THE EFFECT OF LIGHT INTENSITY ON THE PHOTOSYNTHETIC EFFICIENCY OF TOMATO PLANTS

By

ALTON MILLETT PORTER

A THESIS

Submitted to the faculty of the Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Horticulture Department

East Lansing, Michigan

1936

Approved: Aug. 20, 1936. - V. R. Gardner

ACKNOWLEDGEMENTS

The writer is grateful to Dr. J. W. Crist for guidance and aid in conducting this study and reviewing the manuscript; to Professor V. R. Gardner for suggestions in the preparation of the manuscript; to Professor F. C. Bradford for advice in reviewing the manuscript; to Dr. William W. Smith for assistance in collecting data; and to Professor G. Safford Torrey and Dr. H. E. Hill for help with the photographic work.

Introduction

The tomato stands foremost among the several vegetable plants which are cultivated as greenhouse crops. In its culture under glass, especially in the northern states, the question of a sufficiency of light for its best development and highest productivity arises and becomes acute. The light of the natural day, during the winter months, appears to be inadequate with respect to its duration and also its ordinary intensity.

The possibility of using artificial light, to reinforce daylight, exists. As matter of fact, this has already been tried in not a few instances.

Certainly photosynthesis is one of the most fundamental processes which condition plant behavior and production, and light is a major factor in its dynamic complex. Neglecting the characteristics of light, other than its intensity, how is its intensity related to the rate, the so-called efficiency, of photosynthesis? More particularly, what is this relationship respecting the tomato plant, when grown under greenhouse conditions? A study of this, - induced by the desire to extend the knowledge disclosed by investigations already made and reported, - was made and is herein presented.

Review of Literature

The effects of strong, diffused light on photosynthesis were extensively studied by Muntz (11) in 1913. He found from field observations that alfalfa produced less dry matter per square centimeter of leaf area in the summer of 1911, - a summer unusually free from clouds - than in 1910, when cloudy skies prevailed much of the time. Additional observations were made in the laboratory where it was possible to equalize the amounts of water received by the lots of plants grown under different light intensities. The results of the laboratory experiments accorded with those obtained from the work in the field. He concluded that carbon assimilation is governed and limited by the intensity of the light.

Lubimenko (9) and Popp (17) found that in heliophilous plants the rate of the accumulation of elaborated materials was increased with increase in the light intensity, up to an optimum point, and that any increase beyond this optimum resulted in a decrease in the rate. Heliophobous plants behaved in the same manner, the optimum, however, being at a much lower point than that for the heliophilous types.

Arthur, Guthrie and Newell (1) working with 30 different species of plants found the tomato to be the most sensitive to light. Light intensities of 350, 450, 760, 800, 1200 and 1400 foot-candles were used conjointly with lengths of day which ranged from five to 24 hours. This revealed the fact that the "time factor" was of importance. The peak of increase in carbohydrate production was reached at higher light intensities with the 12-hour day. Injurious effects resulted when the day was lengthened to 17 and 19 hours. The maximum carbohydrate increase was reached with the 17 and 19-hour day when lower light intensities were used, or at the point of injury for the higher intensities.

Combes (2) working with potatoes, and other tuber-forming species, found that the higher the light intensity, the greater the accumulation of elaborated organic compounds in the storage parts of the plants. Apparently, at lower intensities the storage function ceased and the entire amount of the products of photosynthesis was consumed in the growth of the aerial parts of the plant.

DeBesteriro and Durand (3) obtained very definite results experimenting with the garden pea. The plants' dry-weight increase was in direct proportion to the intensity of the light employed for its irradiation.

Folmer (5) and Yoshii (24) experimented with several of the different environmental factors, and of these several factors, light intensity had the greatest effect on the production of carbohydrates in cereals and peas. Their data show a greater production of carbohydrates under the condition of short days with bright sunlight than that of long days with reduced sunlight, although the product of the intensity and the duration of light was higher in the latter case.

Kostytschew and Kardo-Sys-Soiewa (8) found that desert plants increased in carbon assimilation up to an optimum light intensity and decreased as the intensity went above this point. Later in the day, as the light intensity fell to the optimum point, the carbon assimilation again reached a maximum causing the daily curve of photosynthesis to show two peaks in its outline.

The literature which bears directly on the question of the response of the photosynthetic function to the factor of light intensity is not so plentiful. The foregoing references are not all, but are representative of those of greater importance, and also, are sufficient to show the existence of a quantitative relationship between these two phenomena.

Besides a direct effect of light, with respect to its intensity, upon the behavior of the photosynthetic process, acting as a catalytic and energizing agent, it appears to affect certain other factors, which are essential in the process. Among these are the chlorophyll content of the leaf, and its anatomical structure, - the latter being important with reference to the rate of the diffusion of gases within the leaf's interior.

Willstätter and Stoll (23) observed that the rate of photosynthesis increased with the chlorophyll content, but were unable to establish a definite quantitative relationship between the two, - the function and the independent variable.

Palladin (14) and Lubimenko (9) state on the basis of their experiments that heliophobous plants are relatively higher in chlorophyll content than heliophilous plants. The latter investigator was able to establish the fact that the optimum light intensity for photosynthesis is lower in correspondence with reduced content of chlorophyll. Shade plants, at the lower light intensities were as efficient in photosynthetic activity as nonshade plants at these same light intensities.

A number of more recent investigators, Johnson (7), MacDougal (10), Spoehr (19) and Wiesner (21), working with long day plants, report that the amount of chlorophyll in the leaves of plants increased in direct proportion to the average quantity of light received by them.

Sprague and Shive (20) demonstrated that there was a degree of relationship between the total chlorophyll content and the dry weights of tops in corn. The total quantity of chlorophyll contained in the leaves of the various strains of maize correlated closely with their dry weights at successive harvests. Strains that showed a high chlorophyll concentration per unit of leaf area also had high average rates of increase in dry weights of tops, and vice versa. This ratio between the total chlorophyll and dry weight of tops was practically identical with all three strains of corn tested.

Emerson (4), working with Chlorella, observed that plant cells low in chlorophyll reached their maximum rate of photosynthesis at approximately the same light intensity as normal cells. In working with different chlorophyll concentrations in plants that were kept constant in these variations, with the same light intensity, he found that the rate of photosynthesis increased at the same speed regardless of the chlorophyll concentration. The conclusion was that chlorophyll is probably a chemical reactant in photosynthesis as well as being the photosensitizer which absorbs the radiant energy necessary in the process.

Hayden (6) and Poole (15) found the spongy parenchyma cells (mesophyll) of the leaves were poorly developed in sun plants, but in shade plants these cells replaced the palisade cells.

Shibata (18) observed that light intensity had a definite effect on the anatomy of the leaves, in that the epidermal cells are smaller in short day plants. Osterhout (13), and Nightingale and Mitchell (12) observed that leaves were thicker and had more elongated, more densely packed, palisade cells, as the average light intensity was maintained at a higher point.

The literature leaves no doubt concerning the direct, and also indirect, importance of light intensity in the plant's photosynthetic behavior. The results cited from the work of Arthur, Guthrie, and Newell (1) are especially significant and helpful, since the tomato plant itself was among those used in their experiments. However, additional contributions from controlled experimentation are desirable, and necessary, before the matter of the use of artificial light in forcing houses, devoted to t omato growing and production, can be certainly and soundly determined.

General Procedure

The tomato plants used in the experiment were of the Grand Rapids Forcing variety. The seeds were sown in greenhouse flats on January 26, 1933. On February 3, a large number of seedlings were selected and pricked off into two-inch pots. These were transferred on February 12 into four-inch pots and left therein until March 1, or until their development was such that they were ready for final transplantation. On that date, 36 of the plants were selected from the remaining 108, and transferred to 14-inch pots, in which they were grown singly and to full maturity.

The soil was a fairly rich orchard loam, which had been previously screened and thoroughly mixed, by having been shoveled over, in bulk. Its uniformity was as good as could be expected and secured.

The 36 plants were divided into three lots of 12 each, and each of the lots placed, with wide spacing, on a separate greenhouse bench where the pots were surrounded by moist sand, (afterwards kept moistened) to a depth of five inches. During the course of the experiment, the individual pots within each lot were systematically shifted, twice each week, in their positions. This insured greater uniformity in their exposure to the environment, particularly the factor of light. The number of clusters of fruit per plant was restricted to five.

A 14-hour day was maintained over the plants of each lot. Extension of the regular daylight period was accomplished by means of a 1000-watt electric lamp, with dome reflector and adjustable in height, suspended centrally above each group of plants. A wooden frame was constructed above each of two of the benches, under each light, and made to be vertically moveable. One of these frames was covered with one layer of white cheese-cloth, the other with two layers. This effected three respective intensities of the light, both natural and artificial, for the plants: no shade or full intensity - one-half intensity (50.4%) - and a little less than one-fourth intensity (22.3%). The shades were kept adjusted in their heights so as always to be approximately 24 inches above the tops of the growing plants.

It was aimed, of course, to keep the conditions of the environment, aside from the controlled variations in light intensity, the same for the three benches. Data were recorded for relative humidity, air temperature, and soil temperature, under each of the three light conditions, from March to July, by the use of hygrothermographs and soil thermographs.

Additional information regarding methods - those more particularly technical - is given, where appropriate, in the following section, with its presentation of the data obtained.

