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GROWTH OF PEAS IN WATER CULTURE
UNDER VARIOUS LIGHT EXPOSURES

THESIS FOR THE DEGREE OF PH. D.

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GROWTH OF PEAS IN WATER CULTURE UNDER

VARIOUS LIGHT EXPOSURES

by

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THESIS

1

GROWTH OF PARS IN WATER CULTURE UNDER
VARIOUS LIGHT EXPOSURES

1. Carbohydrate-Nitrogen Relationships

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Introduction

A voluminous literature has grown up on the subject of the balance between the organic constituents in plants. The greater part of the evidence has supported the hypotheses advanced by Kraus and Kraybill (13), but not all the results have substantiated their views. The tendency has been to employ radical treatments, especially as regards control of nitrogen supply, conclusions being advanced on comparisons between a very low and a very much higher level of nitrate nitrogen in the culture medium. Such wide differences of treatment were perhaps necessary in order to prove or disprove the soundness of the primary hypothesis. However, in the present work, it was considered advisable to keep the nitrogen supply within the same order

(1) The writer is indebted to Dr. R. F. Hibbard, Michigan State College, for patient guidance during the course of the experiments. He is further indebted to Dr. H. F. Clements, Washington State College, for suggestions in the planning of the work, and to Dr. P. J. Anderson for permission to complete the necessary analytical work in the laboratory of the Tobacco Sub-station, Connecticut Agricultural Experiment Station.

of magnitude in all cultures. The employment of differential water cultures of the same total osmotic concentration permitted this control, as well as that of the other nutrient materials.

The use of several light exposures was a necessary complement to this study, in view of the well-established effect of light duration on growth and reproduction.

Historical

The literature on water cultures has been thoroughly reviewed by a number of writers, among others by Tottingham (26), Shive (22), Hoagland (10) and Hibbard (2) and (9). In view of the divergence of theme under which workers have published, it hardly seems necessary to enlarge on the general literature. A great variety of salt combinations have been developed, but the simplest and the one most widely used at the present time is that of Shive (23). It has been shown by McHargue (16), Somner and Lipman (24), Brenchley (3), Maze (18) and others that plants require very small amounts of various elements. The requirements for such elements as aluminum, zinc, chlorine, manganese, silicon, iodine, boron and perhaps others are so small that they are usually supplied by impurities in the chemicals used, or by dissolution from containers. This very interesting phase of plant nutrition was touched upon only incidentally in the present work.

The exhaustive studies of Garner and Allard (5), (6), (7), on light effects in plants have been extended by Nightingale (19), (20), Maximov (17), McClelland (15), Tincker (25), and Manser (27). A recent publication of Arthur, Guthrie and Howell (1) summarizes the greater part of this work. The last named authors also attempted to control other climatic factors, such as moisture, temperature,

carbon dioxide concentration of the air, as well as the intensity, quality and duration of light. The generalization that an increase of light period brings about an increase in carbohydrate content and a decrease in nitrogen content is so well established by different workers with various plants that it barely needs repetition.

Plan of Experiment

The experiments of Clements (4), reported in 1928, were performed in the same laboratory as the present work, and it was with a view toward testing some of his conclusions that the following experiments were initiated. He used the triangular system of Tottingham (26) and Shive (23), growing single cultures of 40 plants in three gallon crocks. His most important conclusion was that the supply of potassium has a very marked influence on nitrogen assimilation, at least under longer light exposures. In order to test this finding, it was decided to use the same salt combination, KH_2PO_4 , $\text{Ca}(\text{NO}_3)_2$, and MgSO_4 , and grow duplicate cultures in selected culture solutions. The following were chosen as being representative of different portions of the triangle, as well as giving different combinations of potassium and nitrogen, under the conditions recommended by Livingston (14).

Table 1.

Differential Culture Solutions, Type 1

Osmotic Concentration, 1 atm.

