of this earlier work has been reviewed by Teodoresco (18, 19), who has done very valuable work along this line. He investigated two main spectral regions (the blue-violet and the red-orange) by means of colored solutions and glass filters. Because of the general conclusion of many previous investigators and his own experience that infra-red has no appreciable effect in addition to heating, he did not think it necessary to use water screens between his light sources and the plants. However, in measuring his light intensities a screen of water and copper acetate was used to eliminate the effect of the infra-red upon his measurements. His general conclusions from experiments with a large number of land plants, many of which were duplicated with both glass and solution filters, are: that in the longer wave lengths, internodes were elongated and more numerous, areas of leaves reduced, the leaves themselves were thinner, and a general abnormal configuration resulted. In the shorter wave lengths, growth in length was retarded, leaf area increased as well as leaf thickness. The general appearance of the plants was normal, resembling those grown in white light. In many respects the plants grown in the red-orange region resembled plants grown in darkness except for their green color. As Teodoresco points out, plants grown in darkness became etiolated without chlorophyll assimilation, so that growth ceases. In red light, however, the plants grow for a longer time than in darkness, due to the production of food by photosynthesis. In view of the fact that different color filters usually transmit different amounts of infra-red light, the existence of an effect of radiation in the near infra-red would necessarily qualify the conclusions to be drawn from such experiments. Consequently, the results of the present investigation raise serious doubts as to the validity of this type of experiment, unless it is definitely shown that the different filters transmit the near infra-red in the same degree.

Funke (7), working mainly with aquatic plants, studied the effects of three general spectral regions, red, green, blue, and subdued white light. Any ultra-violet or infra-red passing through his filters was neglected. The intensities behind these filters were approximately 25 per cent of the energy of diffused daylight. For many species the light intensity was insufficient. Results were obtained for plants in which photosynthesis was greater than respiration. The anatomy and behavior of plants in the blue light resembled those in full daylight. Those in red were " etiolated as in darkness (except of course that chlorophyll is formed). In green, phenomena are either the same as those in red or development is reduced to a minimum; the latter is undoubtedly due to a total absence of assimilation of carbonic acid. In gray, development now resembles that in blue, now that in red, depending on the needed quantity of blue rays being small or great."

Arthur, Guthrie, and Newell (3) have carried out a great many experiments on the growth of plants under artificial conditions and find the tomato the most sensitive to high light intensity in combination with a long day period of illumination. In three series they used respectively 5, 7, 12, 17, 19, and 24 hours of illumination daily, with an intensity of 450, 800, and 1,200 foot-candles. The air temperature of the first and second series was maintained at 78° F. and the third at 68° F. Their results show that the tomato will not withstand a 24-hour day of illumination at intensities which cause little or no injury to other plants. Even 19- and 17-hour days are injurious at the higher intensities. In the greenhouse experiments, where the plants were exposed to 12 hours daylight and 12 hours artificial light, the plants were injured. However, the rate of development of this injury was decreased by this combination of daylight and artificial light. The injury was characterized by the leaves becoming faintly mottled with necrotic areas appearing along the veins. The plants also had yellow leaves. The first signs of injury appeared in five to seven days.

In commenting on the illumination used these authors state:

> The energy value in the constant-light room calculated at 0.3 gram calory per square centimeter per minute amounts to approximately 12,960 gram calories per month of 30 days. The total for the month of solar and sky radiation as published by the New York Observatory for June, 1929, was approximately 11,903 gram calories. The two energy values are similar but, as already pointed out, the spectral distribution is in no way comparable. The glass-water filter in the constant-light room absorbs practically all radiation of wave-length longer than 1,400 mμ so that the total energy value of 12,960 gram calories includes only the visible region and the near infra-red of wave-length shorter than 1,400 mμ.

The experiments described in the present paper set forth the general growth characteristics of tomato plants grown under two ranges of wave lengths for two different intensities. One group of plants was exposed to light, a large proportion of whose energy was in the red and near infra-red region, the other exposed to light limited to the visible wave length region. Thus, an attempt is here made to separate any near infra-red effects from those brought about by other wave lengths.