EXPERIMENTAL RESULTS

Growth Response - Leaf Area:

Possible relationships between each of several different linear measurements of the tomato leaf and its total area were examined in a previous experiment (16). The length of the leaf from the base of its first leaflets to the tip of the midrib proved to be the most accurate index. The type of association was clearly curvilinear, and specifically, parabolic in the second degree. The derived equation was $y \text{ (area)} = 3.16 + 0.417\,x + 0.307\,x^2$.*

All of the leaves on each plant in each of the three lots were measured, in the manner indicated above, and at intervals of three to seven days during the course of the present experiment, and their areas calculated through the given equation. The data are presented in Table 1.

* This leaf area equation was tested out on about 20 leaves from each set of plants and it was found that the formula applied equally well to all three types of illumination.

Table 1: Growth Response - In Terms of Leaf Area

Date of Measurement	Average leaf area per plant in sq. cm.			Average daily increase in leaf area per plant in sq. cm.		
	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth
March 28	1350	1503	1652			
April 4	1649	2253	2473	42.7	107.0	116.0
April 8	1888	2687	3122	59.7	105.8	162.1
April 11	2088	2894	3594	66.6	100.4	157.1
April 15	2358	3408	4202	67.5	107.5	152.0
April 18	2668	3646	4694	102.8	77.7	158.5
April 22	3188	3901	5294	130.0	63.6	147.5
April 29	3754	4303	6259	80.7	57.3	139.0
May 6	4164	4680	6649	58.5	56.1	55.6
May 13	4325	5033	6764	23.0	48.0	16.4
May 20	4485	5433	6868	13.3	57.0	14.8
June 5	4563	5559	7072	6.5	7.9	12.7
July 3	4563	5559	7072			

As shown in Table 1, expansion in leaf area was both continuously and finally the greatest for the plants under the lowest light intensity; next greatest where medium intensity prevailed, and least in the unshaded condition. The orderliness of the change in the daily rate of the increase in the foliar surface of the unshaded plants is outstanding. This rose over gradual steps to a distinct maximum (April 22), and thereafter fell off consistently to zero at the end. Differing from this, the two other maxima were reached more quickly and much earlier in the life of the plants, and were maintained over longer periods of time.

Thus, the usual result was obtained. Growth, when measured in terms of leaf area, augments under reduced light intensity. The leaves attain greater size, but commonly are thinner and may have even less total mass. The greater spread of leaf surface gives increased exposure to the light, such as it is, and tends in some degree to compensate on the whole for the lesser quantity of light received per unit of exposed surface.

Growth Response - Stem Elongation:

The measurements taken for leaf area were accompanied by determinations which gave the growth rate of the main axis of the plants, under each light treatment. The distance measured was that of the stem axis. The period of these intermittent measurements was April 4 to June 5, when the plants were pinched out at the top, and thus restricted to the production of but five fruit clusters per plant. Table 2 gives the data.

Table 2. Growth Response - In Terms of Stem Elongation

Date Measured	Average Height of Plant in Cm.			Daily Increase in Height per Plant in Cm.			Internodal Length		
	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth
April 4	45	61	70				4.8	5.5	6.2
April 8	50	68	76	1.25	1.75	1.50	4.8	5.5	6.0
April 11	54	73	87	1.33	1.66	3.66	4.8	5.6	6.2
April 15	59	82	95	1.25	2.25	2.00	4.5	5.9	5.7
April 18	64	94	100	1.66	4.00	1.66	4.7	6.7	5.9
April 22	70	96	105	2.00	.50	1.25	5.1	6.5	6.2
April 29	74	98	112	.57	.28	1.00	5.2	6.4	6.5
May 6	78	100	116	.57	.28	.28	5.2	5.9	6.6
May 13	81	102	117	.42	.28	.14	5.4	6.0	6.2
May 20	81	102	117	0	0	0	5.4	6.0	6.2
June 5	81	102	117	0	0	0	5.4	6.0	6.2

The responses in stem elongation shown in Table 2 were akin to those shown for increases in leaf area. Growth in height, as reflected in more attenuated internodes, was more rapid as shading was heavier, and the plants taller at the time of being topped. The maxima for the rates of elongation were in the same order as those followed by the leaves, and their occurrences in time practically identical with those which obtained for the leaves.

Growth Response - Fruit Production:

The records taken on fruit production show a definite fruit set and production in direct relation with the light received by the plants. These measurements were made by tagging the fruit with the date set on each cluster and recording the number of days necessary for each fruit to ripen and its weight. This information was assembled and totaled giving comparative figures to illustrate the value of light intensity on fruit production and on the efficiency of the plant leaf area. These data are presented in Table 3.

Table 3. Growth Response - In Terms of Fruit Production

Cluster No.	Total Number of Fruits			Total Weight of Fruit in Grams			Average Wt. of Single Fruits in Grams			Average Days to Ripen, from Set		
	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth
1	57	29	0	3335	1572	0	58.5	54.2	0	48.9	53.6	0
2	75	54	20	5866	3629	1555	78.2	67.2	77.7	47.7	49.6	54.7
3	58	57	39	5277	4062	2761	90.9	71.2	70.9	47.7	49.1	53.8
4	61	47	56	5797	3896	4590	95.0	82.9	82.0	46.0	48.0	53.6
5	20	18	27	1759	1448	1913	87.9	80.4	70.8	43.1	47.2	52.0
Totals	271	205	142	22034	14607	10819	-	-	-	-	-	-
Average per plant	22.5	17.0	11.8	1836.1	1217.2	901.5	-	-	-	-	-	-
Average per sq.m of leaf area				7288	3894	2229						

The amount of fruit set under reduced light intensity is much less than under normal light, as can be seen in Table 3. In the early part of the season when the plants were receiving a relatively small amount of light the fruit set was in inverse proportion to all amounts of shading, but as the season progressed and light intensity became higher, the fruit set correlated best with the heaviest shading as would be expected. This may be accounted for by the fact that the light intensity received by the heaviest shaded plants was originally at or near the minimum for fruit set. Then as the season progressed and light increased beyond the minimum, other environmental factors entered, causing a greater proportion of fruit set under shaded conditions than was originally the case. The amount of fruit when ripened, however, correlates closely with the foot candle hours of light, (Table 7), to which the plants were exposed.

Fruit production requires a greater area of leaves in proportion to the amount of shading the plants receive. The fruits attain greater weights and ripen sooner when the light intensity is not reduced. Doubtless the great assimilation of plant food by the leaves tends to speed up fruit growth and ripening.

Growth Response - Total Plant Production:

The data for total plant production determined on twelve individuals under each of the three different light intensities are shown in Tables 5, 6 and 7. A cursory glance at these data shows that individual tomato plants vary within wide limits. The weights taken for total plant production show a variation in plant food under each light treatment that is less than the differences in light intensity.

Table 4. Growth Response - In Terms of Total Plant Production by Plants Not Shaded

Plant	Fresh Weight in Grams				Dry Weight in Grams				Ash Weight in Grams				#Plant Food Weight in Grams			
	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total
1	629	131	2217	2977	91	22	113	226	16.4	7.9	7.9	32.2	74.6	14.1	105.1	193.8
2	382	42	1823	2247	58	8	93	159	12.2	1.6	6.5	20.3	45.8	6.4	86.5	138.7
3	409	60	1710	2179	58	7	87	152	13.9	1.4	6.0	21.3	44.1	5.6	81.0	130.7
4	574	187	2236	2997	73	28	114	215	16.8	9.8	7.9	34.5	56.2	18.2	106.1	180.5
5	604	104	2608	3316	82	15	130	227	16.4	8.0	9.1	33.5	65.6	7.0	121.3	193.9
6	523	85	1590	2198	76	12	81	169	14.5	5.4	5.6	25.5	61.5	6.6	75.4	143.5
7	382	82	1762	2226	52	12	90	154	11.4	4.1	6.3	21.8	40.6	7.9	83.7	132.2
8	476	156	1754	2386	65	26	89	180	11.7	9.6	5.9	27.2	53.3	16.4	83.1	152.8
9	529	81	1928	2538	67	12	98	177	12.2	4.8	6.8	23.8	54.8	7.2	91.2	153.2
10	464	141	1025	1630	70	26	52	148	12.4	6.2	3.6	22.2	57.6	19.8	48.4	125.8
11	507	182	1755	2444	80	33	90	203	14.8	9.9	6.3	31.0	65.2	23.1	83.7	172.0
12	608	206	1626	2440	76	23	83	182	13.8	5.7	5.8	25.3	62.2	17.3	77.2	156.7
Total	6087	1457	22034	29578	848	224	1073	2145	166.5	74.4	74.4	315.3	681.5	149.6	998.6	1829.7
Avg. per Plant	507	121	1836	2466	70	19	89	179	13.9	6.2	6.2	26.3	56.8	12.8	82.8	152.6
Avg. per sq.m. of leaf area	2013	480	7288	9790	282	75	353	711	55	25	25	104	227	50	328	607

Dry weight minus ash weight

Table 5. Growth Response - In Terms of Total Plant Production by Plants Shaded with 1 Layer of Cheesecloth