Solution Number	Molecular Proportions			Partial Volume Molecular Proportions		
	KH_2PO_4	$\text{Ca}(\text{NO}_3)_2$	MgSO_4	KH_2PO_4	$\text{Ca}(\text{NO}_3)_2$	MgSO_4
1-1-6	1	1	6	.0027	.0027	.0161
1-6-1	1	6	1	.0020	.0122	.0020
2-2-4	2	2	4	.0049	.0049	.0099
3-3-2	3	3	2	.0068	.0068	.0045
5-1-2	5	1	2	.0123	.0024	.0049

In addition to the salts employed above, small amounts of iron, manganese and boron were added to the culture solutions. Preliminary tests showed that 2.2-4.0 p.p.m. iron in ferric tartrate, 0.66-2.0 p.p.m. boron in boric acid, and 0.55-2.0 p.p.m. manganese in manganous chloride were the optima, and the lower amounts were used in subsequent experiments.

The culture solutions were changed once a week. Transpiration losses were made up by the addition of distilled water during the latter part of the growing period. The cultures were aerated for a period of two hours every day.

Light exposures of ten, thirteen and seventeen hours were chosen as representing the range of light period under which normal growth might be expected. The longer periods were in part artificial light, the ten cultures of each group being arranged under a battery of lights suspended five feet above the greenhouse benches and supplying 2000 watts at 110 volts. Measurements of light intensity were not made, as the duration of light has been found by Garner et al (7) to be the most significant factor, provided the intensity is not too low. However, comparison of illumination per unit area, as used in these experiments, with that employed by Arthur et al (1) would indicate that the intensity was quite high.

No water screens between the lights and the plants were available, but the heating effect was not noticeable. As the plants grew taller, the lights were raised.

The 10 hour plants received only solar light, altered, of course, by the glass of the greenhouse. These cultures were grown in large wooden boxes which were fitted with light tight covers and ventilated by a shutter arrangement similar to that employed in photographic dark rooms. The period of illumination of these cultures was 8 A. M. to 6 P. M.

The 13 hour plants were protected from the artificial light source of the 17 hour plants by curtains of fine weave, black cambric cloth. These curtains were drawn around the bench at the end of the 13 hour period and withdrawn early in the morning.

Knott's Excelsior field peas, obtained from the Michigan State Farm Bureau, Lansing, Michigan, were used throughout the experiments. They were found to be an excellent type for this work, having a sturdy growth habit and flowering freely. Before being placed in the germinator the seeds were sterilized in 1-250 formalin for 20 minutes, washed in tap water and soaked for a few hours. They were then placed between layers of moist paper towelling in a large galvanized iron pan. After about three days a uniform lot of the more vigorous

seedlings with roots measuring one inch in length was selected for the experiment. These selected seedlings were fitted into perforated corks each of which held five plants. The three gallon culture jars were fitted with perforated aluminum covers, each of which held eight corks, making a total of 40 plants per culture.

In the first two series, the seedlings which were damaged in handling were replaced during the first few days of the experiment. In the final series a number of extra corks were prepared and allowed to remain in contact with tap water until the experiment had progressed about two days when replacement of corks not having a complete stand was made. By the latter technique, a somewhat more uniform stand was obtained.

The chemical analyses made in connection with this work were only on the tops and pods and were as follows: Nitrate nitrogen, total nitrogen not including nitrates, simple sugars, sucrose, starch and hemi-cellulose. Physical measurements included top length in centimeters, green weight of tops (and pods when found), dry weight of tops, roots and pods.

Chemical Methods

In order to obtain comparable results, the chemical methods for carbohydrates and total nitrogen not including nitrates (organic nitrogen) were the same as those reported by Clements (4). All samples for carbohydrate analyses were preserved in alcohol to which a small quantity of ammonium hydroxide was added to neutralize plant acids. A laboratory experiment with ripe tomato pulp showed that this base was much preferable to calcium carbonate especially when the latter was used in excess of requirements to neutralize plant acids.

The Nevada method for nitrate nitrogen was tried but gave such unreliable results that it was soon discarded. The impossibility of preventing the breakdown of the simpler nitrogenous compounds such as amino-acids, and amides, and the consequent high results, renders the method worthless for plant material. The modification of the Gilbert method by Holtz and Larson (11) gave very good results. All figures reported are on a dry-weight basis.