The growth of these tomato plants as measured by their total dry weights clearly shows that the plants receiving infra-red radiation were considerably heavier, with less difference occurring in the stronger light. It is conceivable that if the illumination were further increased the plants receiving no infra-red would surpass in weight those receiving these longer wave lengths. Such an increase in illumination would undoubtedly have been beneficial since Arthur (2) found that where light of the same composition as sunlight was reduced to 35 per cent of full sunlight tomato plants thrived best. Assuming 10,000 foot-candles as a value for full sunlight, then an illumination of 3,500 foot-candles would be the optimum illumination for tomatoes. In these experiments the higher estimated intensity was 1,966 foot-candles, approximately half their optimum intensity.

The general form of the plants grown under the near infra-red radiation was somewhat characteristic of plants grown under shade conditions in that the internodes were long. However, the leaves were not small as might be expected for shade conditions. The water requirement was also lower than that of the plants receiving only visible radiation. This point is rather interesting because shading is usually considered an environmental factor increasing the water requirement of plants. Thus, some general growth habits of the plants exposed to the near infra-red radiation are common to plants grown under shade conditions and others to those grown under normal light conditions.

Although the dry weight production was greater for plants exposed to the infra-red radiation, these plants were distinctly less green than those receiving only the visible wave lengths. In the higher intensity of the infra-red the lower leaves were rather yellow. This evident destruction of chlorophyll in the near infra-red region is extremely interesting. Although considerable work has been done on growing plants in different colored lights, many of the early results are questionable because of inadequate light filters and a lack of suitable measuring devices for evaluating the intensity factors. In recent years many of these difficulties have been overcome.

Light within certain wave length and intensity limits is generally considered essential to chlorophyll formation, although it is true that certain pine seedlings and a few algae become green in darkness. As early as 1874 Wiesner (21) found that chlorophyll was formed in plants when illuminated by light passed through solutions of potassium bichromate and copper sulphate. These filters divided the visible spectrum into two parts. He also showed that no greening occurred in the nonluminous heat rays.

Sayre (15) studied the development of chlorophyll in seedlings of several varieties of plants by growing them under Corning glass ray filters and noting the relative greenness as compared with seedlings grown in full daylight. No greening was observed in wave lengths longer than 6,800 A. In the visible spectrum he found that for approximately equal energy values the red wave lengths were more effective for the development of chlorophyll than the green and the green more effective than the blue. The effectiveness apparently increased with increasing wave length up to 6,800 A, where it ended abruptly.

Shirley (16) working with several types of plants grown in the spectral greenhouses at the Boyce Thompson Institute for Plant Research found an increase in chlorophyll concentration with decreasing intensity to a point so low as to hazard the health of the plant. At approximately 10 per cent of full sunlight intensity the chlorophyll content was practically the same for wave lengths 3,890-7,200, 3,740-5,850 and 4,720-7,200 A.

Plants grown at high altitudes were found by Henrici (9) to contain less chlorophyll than similar ones grown at lower altitudes. As noted by Spoehr (17) "this is presumably due to the greater intensity of light at higher altitudes. However, whether the lower chlorophyll-content of plants grown under high illumination intensity can be directly ascribed to the destructive action of such light (especially the red-yellow rays) on chlorophyll, does not seem entirely established."

Tomato plants grown under ordinary greenhouse conditions and then placed under continuous artificial illumination were found by Guthrie (8) to show a marked decrease in their chlorophyll content in a few days. The leaves turned yellow and later showed necrotic areas. By analysis the chlorophyll decrease was greater on the dry-weight than the fresh-weight basis, due to a very large increase in carbohydrates. It is interesting to note that this author found a consistent lowering of the chlorophyll *a*/chlorophyll *b* ratio. Both *a* and *b* decreased under the effect of the light, but *a* decreased faster.

If radiation within certain wave length and intensity limits is necessary for the formation of chlorophyll and if, as appears probable, other radiation limits are destructive either directly or indirectly, then the amount of chlorophyll present in a leaf at a given time is the resultant of these two processes of production and destruction. According to Sayre, as noted above, the effectiveness of the wave lengths apparently increases up to 6,800 A., where it ends abruptly. In earlier experiments it appears that no distinction was made between the near and far infra-red, so that definite conclusions cannot be drawn. From the present experiments it would appear that the near infra-red has a decided destructive action on chlorophyll, even great enough to surpass its rate of formation in the presence of wavelengths shorter than 6,800 A. It should be remembered, however, that these tentative conclusions are based on the appearance of the leaves. Before definite conclusions can be drawn the experiments should be repeated and chlorophyll determinations made.