Plant	Fresh Weight in Grams				Dry Weight in Grams				Ash Weight in Grams				#Plant Food. Weight in Grams			
	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total
1	465	144	854	1463	62	13	45	120	11.2	4.6	2.9	18.7	50.8	8.4	42.1	101.3
2	460	187	1048	1695	65	25	55	145	14.3	11.8	3.5	29.6	50.7	13.2	51.5	115.4
3	560	116	1495	2171	66	11	78	155	13.2	2.2	4.9	20.3	52.8	8.8	73.1	134.7
4	496	140	1397	2033	56	18	73	147	12.3	6.8	4.6	23.7	43.7	11.2	68.4	123.3
5	657	213	1037	1907	77	35	54	166	16.2	17.5	3.4	37.1	60.8	17.5	50.6	128.9
6	613	280	1009	1902	63	47	53	163	12.6	19.7	3.3	35.6	50.4	27.3	49.7	127.4
7	425	269	942	1636	54	49	50	153	11.8	15.7	3.1	30.6	42.2	33.3	46.9	122.4
8	521	179	873	1573	58	23	46	127	12.7	6.4	2.9	22.0	45.3	16.6	43.1	105.0
9	554	120	1805	2479	61	17	95	173	18.3	3.4	6.0	27.7	42.7	13.6	89.0	145.3
10	458	147	1132	1737	52	20	59	131	15.6	5.0	3.7	24.3	36.4	15.0	55.3	106.7
11	563	248	1709	2520	75	38	90	203	18.7	19.8	5.7	44.2	56.3	18.2	84.3	158.8
12	502	231	1308	2041	69	38	69	176	18.6	11.4	4.3	34.3	50.4	26.6	64.7	141.7
Total	6274	2274	14609	23157	758	334	767	1959	175.5	124.3	48.3	348.1	582.5	209.7	718.7	1510.9
Avg. per Plant	522	189	1217	1928	63	28	64	163	14.6	10.3	4.0	29.0	48.5	17.5	59.8	125.8
Avg. per sq.m. of leaf area	1670	605	3894	6169	201	89	204	499	46	33	13	93	155	56	191	406

\# Dry weight minus ash weight

Table 6. Growth Response - In Terms of Total Plant Production by Plants Shaded with 2 Layers of Cheesecloth

Plant	Fresh Weight in Grams				Dry Weight in Grams				Ash Weight in Grams				#Plant Food, Weight in Grams			
	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total	Tops	Roots	Fruit	Total
1	692	155	726	1573	79	21	40	140	21.3	4.2	2.4	27.9	57.7	16.8	37.6	112.1
2	414	132	885	1431	55	16	49	120	17.6	3.2	2.9	23.7	37.4	12.8	46.1	96.3
3	492	120	983	1595	54	15	54	123	11.3	2.7	3.3	17.3	42.7	12.3	50.7	105.7
4	480	199	945	1624	68	23	52	143	19.0	5.1	3.1	27.2	49.0	17.9	48.9	115.8
5	495	77	933	1505	64	9	51	124	15.4	1.6	3.1	20.1	48.6	7.4	47.9	103.9
6	476	142	1016	1634	60	18	56	134	18.0	4.5	3.4	25.9	42.0	13.5	52.6	108.1
7	540	124	878	1542	56	13	48	117	16.8	2.3	2.9	22.0	39.2	10.7	45.1	95.0
8	582	87	510	1179	69	12	28	109	13.8	2.1	1.7	17.6	55.2	9.9	26.3	91.4
9	616	91	892	1599	78	11	49	138	17.2	2.6	2.9	22.7	60.8	8.4	46.1	115.3
10	539	32	849	1420	62	5	47	114	13.0	1.2	2.8	17.0	49.0	3.8	44.2	97.0
11	434	68	1327	1829	57	7	73	137	13.7	1.4	4.4	19.5	43.3	5.6	68.6	117.5
12	554	35	875	1464	58	6	48	112	19.1	2.7	2.9	24.7	38.9	3.3	45.1	87.3
Total	6314	1262	10819	18395	760	156	595	1511	196.2	33.6	35.8	265.6	563.8	122.4	559.2	1245.4
Avg. per Plant	526	105	902	1533	63	13	50	126	16.4	2.8	3.0	22.1	45.3	10.2	46.6	103.8
Avg. per sq.m. of leaf area	1300	259	2230	3790	156	32	121	312	40	7	7	54	116	25	114	258

\# Dry weight minus ash weight

In accordance with expectations, increases in light available for carbohydrate formation showed a greater quantity of fresh, dry, ash and plant food weights in the average case. The rate of photosynthesis was slowed up according to the amount of light reduction in each block. The differences in light intensity appeared to have less effect on the ash content of the plants, but are in a rather definite relation with the average results on the fresh, dry and plant food weights in all parts of the plants. The plant food manufactured per unit leaf area is greatest under the no shade condition and is reduced according to the amount of shade the plants receive. This efficiency in food manufacture seems to have a definite effect on the plant material used in fruit production and is in approximately the same ratio as the average decreased plant efficiency where shaded. It would seem from this information that differences in light intensity during the seasons of the year are the direct causes for variations in plant efficiency in growth and fruit production, but Plant 10 in Table 4, Plant 11 in Table 5, and Plant 11 in Table 6 are practically equal in their efficiency under each respective condition. This appears to indicate that plant variation is responsible for some of the differences in photosynthetic activity under the different light intensities.

Environmental Conditions.

The experimental aim, as stated earlier, was to have the same length of day (14 hours) for the three lots of plants, while having them exposed to three different light intensities. Light measurements were made daily, at two hour intervals, throughout the period of growth, by means of a Clements Photometer. The data for these measurements are presented in Table 7.

Table 7. Light Intensity for Plants under the Different Treatments

Month	Average Daily Light Intensity per Hour, in Apparent Foot Candles			Total Hours Daylight	#Total Foot Candle-Hours			Percentages No Shade = 100		
	No Shade	1 layer Cheese-cloth	2 layers Cheese-cloth		No Shade	1 layer Cheese-cloth	2 layers Cheese-cloth	No Shade	1 layer Cheese-cloth	2 layers Cheese-cloth
Mar. 1 - 31 incl.	532	251	114	434	230888	108934	49476	100	47.2	21.4
Apr. 1 - 30 incl.	980	497	212	420	411600	208740	89040	100	50.7	21.5
May 1 - 31 incl.	1133	591	246	454	514382	268314	111684	100	51.9	21.7
June 1 - 30 incl.	1872	973	468	459	859248	446607	214812	100	52.1	25.0
July 1 - 3 incl.	1774	892	355	46	81604	41032	16330	100	50.2	20.0
Daily Average During Crop Growth	1139.9	583.1	261.0							
Total for Producing Crop				1813	2,097,722	1,073,627	481,342			

Daily Average Intensity x Number of Hours

It is clear, from examination of Table 7, that the gradations of light intensity, established in the beginning by means of shading, maintained with close approximation, as the season advanced and ended. While the general intensity of the sunlight increased gradually for all, the three experimental conditions of full intensity, one-half intensity, and one-fourth intensity, continued to hold and to be effective.

General correlation of these controlled variations in light intensity - previously shown with the differences in growth responses of the three lots of plants - is obvious. The relationship is itself negative in character for leaf area, and stem elongation, and positive for fruit production, and total plant production. In order to facilitate inspection, certain figures from the preceding tables are brought together in Table 8.

Table 8. The Relationship of Light Intensities to Growth Responses of the Plants

Light Intensity	Total Foot-Candle-Hours of Light (Table 7)	Average Leaf Area Per Plant in sq.cm. (Table 1)	Average Height of Plant in cm (Table 2)	Total Weight Fruit in gm. (Table 3)	Total Fresh Weight of Plants in gm. (Tables 4, 5, 6)
Unshaded	2097722	4385	81	22034	29578
1 Layer Cheesecloth	1073627	5559	102	14607	23157
2 Layers Cheesecloth	481342	7072	117	10819	18395

However, the association which is apparent in Table 8 can have validity only in case certain other factors which are known to condition the photosynthetic rate, and consequently, growth, remained sufficiently constant during the experimental period. Table 9 gives data respecting three such factors, - these being the principal ones which required consideration and attempted control.

Table 9. Air Temperature, Soil Temperature, and Relative Humidity, during Growth Period

Month	Air Temperature Degrees F.									Soil Temperature Degrees F.								
	No Shade			1 Layer Cheesecloth			2 Layers Cheesecloth			No Shade			1 Layer Cheesecloth			2 Layers Cheesecloth		
	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.
March	73	56	62	82	58	66	80	58	67	62	62	62	66	61	63	72	60	64
April	88	55	65	86	55	66	86	56	66	63	60	62	67	60	64	70	60	66
May	86	55	66	90	55	67	90	55	66	63	60	62	69	60	63	74	60	66
June	98	46	73	95	48	71	95	48	71	65	58	62	76	59	66	82	53	74
July	106	55	76	100	54	73	102	56	70	67	59	63	77	60	71	82	65	74

Month	Relative Humidity								
	No Shade			1 Layer Cheesecloth			2 Layers Cheesecloth		
	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.	Max.	Min.	24 hr. Avg.
March	76	40	61	80	41	65	80	41	62
April	83	32	64	84	38	73	84	38	65
May	84	27	68	90	42	79	84	30	72
June	84	30	68	90	34	75	84	30	73
July	91	28	63	85	30	72	84	30	70

These three factors are relatively uniform for each block of plants. The variations of these factors in the three treatments is probably regulated somewhat by the light intensity. This light intensity variation has evidently accounted for the plant growth responses under each condition, and the effects of the other environmental conditions are regulated by this light.