Experimental Results

Series I was started on March 13, 1928 and ran until May 14, 1928, a period of nine weeks. Blossoms appeared under 17 hour light three weeks after transplanting of the seedlings. Both the longer light periods produced pods abundantly and at the time of harvest the pods were beginning to ripen. The short light plants blossomed toward the end of the period, but developed only a very few pods. Control of the temperature in the greenhouse was not difficult during these months, and culture conditions were generally satisfactory. It was necessary to use "Lemon Oil Spray" to control red spiders in the greenhouse and to give the cyanide treatment for white flies and aphids. The plants were not at any time seriously affected by these insects.

Series II ran from June 13, 1928 to July 31, 1928 a period of seven weeks. Due to the higher air temperature in the greenhouse at this time, the plants matured more rapidly, and the uniformity of plants in a single culture was not as satisfactory. The light intensity was also higher at this later time, and this apparently had some effect on the growth in height and carbohydrate content of the plants.

In Series III it was decided to limit the experiment to 10 and 13 hour light periods, to have treatments in

triplicate and to terminate the experiment when the plants were vegetatively developed but had not set fruit. The cultures were started May 14, 1929 and ran until June 12, 1929, a period of four weeks. At this season of the year, the days were long enough to omit the use of artificial light for any part of the 13 hour period.

The average top length was usually greatest in the solutions supplying the highest proportion of nitrates, indicating the greater tendency for vegetative growth with a more liberal supply of nitrates. The dry weight of tops was highest with high nitrates in an equal number of groups but not in the same cultures in every case.

In order to establish the relative value of the various treatments in dry weight production, the total dry weight per plant, exclusive of pods, was reduced to a ratio, taking the best treatment in each group as unity. These ratios are given in the last column of tables 2, 3, and 4.

Table 2

PHYSICAL MEASUREMENTS OF PEAS GROWN IN WATER CULTURE.

Series I.

Treatment(1)	Ave. top length in centimeters	<u>Ave. dry wt. per plant in gms</u>			Dry(2) Weight Ratio
		Tops	Roots	Pods	
<u>17 hours light</u>					
1-1-6	52.5	.8363	.1860	.6390	.80
1-6-1	52.5	1.0865	.2774	.7719	1.00
5-1-2	47.0	.7649	.1904	.5500	.70
3-3-2	51.6	.9184	.2755	.6210	.87
2-2-4	45.5	.6216	.1559	.5206	.57
<u>13 hours light</u>					
1-1-6	50.8	.7886	.1535	.4051	.70
1-6-1	50.6	.8404	.1817	.3264	.76
5-1-2	49.9	.9025	.2349	.3704	.85
3-3-2	53.9	.9300	.3826	.4315	.98
2-2-4	50.8	1.0812	.2527	.5277	1.00
<u>10 hours light</u>					
1-1-6	39.0	.4537	.1058		.67
1-6-1	45.6	.7007	.1361		1.00
5-1-2	33.5	.4195	.1066		.62
3-3-2	40.8	.4984	.1429		.76
2-2-4	41.5	.4402	.1506		.71

(1) Culture solution, Shive's 1.00 atmosphere. 1st figure $\text{KH}_2(\text{PO}_4)$, 2nd figure $\text{Ca}(\text{NO}_3)_2$, 3rd figure MgSO_4 .

(2) Dry weights of tops and roots, but not of pods, were computed to a ratio by giving the highest weight in the group the value of 1.00, and reducing others to decimal parts of this value.

Table 3

PHYSICAL MEASUREMENTS OF PEAS GROWN IN WATER CULTURE.

Series II

Treatment(1)	Ave. top length in centimeters	<u>Ave. dry wt. per plant in gms</u>			Dry(2) Weight Ratio
		Tops	Roots	Pods	
<u>17 hours light</u>					
1-1-6	36.5	.6640	.0962	.1854	.71
1-6-1	38.8	.9160	.1456	.2703	1.00
5-1-2	36.3	.7541	.1328	.2105	.83
3-3-2	39.7	.8785	.1297	.1171	.94
2-2-4	34.4	.7158	.0979	.1248	.76
<u>13 hours light</u>					
1-1-6	33.3	.5183	.0824	.0578	.75
1-6-1	42.0	.7092	.0896	.1000	1.00
5-1-2	39.0	.6612	.1152	.0567	.97
3-3-2	36.9	.6142	.0898	.1153	.89
2-2-4	31.0	.4919	.0792	.0828	.77
<u>10 hours light</u>					
1-1-6	21.3	.2759	.0337		.31
1-6-1	24.2	.2296	.0400		.70
5-1-2	24.3	.2604	.0527		.79
3-3-2	25.3	.3313	.0624		1.00
2-2-4	23.5	.2233	.0467		.68

(1) Culture solution, Shive's 1.00 atmosphere. 1st figure $\text{KH}_2(\text{PO}_4)$, 2nd figure $\text{Ca}(\text{NO}_3)_2$, 3rd figure MgSO_4 .