From the experiments of Arthur (1) on the production of pigment in apples it appears that the near infra-red radiation alone or in the presence of visible light has a marked detrimental effect on apples. Under these rays a typical wrinkled, necrotic area soon develops. In his work with tomato plants Arthur found that injury occurred with the use of continuous illumination even as low as 150 foot-candles. The fact that the rate of injury was greatly decreased where half sunlight and half artificial light was used emphasizes the necessity for a more thorough investigation of light sources whose distributions differ from that obtained with the Mazda lamp.

One point should not be lost sight of, namely, that in the region of the strongest chlorophyll absorption bands the plants grown in the distribution including the infra-red receive some three times greater intensity of radiation. This very likely in large measure accounts for the greater increase in dry weight exhibited by the plants grown under this distribution. It is furthermore likely that the higher internal temperatures produced by the more penetrating near infra-red would account to some extent for other differences exhibited. In a future experiment it is hoped to compare two distributions in which the radiation in this region is approximately equalized. For this purpose it will be necessary to secure heat-absorbing filters which cut off at longer wave lengths.

CONCLUSIONS

The tomato plants that received both visible and excessive near infra-red radiation under the artificial conditions of these experiments showed some general growth habits common to both normal and shade-grown plants. The internodes were larger, the leaves larger, and the water requirement less than in plants grown under the visible radiation alone.

A marked decrease in chlorophyll occurred in the leaves of the tomato plants grown under the full visible and infra-red range of wave lengths. A distinct yellowing and death was noted in extreme cases. It appears that, if not actually destructive, this infra-red region of the spectrum is of little or no benefit to chlorophyll formation.

It would appear that normal growth of the tomato plant can be obtained under artificial light conditions where the infra-red is cut off and the intensity great enough.

From a review of the literature and from the results obtained in these experiments with the tomato plant it appears that the near infra-red region of the spectrum is of considerable biological importance.

Furthermore, experiments comparing the effects of different portions of the visible region must be scrutinized for the possible presence of different amounts of near infra-red.