Daily Periods of Measurement:

The data which have been presented show, beyond doubt, a relationship between the behavior of the plants and the different light intensities under which they grew and matured. The evidence, however, is general in nature and not such as to be adequate for those mathematical processes which yield quantitative expressions of correlation.

The plant materials manufactured by the plants on 12 dates, spread over the period of growth, were determined on seven periods during each of the days. This procedure for estimating the photosynthetic activity was that termed the Modified Sachs Method. It consisted of taking two square centimeters of foliage from each plant every two hours in sample bottles and weighing in the fresh condition. These small discs of the leaves were then heated in the oven at 70°C. for 12 hours and then at 95°C. for six hours, when they were reweighed. After drying they were put in crucibles and ashed, and again reweighed. The dry weight minus the ash weight was the amount of photosynthesized product in each sample. Correction for respiration and translocation was determined by adding the average loss in weight per two hours during the night to the difference in weight of the two hour samples during the day.

Light in each block of plants was measured at two hour intervals with a Clements Photometer in which solio paper is used, and comparisons made with a standard. On days when photosynthetic activity was determined, the Macbeth illuminometer was also used in order to get readings in actual number of foot-candles. The data are presented in Tables 10, 11, and 12.

Table 10. Photosynthate and Light Intensities for Unshaded Plants

Date	Variables	Period of Day						
		4-8 A.M.	8-10	10-12	12-2 P.M.	2-4	4-6	6-8
April 7	Photosynthate	1.60	1.46	0.16	2.16	4.20	1.40	1.64
	Light Intensity	200	400	444	387	256	139	87
April 24	Do	1.12	1.11	1.60	2.96	5.84	2.44	0.36
	Do	606	1200	1411	2408	2314	1207	117
April 29	Do	1.64	3.06	3.06	4.08	1.24	2.28	1.60
	Do	732	1464	2553	2553	1445	806	337
May 5	Do	1.48	1.46	1.44	1.60	1.76	0.56	0.27
	Do	212	424	393	394	287	116	87
May 13	Do	1.06	1.06	1.44	2.64	0.88	0.72	0.34
	Do	237	446	286	1285	2408	2408	337
May 14	Do	1.28	1.40	2.00	3.96	1.68	1.80	0.36
	Do	1164	2078	2409	2503	1800	687	140
May 23	Do	2.48	1.80	0.76	1.84	7.84	1.24	1.68
	Do	1206	2172	2588	2937	2730	1376	736
May 24	Do	1.52	3.20	4.96	1.32	2.92	1.76	1.60
	Do	637	1230	2499	2435	2100	1350	736
June 9	Do	3.76	3.32	2.76	6.04	3.00	2.92	1.96
	Do	739	1369	2533	2855	2344	964	674
June 15	Do	1.84	1.40	2.76	4.88	2.96	2.76	2.16
	Do	100	186	277	278	944	910	121
June 16	Do	1.88	2.76	5.44	7.20	5.12	1.60	1.40
	Do	210	330	3480	3906	3773	3039	1674
June 17	Do	4.03	2.64	1.52	9.20	5.12	1.60	1.08
	Do	940	1734	1503	3155	4235	3115	1769
Average	Photosynthate	1.89	2.05	2.32	3.99	3.54	1.75	1.20
	Light Intensity	582	1086	1520	2091	2053	1426	578

Table 11. Photosynthate and Light Intensities for Plants Shaded with 1 Layer of Cheesecloth

Date	Variables	Period of Day						
		4-8 A.M.	8-10	10-12	12-2 P.M.	2-4	4-6	6-8
April 7	Photosynthate	1.00	0.76	0.16	0.28	3.44	1.44	0.36
	Light Intensity	100	202	246	236	128	49	24
April 24	Do	1.00	1.06	1.36	1.28	2.16	2.80	0.80
	Do	337	648	768	1245	1135	544	49
April 29	Do	0.92	1.60	1.72	1.84	1.84	2.00	0.60
	Do	462	739	1182	1281	813	739	247
May 5	Do	1.42	0.88	1.60	1.04	1.60	0.12	0.16
	Do	104	241	187	187	136	83	64
May 13	Do	0.80	0.60	1.80	1.32	0.52	0.24	0.28
	Do	106	207	182	677	1163	1231	187
May 14	Do	1.00	1.64	1.60	1.16	1.72	0.88	0.16
	Do	737	1207	1251	1409	914	352	47
May 23	Do	1.68	1.48	0.16	1.28	1.32	1.12	0.04
	Do	737	894	1191	1113	1113	689	306
May 24	Do	1.68	2.24	1.48	1.04	1.52	0.96	0.40
	Do	331	532	1170	1180	1259	532	306
June 9	Do	0.76	0.12	1.16	0.32	1.20	2.48	0.16
	Do	312	692	1069	1424	1177	409	394
June 15	Do	0.40	1.06	1.40	2.36	1.28	2.24	0.04
	Do	100	153	128	157	476	451	86
June 16	Do	1.46	2.74	0.12	2.64	2.40	1.28	0.40
	Do	96	823	1793	1946	1891	1562	815
June 17	Do	4.12	2.28	2.80	4.20	4.96	2.08	0.18
	Do	431	586	796	1025	2124	1515	815
Average	Photosynthate	1.35	1.37	1.28	1.56	1.91	1.47	0.29
	Light Intensity	321	577	830	990	1024	679	279

Table 12. Photosynthate and Light Intensities for Plants Shaded with 2 Layers of Cheesecloth

Date	Variables	Period of Day						
		4-8 A.M.	8-10	10-12	12-2 P.M.	2-4	4-6	6-8
April 7	Photosynthate	0.52	0.44	1.12	.00	2.08	1.24	0.32
	Light Intensity	87	92	104	148	96	45	16
April 24	Do	0.20	0.44	0.72	1.24	2.60	2.68	0.40
	Do	92	341	354	684	578	257	26
April 29	Do	0.20	1.32	1.68	1.32	1.20	1.68	0.40
	Do	141	371	600	661	407	303	124
May 5	Do	0.16	0.12	0.60	1.16	1.24	1.00	0.32
	Do	109	116	101	75	72	37	24
May 13	Do	0.46	0.32	0.36	0.76	0.24	0.24	0.28
	Do	83	123	99	384	561	647	90
May 14	Do	0.36	0.20	0.64	0.72	0.44	0.56	0.26
	Do	361	683	630	754	456	106	24
May 23	Do	0.68	1.56	0.28	1.08	2.80	1.44	0.40
	Do	337	491	573	602	520	297	152
May 24	Do	1.12	0.96	1.28	0.72	2.76	1.04	0.32
	Do	113	225	552	519	635	225	147
June 9	Do	0.60	0.06	0.16	0.84	0.88	1.48	0.56
	Do	185	386	548	760	680	230	155
June 15	Do	0.20	0.86	0.40	3.20	1.40	0.72	0.28
	Do	40	90	91	85	238	213	107
June 16	Do	0.60	0.37	0.20	3.24	1.36	1.36	0.16
	Do	40	490	937	951	946	744	521
June 17	Do	4.20	2.52	1.04	1.83	4.04	1.32	0.10
	Do	261	276	467	524	1080	784	521
Average	Photosynthate	0.77	0.76	0.70	1.34	1.75	1.23	0.32
	Light Intensity	154	307	421	512	522	324	158

The source of energy for the plant world is sunlight and it evidently regulates the amount of plant food manufactured according to its intensity as is demonstrated in Tables 10, 11, and 12. It appears that this carbon assimilation changes gradually or violently in relation to the variation in light intensity received by the plants.

The unshaded plants show that a greater amount of light is necessary for each gram of photosynthate manufactured. Furthermore, the amounts of plant food appear to increase until 12-2 P.M. when the light intensity reaches it maximum and then decreases at a relatively similar rate with the light. Differing from this, the plants shaded show a slower increase in food manufacture relative to the light increase until the 2-4 P.M. period, when they reach the maximum, and then they decrease more rapidly in ratio with the light intensity. Greater reduction in light shows a more gradual increase in photosynthesis and there appears to be an accumulation of plant food over a longer period, or a lagging in photosynthate manufacture, when the light is decreased due to heavy shading. This appears to result in the plants exposed only to light of low intensities having a much lower basal metabolism than no shade plants. The simple coefficients of correlation for photosynthate and light: $r = .5454 \pm .0527$; $r = .3012 \pm .0681$ and $r = .3034 \pm .0679$ demonstrate the importance of the light to the plant food manufacture under the no shade condition as compared with shaded plants.

While temperature and humidity are similar or relatively uniform for the three lots of plants, it varied the same for each, as the day advanced. Naturally, this would be expected to be true, due to their relationship to light intensity and its variation. Consequently, data on temperature and humidity were taken for each of the two hour periods. The simple coefficients of correlation for photosynthate and temperature: $r = .2968 \pm .0681$; $r = .1924 \pm .0725$; and $r = .1704 \pm .0727$ signify that the temperature is in close relation with the light intensity and probably is intercorrelated with it. Their being lower than those for light demonstrates their slighter importance in photosynthetic activity.

The simple correlation coefficients for photosynthate and humidity: $r = -.2099 \pm .0714$; $r = -.4955 \pm .0565$; and $r = -.3377 \pm .0663$ indicates that humidity is possibly too high for proper plant food manufacture. Their negative character signifies that the high humidity might have a tendency to hinder photosynthesis and the higher the negative correlation the greater it is reduced. This appears to be one of the contributing causes of lower plant food manufacture when the plants are shaded.