(2) Dry weights of tops and roots, but not of pods, were computed to a ratio by giving the highest weight in the group the value of 1.00, and reducing others to decimal parts of this value.

Table 4

PHYSICAL MEASUREMENTS OF BEANS GROWN IN TANK CULTURE.

Series III

Treatment(1)	Ave. top length in centimeters	<u>Ave. dry wt. per plant in gms</u>		Dry(2) Weight Ratio
		Tops	Roots	
<u>13 hours light</u>				
1-1-6	24.6	.3386	.0830	.89
1-6-1	32.4	.3832	.1012	1.00
5-1-2	30.0	.3275	.0936	.86
3-3-2	30.6	.3526	.0939	.92
2-2-4	25.4	.3327	.0785	.84
<u>10 hours light</u>				
1-1-6	24.3	.2609	.0604	.92
1-6-1	25.7	.2758	.0722	1.00
5-1-2	20.3	.2368	.0624	.86
3-3-2	22.8	.2760	.0657	.98
2-2-4	24.7	.2500	.0614	.89

From these ratios it can be seen that solution 1-6-1 was the best in six out of eight groups, while solution 3-3-2 was second best in the same number of cases. The remaining three treatments were all distinctly inferior. A weighted average of these ratios shows that solution 3-3-2 was 98.9% as efficient as solution 1-6-1 in production of dry weight. Both of these solutions are the highest in

- (1) Culture solution, Shive's 1.00 atmosphere. 1st figure $KH_2(PO_4)$, 2nd figure $Ca(NO_3)_2$, 3rd figure $HgSO_4$.
- (2) Dry weights of tops and roots, but not of pods, were computed to a ratio by giving the highest weight in the group the value of 1.00, and reducing others to decimal parts of this value.

calcium nitrate of those employed. Solution 5-1-2, high in potassium, produced 36.9% of the dry weight of the 1-3-1 treatment, while 1-1-6 and 2-2-4, both high in magnesium, each produced 83.2%. Under the conditions employed, a high supply of calcium nitrate was the most favorable for vegetative growth.

Results of carbohydrate analyses of Series I, tops, are shown in Table 5. The term "tops", as used in this paper, includes stems, petioles, and leaves, and does not include pods. It was not possible to separate the aerial parts and secure samples large enough for analysis. All carbohydrates are computed to d-glucose using Munson and Walker's table (2).

The figures presented here are the average of the duplicate cultures, with duplicate determinations of each sample. Thus each entry represents the average analysis of a group of 20 plants.

As an aid to interpretation of the results, the ratio system was again employed. Ratios were computed upon the total sugars (sum of the simple sugars and sucrose), total non-sugars (sum of starch and hemicellulose) and total carbohydrates.

In this series, the culture solutions supplying a high proportion of magnesium sulphate were the most efficient in promoting the elaboration of sugars. This

was true in all light exposures, the only discrepancy being in the 2-2-4 treatment in 17 hour light. Solution 5-1-2, high in potassium, was not as efficient as the magnesium group, while the solution high in calcium nitrate was only 70 per cent as high in total sugars as the 1-1-6 treatment.

In the formation of more stable carbohydrate compounds, the most efficient solution was found to be the high potassium treatment. Altho it did not consistently lead in all light exposures, the average of the ratios for all light treatments placed it in the fore. Solution 1-6-1, was again the least efficient, while the magnesium treatments were consistently good.