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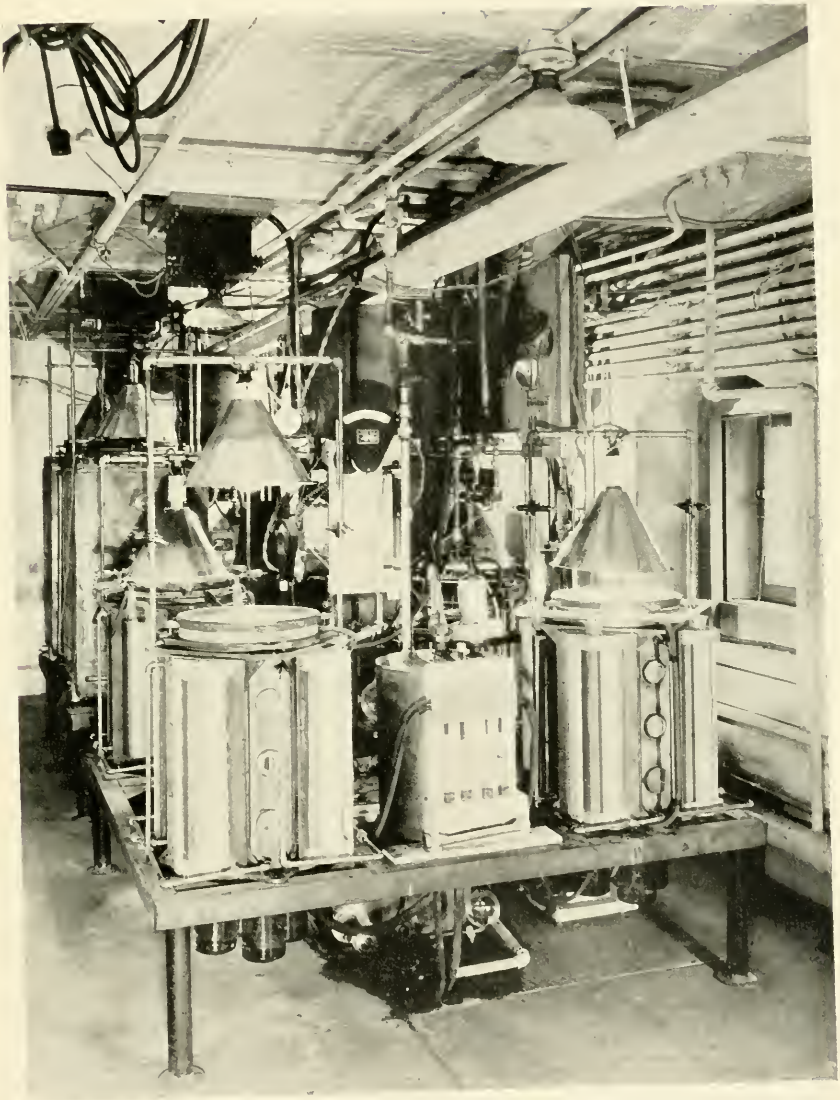
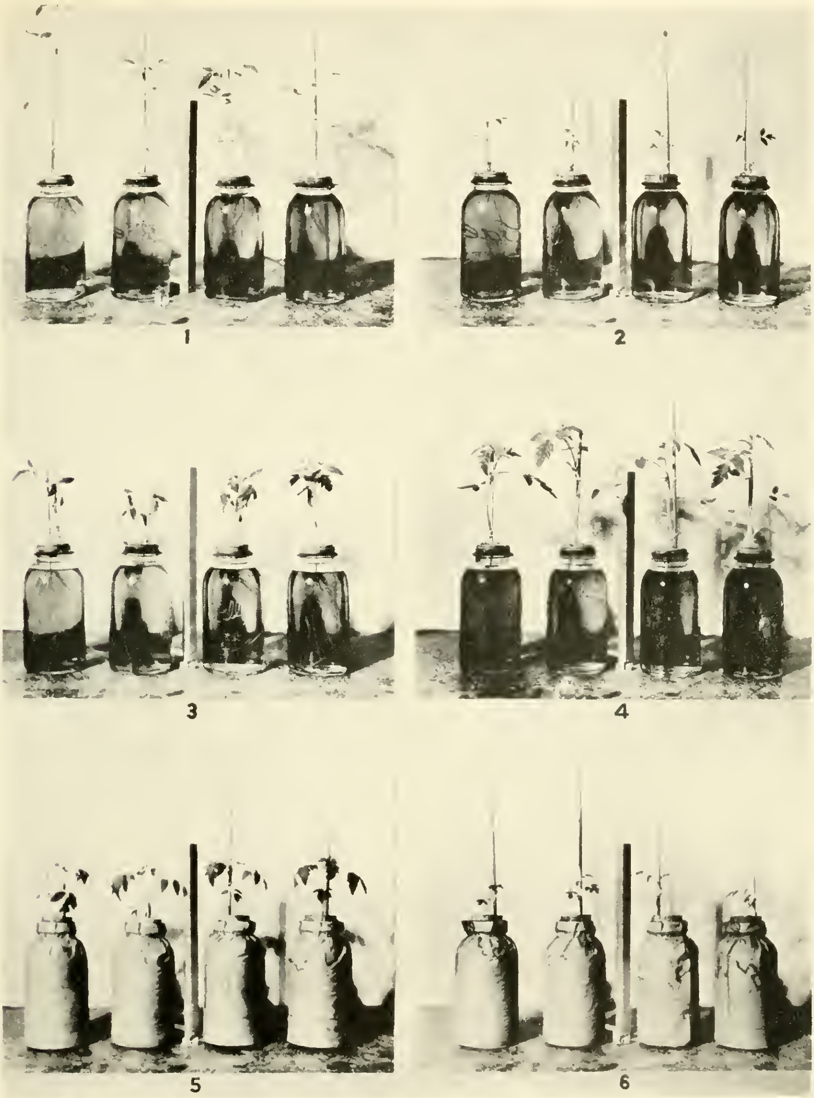


General View of Plant Growth Chambers and Equipment for Control of Experimental Conditions

APPEARANCE OF TOMATO PLANT AFFECTED WITH OEDEMA BROUGHT ABOUT BY POOR VENTILATION



APPEARANCE OF THE SIX GROUPS OF TOMATO PLANTS AFTER TWO WEEKS OF GROWTH

Low light intensity:	
Visible plus near infra-red	1
Visible only	2
High light intensity:	
Visible plus near infra-red	4
Visible only	3
Natural illumination:	
In west window of tower	5
In north window of laboratory	6

APPEARANCE OF REPRESENTATIVE TOMATO CULTURES FROM EACH OF THE GROUPS ILLUSTRATED IN PLATE 3

Low light intensity:
Visible plus near infra-red........ 1
Visible only 2

High light intensity:
Visible plus near infra-red......... 4
Visible only 3

Natural illumination:
In west window of tower.......... 5
In north window of laboratory...... 6