Correlation Coefficients.

In order to measure the direct effect of light intensity on photosynthesis, it is necessary to know how much the other environmental factors affect photosynthesis and the relation between all these factors. It appears that the true value of this relationship cannot be obtained directly from the raw figures, but an analysis of the data must be completed in order to determine the numerical measurements. This analysis will show the relative importance of the variation in each of these independent variables on the variation in the dependent variable and can best be demonstrated by the correlation coefficients given in Table 13.

Table 13. Correlation Coefficients for Photosynthate and Environment

r 0 order				r 1st order				r 2nd order				R Multiple			
Subscript	Coefficient			Subscript	Coefficient			Subscript	Coefficient			Subscript	Coefficient		
	No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth		No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth		No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth		No Shade	1 Layer Cheese-cloth	2 Layers Cheese-cloth
12	.5454 ±.0527	.3012 ±.0681	.3034 ±.0679	12.3	.4872 ±.0571	.2421 ±.0309	.2600 ±.0698								
				12.4	.5421 ±.0528	-.0372 ±.0748	.1595 ±.0728	12.34	.5266 ±.0541	.0236 ±.0747	.1711 ±.0727				
13	.2968 ±.0681	.1924 ±.0721	.1704 ±.0727	13.2	.0009 ±.0749	-.0049 ±.0749	-.0087 ±.0749								
				13.4	.2203 ±.0716	-.1436 ±.0733	.0173 ±.0748	13.24	.1025 ±.0741	-.1452 ±.0733	.0649 ±.0745				
14	-.2099 ±.0714	-.4955 ±.0565	-.3377 ±.0663	14.2	.1716 ±.0727	-.4179 ±.0618	-.2235 ±.0717								
				14.3	-.0197 ±.0748	-.4927 ±.0567	-.3002 ±.0678	14.23	.2021 ±.0718	-.4457 ±.0600	-.2348 ±.0708	1.234	.5695 ±.0505	.5108 ±.0553	.3731 ±.0644

X_1 = Photosynthate
X_2 = Light intensity
X_3 = Temperature
X_4 = Humidity

A. No Shade Plants.

The zero order coefficients seem to show a much greater relationship between X_2 and X_1 than between X_3 and X_1 or X_4 and X_1. The relationship between X_3 and X_1 and X_4 and X_1 are questionable because of the possibility of their being obscured by the relationships between the independent variables. Because of this we have separated the effects of the independent variables in order to get the first order coefficients. This separation tends to confirm the tentative conclusions reached with the zero order coefficients. (That the major relationship is that between X_1 and X_2). The conclusions appear to be still slightly questionable because only two of the independent variables have been considered at a time. Because of this we shift to the second order coefficients. This demonstrates that when we consider the effect of variation in light intensity alone (both temperature and humidity being constant), we can explain 27.7% of the variation in photosynthate, while variation in temperature explains but 1% and variation in humidity explains but 4% of the photosynthate variation. The coefficient of multiple correlation shows that the three factors taken together explain 32.4% of the photosynthate variation. Light intensity alone, as we have seen, accounts for 27.7%, showing that temperature and humidity are neglible factors in photosynthesis except where they are correlated with light intensity.

B. One Layer of Cheesecloth Plants.

It appears that the humidity is too high for proper use of light by the plant in photosynthesis. The humidity is consistently higher in this block of plants than in the other blocks. (Table 9). This may account for the reduction in photosynthate as compared with the no shade block of plants. The correlation coefficients demonstrate this fact in every case.

C. Two Layers of Cheesecloth Plants.

The humidity is evidently too high for the plants to utilize light at the best advantage. It appears that light intensity is possibly too low even at the best for proper food manufacture. The total effect of light, temperature and humidity in this block of plants explained only 13.9% of the photosynthate variation which is about one-half that of the no shade plants. This demonstrates that some other factors, that were not taken into consideration, probably have a definite effect on the photosynthetic activity.

Supplementary Consideration: Chlorophyll Content.

The relation of radiation to pigmentation is of very great importance through the necessity of light for the formation of pigments, and due to the fact that the pigments absorb radiant energy which is essential for the photosynthetic activity of the plants. The naturally occuring plant pigments, which are found in the cell structure of the plant foliage are chlorophyll, carotin and xanthophyll. These pigments per unit leaf area were determined for each group of plants, at several periods during the experiment. The modified Willstätter and Stoll method of extraction (22) was used for these determinations and the comparison with a standard was made with the DuBosc Colorimeter.

The data are given in Table 14.

Table 14. **Foliage Pigments**

	No Shade	1 Layer Cheesecloth	2 Layers Cheesecloth
	Chlorophyll - Mgm. per sq. cm.		
April 15	.0368	.0255	.0189
April 15	.0379	.0257	.0189
May 10	.0477	.0353	.0114
May 10	.0468	.0377	.0125
June 17	.0474	.0309	.0110
June 17	.0487	.0392	.0177
June 21	.0401	.0302	.0187
June 21	.0391	.0300	.0186
Total	.3455	.2545	.1277
Average	.0432	.0318	.0159
	Xanthophyll - Mgm. per sq. cm.		
April 15	.0024		
April 15	.0028		
May 10	.0020	.0015	.0008
May 10	.0024	.0014	.0008
June 17			
June 17			
June 21	.0028	.0017	.0010
June 21	.0028	.0014	.0012
Total	.0152	.0060	.0038
Average	.0025	.0015	.0009
	Carotin - Mgm. per sq. cm.		
April 15	.0014	.0014	.0010
April 15	.0017	.0012	.0010
May 10	.0014	.0011	.0006
May 10	.0011	.0011	.0006
June 17			
June 17			
June 21	.0013	.0011	.0006
June 21	.0012	.0010	.0006
Total	.0081	.0069	.0044
Average	.0013	.0011	.0007

It appears that light intensity is essential for proper chromogenesis in the tomato foliage. According to expectations, the no shade plants contain more chlorophyll per square centimeter in leaf area, and the shaded plants showed a variation according to the amount of light the plants received. The reduction in photosynthate manufacture due to shading is relatively proportional to the amount of chlorophyll per square centimeter of leaf area, although this reduction does not affect the chlorophyll efficiency, but it does appear to affect the total plant food manufacture.

Leaf Anatomy. - The internal leaf structure is, in general, an adaptation to the conditions necessary for photosynthesis. Consequently, the six plates demonstrate the modifications of palisade and spongy parenchyma that assist in the plant food manufacture under the existing shaded conditions.

Explanation of Plates

Plate I. A cross section of one of the leaves growing with no shade. This section was made April 30. The cell development under this condition of light has elongated palisade cells, heavy epidermis and cuticle and a thick mass of spongy parenchyma cells with a rather small amount of air space.

Plate II. A cross section of one of the leaves growing with no shade. This section was made June 17. The palisade cells have become much more elongated, chloroplasts appear to have changed, the spongy parenchyma cells are decreased and the air spaces have become more plentiful. This leaf apparently shows the effects of age.

Plate III. A cross section of one of the leaves growing under one layer of cheesecloth. This section was made April 30. The palisade cells are somewhat elongated, chloroplast are arranged full length of them, spongy parenchyma cells are rather scattered, with a large amount of air space throughout the leaf.

Plate IV. A cross section of one of the leaves growing under one layer of cheesecloth. This section was made June 17. The epidermis and cuticle has increased as the leaves become older. The palisade layer remains about the same, but the spongy parenchyma cells have increased in number as the plant gets older.

Plate V. A cross section of one of the leaves growing under two layers of cheesecloth. This section was made April 30. The epidermis, cuticle, and in fact, the entire leaf appears rather thin. The palisade layer of cells is somewhat poorly organized and not elongated as when the leaves receive a higher degree of light intensity. The spongy parenchyma cells are fairly well developed with a large amount of air space between them. The chloroplast are in much smaller number than as shown in the previous plates.

Plate VI. A cross section of one of the leaves growing under two layers of cheesecloth. This section was made June 17. The cuticle, and epidermis have increased somewhat in thickness, but the general thickness of the leaf remains about the same as the previous plate. The palisade cells have become somewhat more elongated as the leaf gets older and the air space seems to have increased in quantity.