In a study of the total carbohydrates, the most striking difference is the low total content in solution 1-6-1, as may also be seen graphically in Figure 1. (In this graph it was necessary to select some one salt and arrange the treatments so as to show the gradations with respect to that salt. The amount of $\text{Ca}(\text{NO}_3)_2$ in the culture solutions decreases from left to right.) Because of the superiority of the magnesium treatments in the production of sugars and the potassium treatments in the transformation of sugars into non-sugars, the two groups were about equally effective in maintaining a high total carbohydrate level.

The influence of potassium on carbohydrate elaboration has been quite thoroughly reviewed by Jannsen and Bartholomew (12). They found that the potassium concentration in the culture medium influenced the production of carbohydrate. However, an examination of their data discloses that only the absence of potassium, or its presence in the lowest concentrations, had any appreciable effect in lowering the percentage of carbohydrates in the plant. The findings of Hightmole, Schenckhorn and Robbins (21) were that carbohydrates may accumulate in potassium-deficient plants. Within the range of treatment employed in the present experiments, an increase in supply of potassium had only the effect of increasing the amount of polysaccharides found, although it is evident from the work cited that more radical effects would attend its complete absence.

It is quite apparent from Figure 1 that the duration of light was the most significant factor in determining the general level of carbohydrate storage in the plant. This is in agreement with work of Arthur et al (1), Garner et al (7), and others (19), (20), (22).

Table 5 also presents the results of organic and nitrate nitrogen determinations in this series. The nitrate nitrogen is at a much lower level than Clements (4) found in his work, due entirely to the difference in