Plate I. 250x

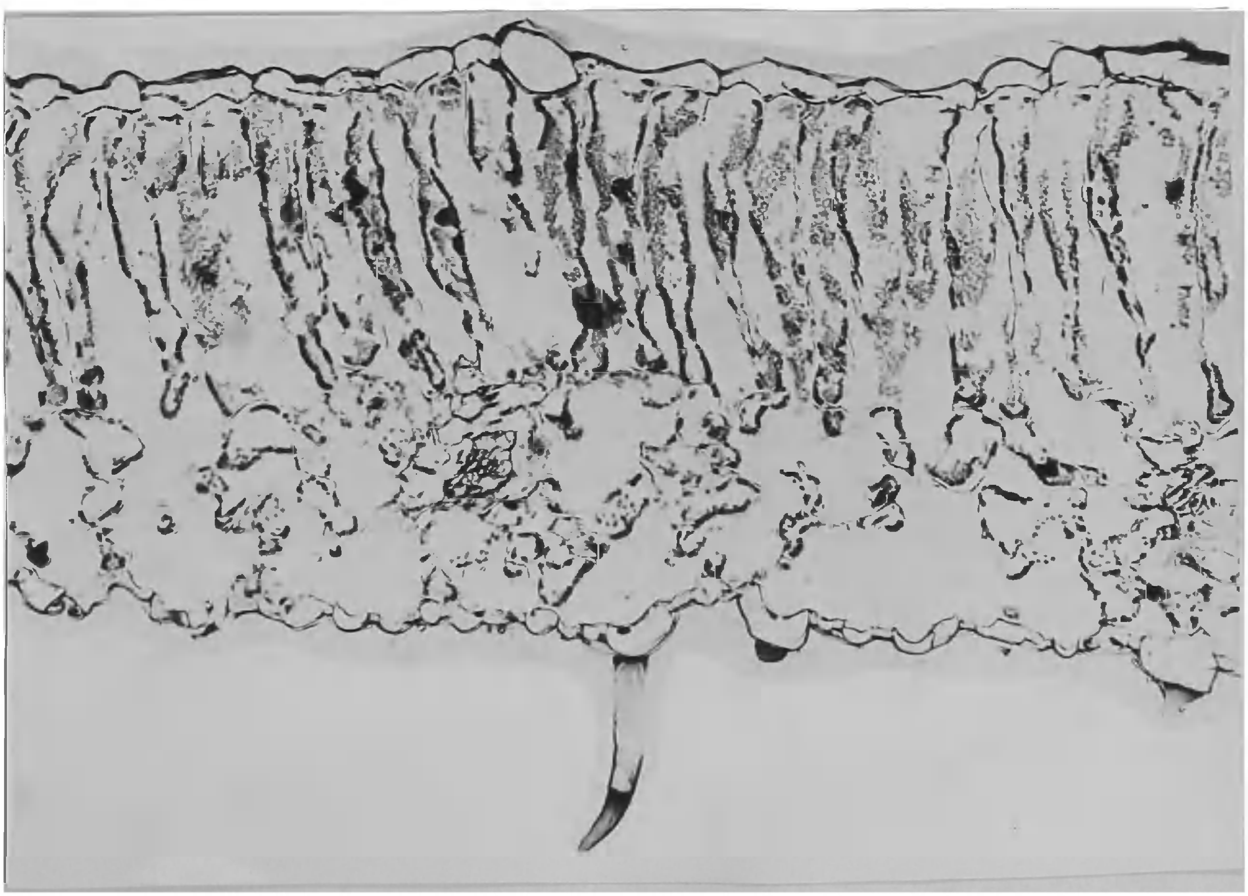

Plate II. 250x

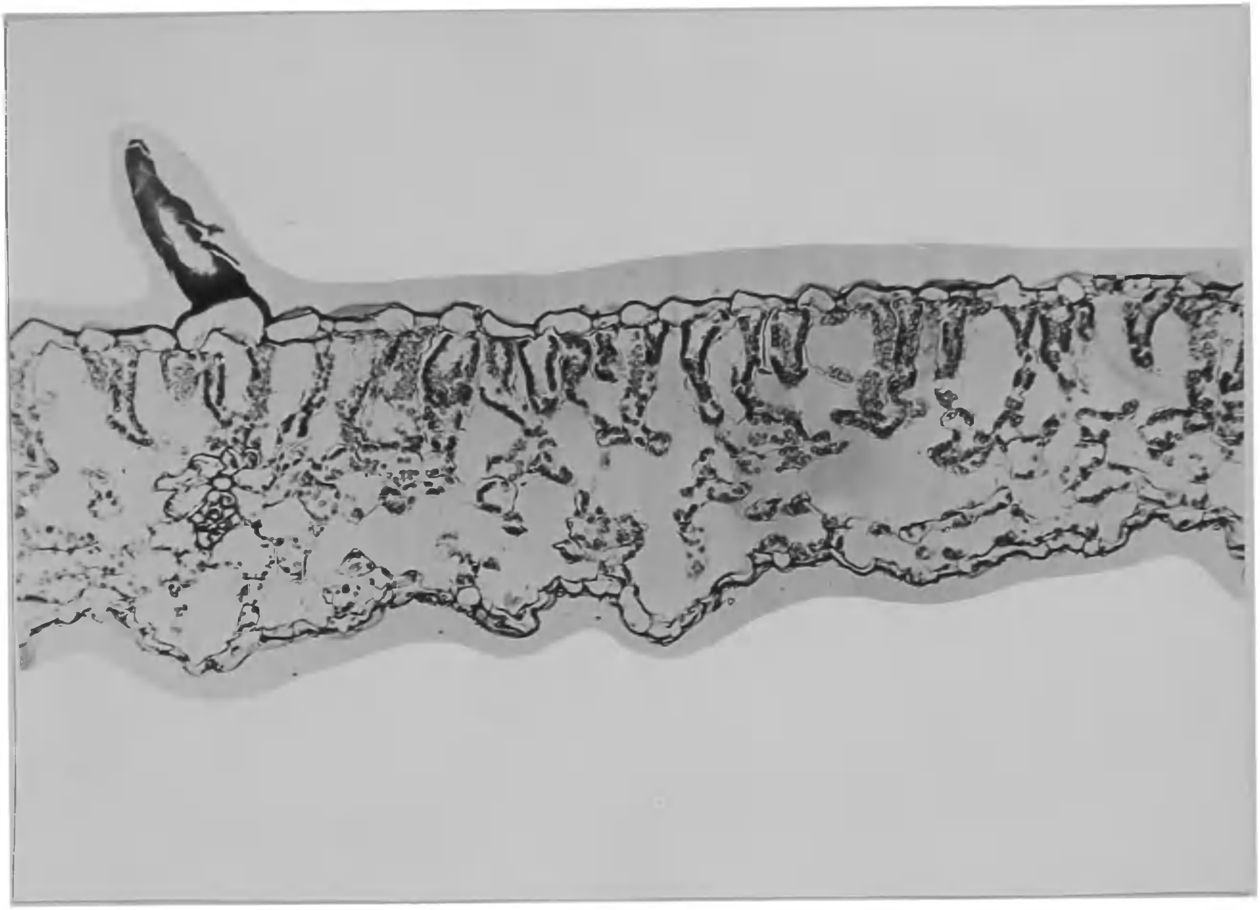

Plate III. 250x

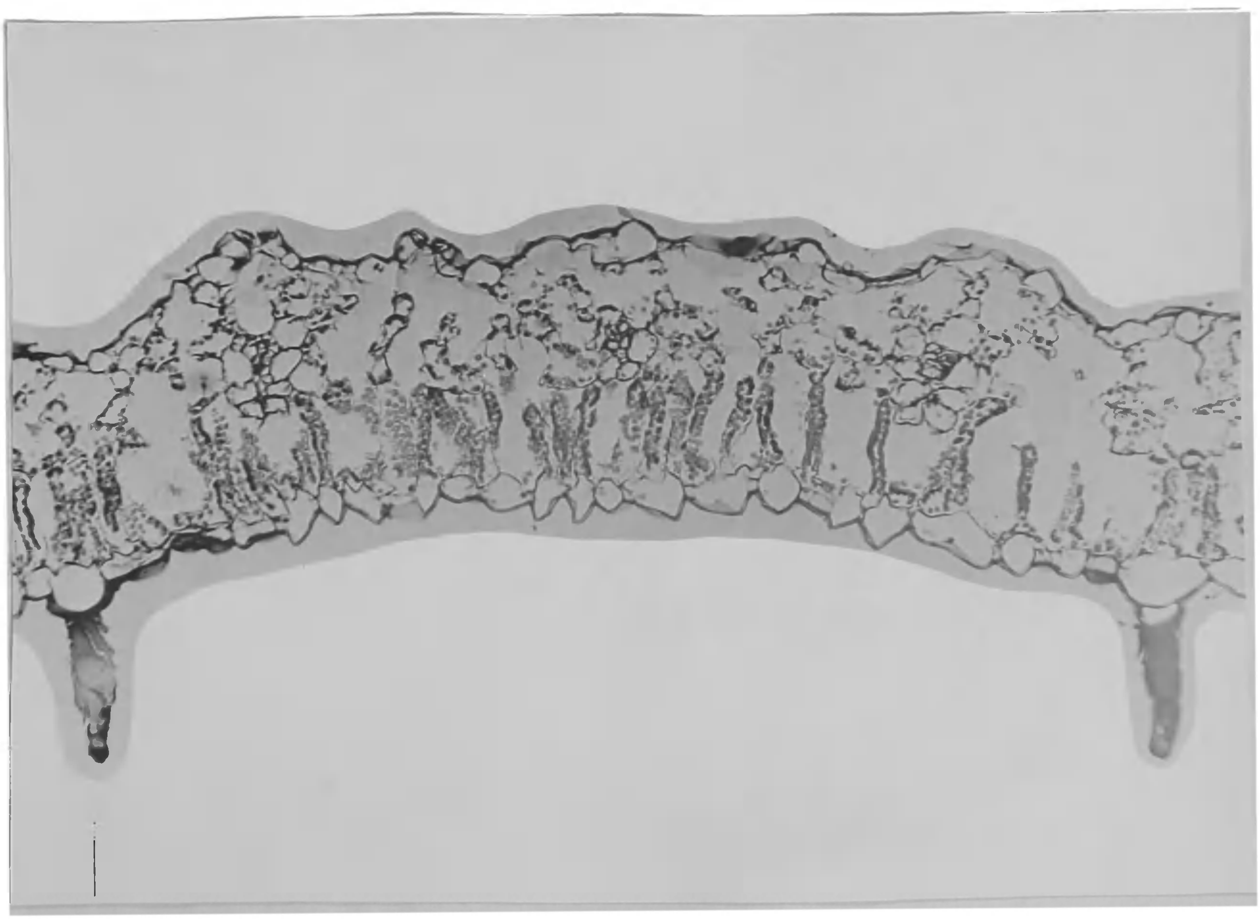

Plate IV. 250x

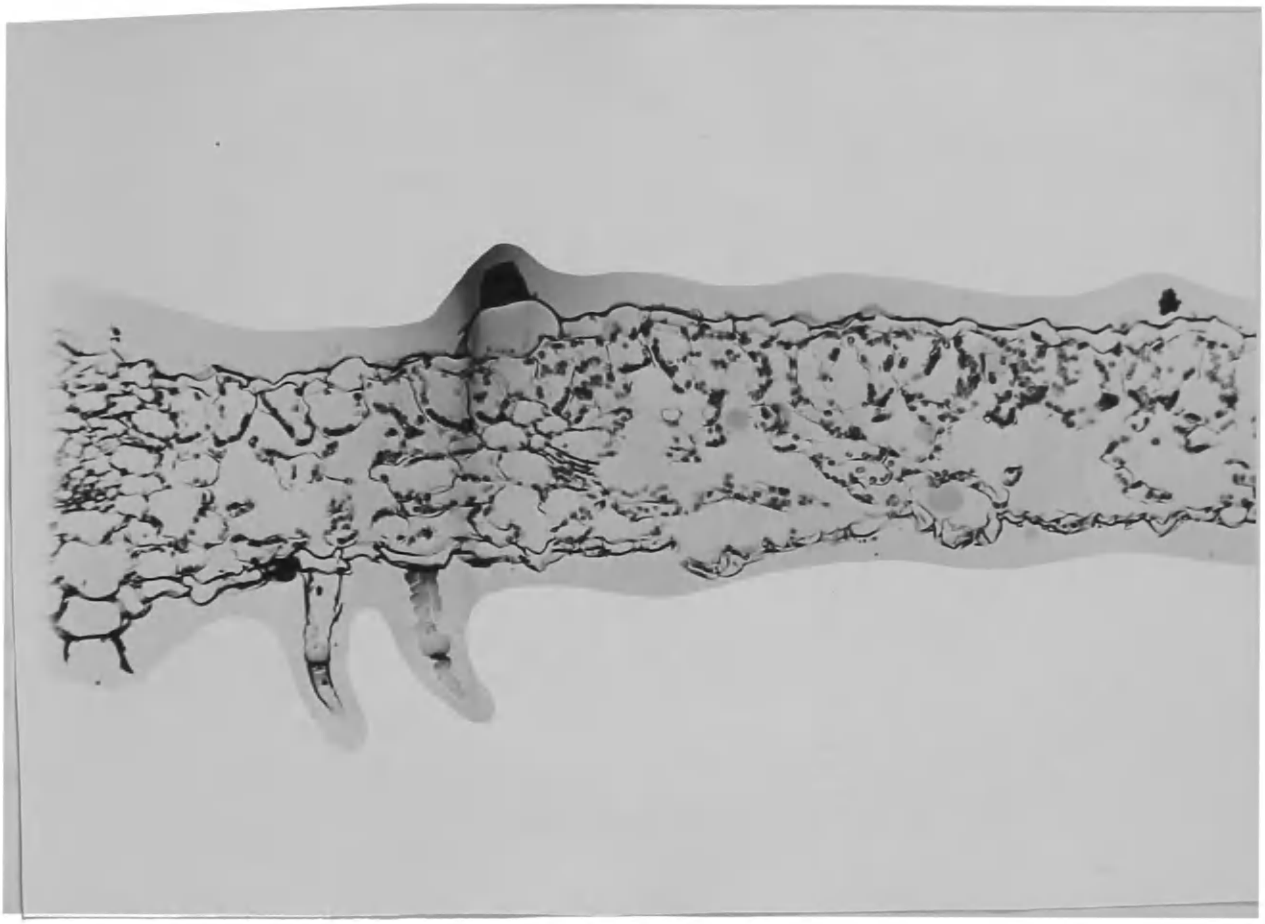

Plate V. 250x

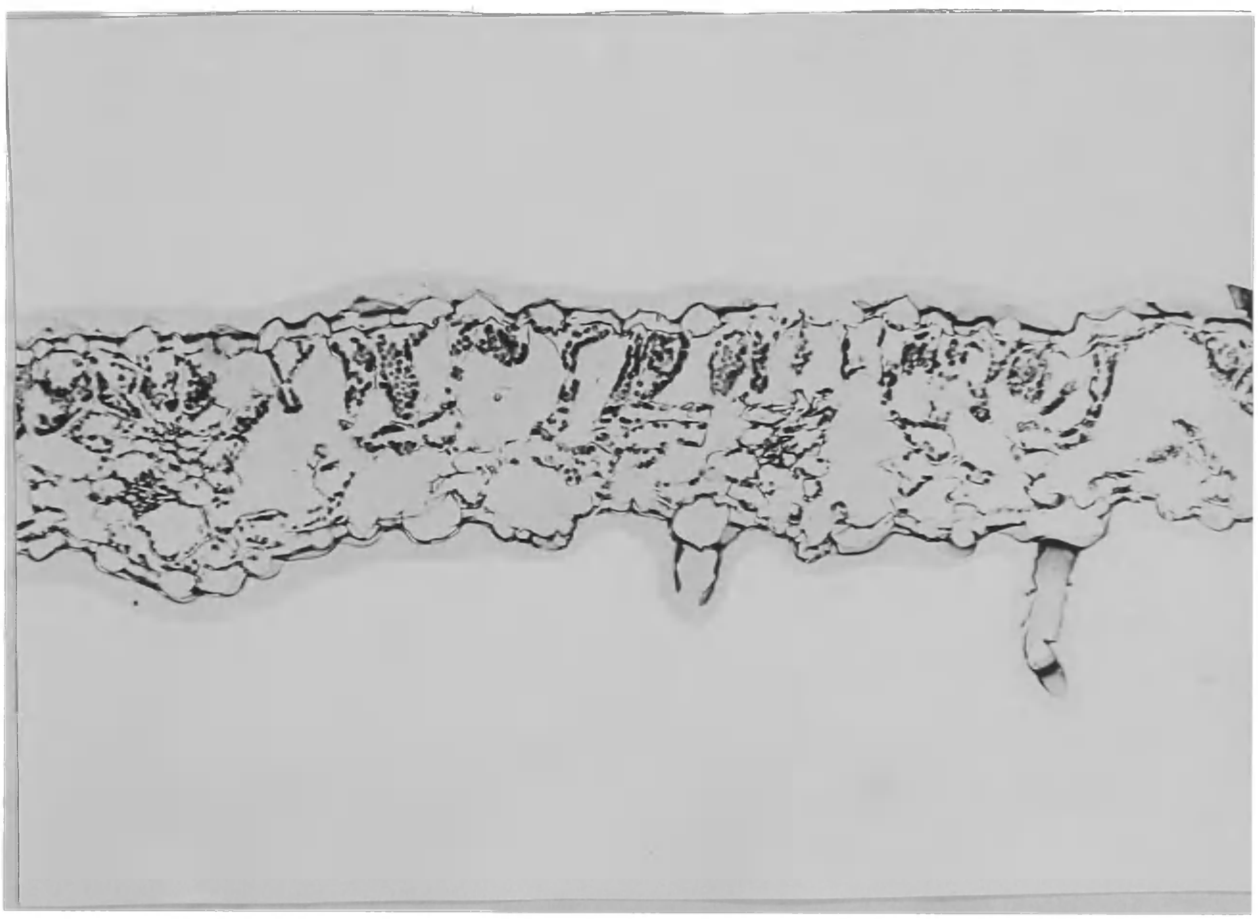

Plate VI. 250x

In general, the cell development of the leaves under the no shade condition is normal, but when shaded the cells in the spongy parenchyma lack regularity in shape and are arranged loosely, so that a large part of their surface is exposed to the intercellular spaces. The greater the shade, the less the palisade parenchyma cells are developed. This demonstrates how the number of palisade layers and the density of the cell structure depends largely, either directly or indirectly, upon light intensity.

These supplementary factors are rather definitely regulated by the amount of light received by the plants, and this appears to be in order with the variation of photosynthetic activity. When the plants are exposed to the no shade condition the palisade cells are well developed and their chloroplasts seem to arrange themselves so as to decrease the surface and transpiration due to the light, but when shaded they are differently arranged so as to increase the surface for receiving light. This latter arrangement appears to increase the chloroplasts' efficiency, and the greater the light reduction the more it is increased. It appears that the reduction in photosynthetic rate did not have an effect on the chloroplast efficiency. As previously stated, the light seems to have a regulatory effect on the chloroplast content and cell structure of the leaves, and this is one of the contributing causes for a decreased photosynthetic activity by the plants when shaded.*

* The cells of the upper part of the thick leaf in the no shade group removes enough red and violet light rays to reduce the effectiveness on the lower leaf cells, but this blocking effect is not as apparent in the thin shaded leaves.

DISCUSSION

This study has dealt primarily with the influence of light intensity on photosynthetic activity of tomato plant leaves, as measured by amount of growth, fruit production, and increases in fresh and dry weights. The results show, as would be expected, that on the whole there is a close relationship between these several factors, viz: with decreased light intensity there is: (a) greater vegetative growth, as measured by leaf area, and both fresh and dry weight of tops and roots, (b) decreased fruit production, and (c) a decrease in the total amount of photosynthate produced by the plants. However, the increase in vegetative growth and the decreases in fruit production and total photosynthate produced are not directly proportional to the decreases in light intensity. Thus, reducing light intensity by a half resulted in only approximately a one-fourth increase in amount of vegetative growth, a one-third decrease in fruit production, and a one-sixth decrease in total photosynthate production. Reducing light intensity to approximately one-fourth normal resulted in only a 40 percent increase in vegetative growth, a one-half decrease in fruit production and a one-third decrease in total photosynthate production. (Table 15). This is but another way of saying that the partially shaded leaves used their limited supply of light more efficiently than the unshaded leaves used their normal supply. That is, a given quantity of light effected a greater

Table 15. Plant Efficiency

	Shading	Fruit per plant Number	Fresh weight of fruit per plant Grams	Leaf area per plant Sq. cm.	Plant food weight per plant Grams	Leaf area necessary for producing each gram of plant food per plant Sq. cm.	Total foot-candle hours of light received during season Intensity x Hours
Table 4 Plant 5	No shade	32	2608	5436	193.9	28.0	2,097,722
Plant 10	No shade	11	1025	4176	125.8	33.2	"
Average for 12 plants	No shade	22.5	1836	4563	152.6	29.2	"
Table 5 Plant 1	1 layer cheesecloth	9	854	5115	101.3	50.5	1,073,627
Plant 11	1 layer cheesecloth	22	1709	6193	158.8	38.9	"
Average for 12 plants	1 layer cheesecloth	17.0	1217	5559	125.8	44.1	"
Table 6 Plant 11	2 layers cheesecloth	14	1327	5642	117.5	48.1	481,342
Plant 12	2 layers cheesecloth	9	875	7566	87.3	86.6	"
Average for 12 plants	2 layers cheesecloth	11.8	902	7072	103.8	68.2	"

photosynthate production in the case of the shaded plants than was true in the case of those unshaded.

Great, however, as were the differences between the growth rates, leaf areas, and fruit and photosynthate production of the several groups of plants exposed to the different light intensities, there were equally great differences, between different plants within the same group, in their apparent ability to utilize their light supply for fruit and photosynthate production. Indeed, some of the individuals (e.g. No. 11) in the moderately shaded group produced nearly as much photosynthate per unit of leaf area as some of those in the unshaded group and one of those in the heavily shaded group (No. 11) produced nearly as much photosynthate per unit of leaf area as the average of those in the moderately shaded group and within 30 percent as much as some of the least efficient in the unshaded group (Table 15).

This latter fact is of especial significance for it suggests the possibility of developing a strain of plants that has a high degree of photosynthetic efficiency under conditions of low light intensity. Obviously, the producer of indoor-grown tomatoes has no control over light intensity - at least he has no practicable means of increasing it. However, if he can obtain that which is especially adapted to the low light intensities and short days of the northern winter season, a substantial contribution will have been made to the solution of the problem of profitably growing tomatoes in the greenhouse during the winter. Little or no effort has thus far been directed toward developing such a physiological strain of tomatoes, present stocks apparently being heterozygous in this respect. The studies here reported point clearly to some of the possibilities that lie in this direction.

SUMMARY

The effect of light intensity on the photosynthetic efficiency of tomato plants was studied by growing Grand Rapids Forcing tomato plants under three different daily average light intensities of 1139.9, 583.1, and 261.0 foot candles. The results were as follows:

1. The responses in stem elongation and leaf area expansion were both continuously and finally the greater when the light intensity was reduced, showing a negative relationship.

2. It was indicated that when the light intensity reached a definite average the fruit would set rather freely and develop.

3. The percentages of dry matter, ash material, water, fresh weight and elaborated food materials correlate rather closely with the light intensity received by the plants. Light intensity variation is the chief cause of differences in plant efficiency.

4. Basal plant metabolism and its contributing factors are regulated by the amount of light received by the plants.

5. The increase in the multiple correlations (when the elaborated food materials are the dependent variable and light

intensity, humidity, and temperature are the independent variables) over the simple correlations under each degree of light intensity is evidence that there is interrelation between factors regulating the plant food manufacture. The coefficients of determination demonstrate that light intensity alone accounts for 32.4% of the photosynthate variation and that temperature and humidity are neglible factors only when correlated with light intensity, - humidity becoming a critical factor in photosynthesis when the light intensity is reduced.

6. The light intensity appeared to have a regulatory effect on the average amounts of chlorophyll per square meter of leaf area. The chloroplasts in the leaves arranged themselves so as to get the greatest amount of light when it was reduced.

7. The leaf anatomy shows abnormal cell development when the plants are shaded. This abnormality consists of loosely arranged, irregular spongy parenchyma cells and a reduction in size, density and number of palisade cells.

8. It is evident that light intensity averaging 1139.9 foot-candles daily during the growth of the tomato plants had a greater effect in promoting chlorophyll formation, fruit production and photosynthetic efficiency than light of a daily average of 583.1 foot-candles and this in turn had a similar greater effect than that on the plants receiving a daily average light intensity of 261.0 foot-candles.

LITERATURE CITED

1. Arthur, John; J. Guthrie, and J. Newell. Some effects of artificial climates on growth and chemical composition of plants. Amer. Jour. Bot. 17:416-482. 1930.

2. Combes, R. Determination des intensités lumineuses optima pour les végétaux aux divers stades du developpement. Ann. Sci. Nat. Bot., 9:ser.; 11. 75-254. 1910.

3. DeBesteriro, D. C. and M. Durand. Influence de la lumière sur l'absorption des matières organiques du sol par les plantes. Compt. rend. acad. sci. Paris 198. 467-70. 1919.

4. Emerson, Robert. The chlorophyll factor in photosynthesis. Amer. Nat. 64:252-260. 1930.

5. Folmer, Swith. Researches on the influence of natural and artificial light on plants. Meldinger Fra Norges Landbruckshoiskole. 13:1-5. 1933.

6. Hayden, A. The ecologic foliage anatomy of some plants of a prairie province in central Iowa. Amer. Jour. Bot. 6:69-87. 1919.

7. Johnson, E. S. The functions of radiation in the physiology of plants. Smithsonian Misc. Coll. 87(14):1-15. 1932.

8. Kostytschew, S. und H. Kardo-Syssoiewa. Untersuchungen über den tagesverlauf der photosynthise in Zentralasien. Zeitschr. Wiss. Biol. Planta 61:117-143. 1930.

9. Lubimenko, V.N. Sur la sensibilité de l'appareil chlorophyllien des plantes ombrophiles et ombrophobes. Rev. Gén. Bot. 17:381-415. 1915. (Cited in Palladin-Livingston Plant Physiology. Phila. P. Blakiston's Son & Co. 1923).

10. MacDougal, D. T. Influence of light upon growth and development. Carnegie Institution of Washington Yearbook. 14:16. 1915.

11. Muntz, M. A. La luninosité et l'assimilation végétale. Compt. rend. acad. sci. (Paris). 156:(5) 368-370. 1913.

12. Nightingale, G. T. and J. W. Mitchell. Effects of humidity on metabolism in tomato and apple. Plant Physiology 9:217-236. 1934.

13. Osterhout, W.J.V. Experiments with plants. 3rd Ed. N. Y. 1906.

14. Palladin, V.I. Plant Physiology. (Ed. by B. E. Livingston) 2nd Amer. Ed. Phila.: P. Blakiston's Son & Co. 1923.

15. Poole, James P. Comparative anatomy of leaf of cycads with reference to Cycadofilicales. Bot. Gaz. 76:203-241. 1923.

16. Porter, A. M. The influence of defoliation and fruit thinning on the growth of tomatoes. Unpublished thesis. Mich. State College. 1932.

17. Popp, H. W. The effect of light intensity on the growth of soy beans and its relation to the autocatalyst theory of growth. Bot. Gaz. 82:306. 1926.

18. Shibata, S. The daily growth rate of bamboos. Jour. Coll. Sci. Tokyo 1900. Trans. in Am. Jour. Bot. 12:384-392. 1925.

19. Spoehr, H. A. Photosynthesis. Chem. Cat. Co. New York. 1926.

20. Sprague, H. B. and J. W. A study of the relations between chloroplast pigments and dry weights of tops in dent corn. Pl. Physio. 4:165-192. 1929.

21. Wiesner, J. Sur l'adaptation de la plante à l'intensité de la lumière. Compt. rend. acad. sci. (Paris) 138:1346-1349. 1904.

22. Willstätter, R. and A. Stoll. Untersuchungen über chlorophyll. Berlin 1913.

23. Willstätter, R. and A. Stoll. Untersuchungen über die Kohlensäure Assimilation. Berlin 1918.

24. Yoshii, Y. Untersuchungen über die Temperatur abhängigkeit der Kohlensaure Assimilation bei bohnen. Zeitschr. Wiss. Biol. Planta 56:81-695. 1928.