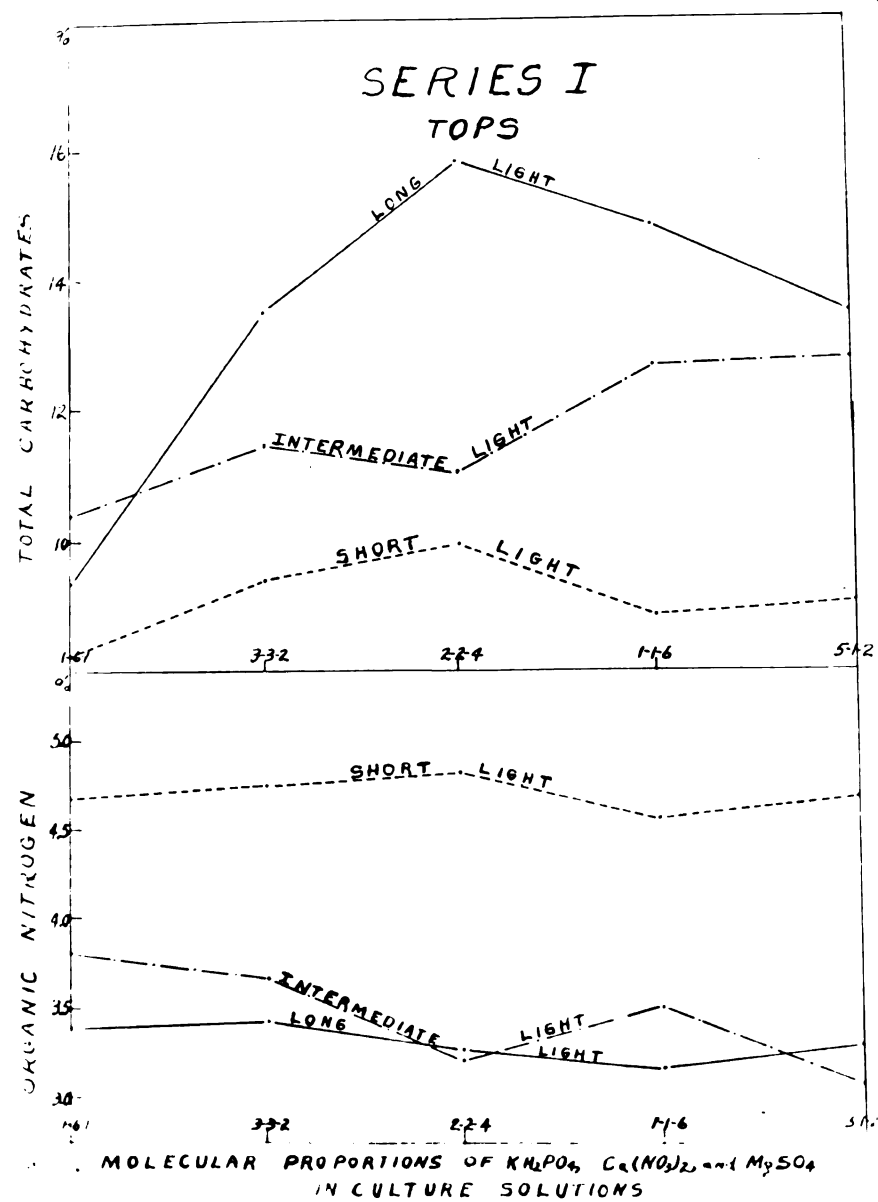


Fig. 1. Carbohydrate and nitrogen content of tops in Series I.

analytical methods. The only values of the data on nitrate nitrogen are to indicate the reserve supply in the plant, over and above the amount it is able to elaborate. It is naturally much higher under short light conditions.

The content of organic nitrogen was entirely inconsistent with the supply of nitrogen in the medium. From figure 1 it might be assumed that in the longer light durations there was some diminution of organic nitrogen as the supply of nitrates became limited, but this is barely more than the limits of experimental error.

The light duration seems to be the most important factor in determining the level of nitrogen assimilation. There is no evidence of a correlation between potassium supply and organic nitrogen synthesis.

Table 6 and figure 2 deal with the solids produced under 17 hours and 13 hours light in this series. This table is of interest because it shows the high level of carbohydrate content in the partly mature fruit but it fails to disclose any consistent relationships with treatment. Here again solution 1-6-1 has the lowest total carbohydrates in 13 hour light, while high potassium leads in longer light. It is evident that the content of organic nitrogen is not affected by nutrient treatment or light exposure.

Table 3

CONTENT OF CARBOHYDRATE AND NITROGEN IN THE TISSUES OF PS

Series I

Treatment	Simple Sugars	Sucrose	Starch	<u>Percentage on dry weight basis</u>			
				cellu- lose	total Carbohy- drates	amino Nitrogen	Nitrate Nitrogen
				<u>17 hours light</u>			
1-1-6	6.13	11.04	6.56	9.79	33.52	3.06	.010
1-6-1	4.93	10.25	7.25	9.02	32.20	3.43	.021
5-1-2	5.41	12.30	8.31	9.58	35.60	3.01	.006
3-3-2	7.22	11.51	5.95	8.30	32.40	3.13	.017
2-2-4	5.63	11.88	6.94	9.22	32.67	3.51	.005
<u>13 hours light</u>							
1-1-6	9.83	10.23	4.17	9.50	34.43	3.12	.010
1-6-1	5.33	5.95	3.26	9.78	24.32	2.95	.088
5-1-2	5.04	7.44	7.11	8.50	28.09	3.24	.014
3-3-2	7.00	10.07	5.07	7.53	29.67	3.62	.070
2-2-4	6.03	13.13	2.79	10.30	32.30	3.19	.027

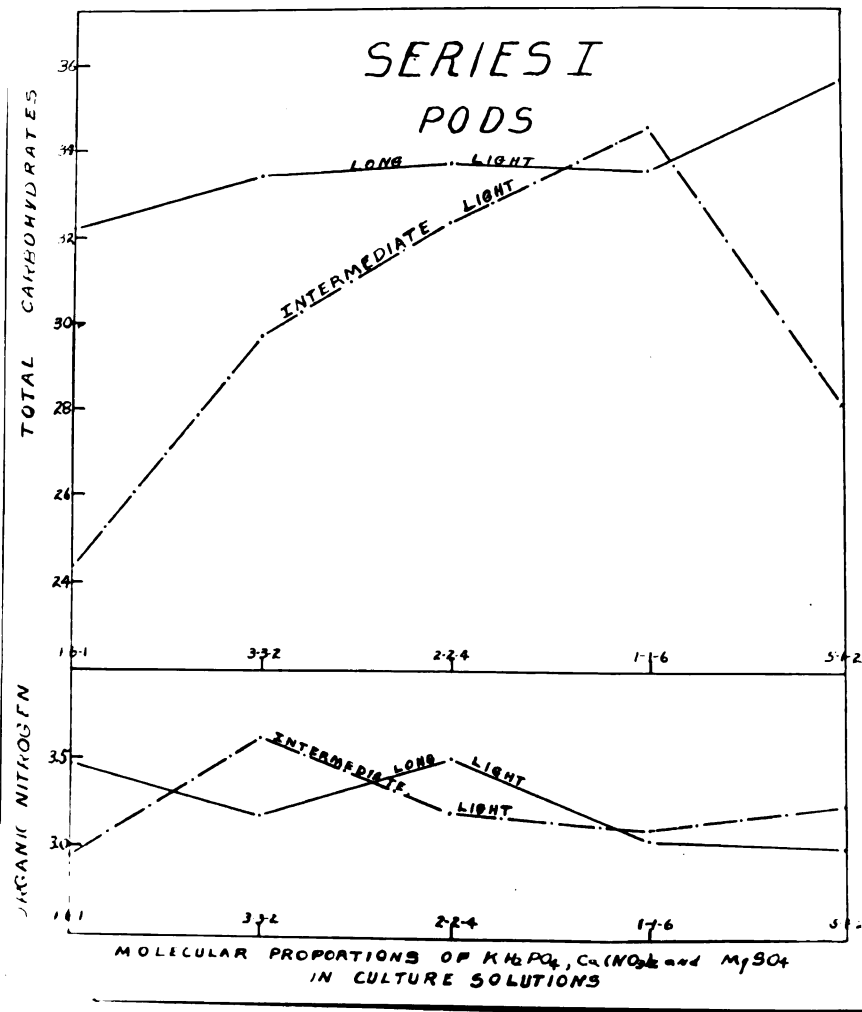


Figure 2. Graph showing carbohydrate and nitrogen content of pods in Series I.

Series II was a repetition of Series I, as far as the outline of the experiment was concerned. No analyses of pods were made. Starch and hemicelluloses were analyzed separately, but are reported together as acid-hydrolyzable carbohydrates. The average content of starch was very low, and did not justify separate mention. The results are given in table 7 and figure 3.

The general level of carbohydrate accumulation in this series was above that of Series I. As mentioned previously, this was perhaps a response to the higher air temperatures in the greenhouse. In this series, there was not a clear distinction between the levels of carbohydrate accumulation in long and intermediate light, the temperature factor apparently overshadowing the light effect.

The effect of high magnesium on the amount of sugars found was similar to that in Series I, altho only treatment 1-1-6 was able to maintain a consistently high level, treatments 2-2-4 and 3-3-2, the latter in particular, being somewhat erratic except in short light. In this series the high potassium culture was not as efficient as the high calcium in production of sugars. The high level of non-sugars in the potassium cultures is an evident corollary of the low sugar content, as rapid translocation must have occurred.

Table 7

CONCENTRATIONS OF CARBOHYDRATES AND NITROGEN IN TOPS

Series II

Treatment	Sample Sugars %	Sucrose %	Total sugars ratio	Carb- hydrate ratio	Total Car- hydrate ratio	Organic nitrogen %	Nitrate nitrogen %
				17 hours light			
1-1-6	10.34	4.00	1.00	7.21	1.00	7.071	.006
1-6-1	10.75	1.21	.38	6.73	.37	3.487	.113
5-1-2	5.73	2.19	.55	7.52	.96	3.241	.003
3-3-2	0.56	2.20	.32	6.50	.81	7.527	.215
2-2-4	9.15	2.21	.79	6.81	.87	3.403	.003
				13 hours light			
1-1-6	8.23	5.40	1.00	5.27	.45	3.967	.004
1-6-1	1.06	4.19	.43	12.74	1.00	3.795	.119
5-1-2	3.98	2.73	.49	11.23	.30	3.770	.005
3-3-2	5.35	2.20	.57	10.31	.30	3.712	.005
2-2-4	5.95	4.40	.76	7.10	.56	3.961	.005
				10 hours light			
1-1-6	3.29	1.39	.91	5.13	.67	4.843	.211
1-6-1	4.43	0.07	.93	7.83	.83	4.711	.215
5-1-2	3.45	0.57	.78	3.90	1.00	4.657	.381
3-3-2	4.10	0.24	1.00	6.65	.74	4.622	.427
2-2-4	3.29	0.22	.58	5.15	.58	4.653	.400

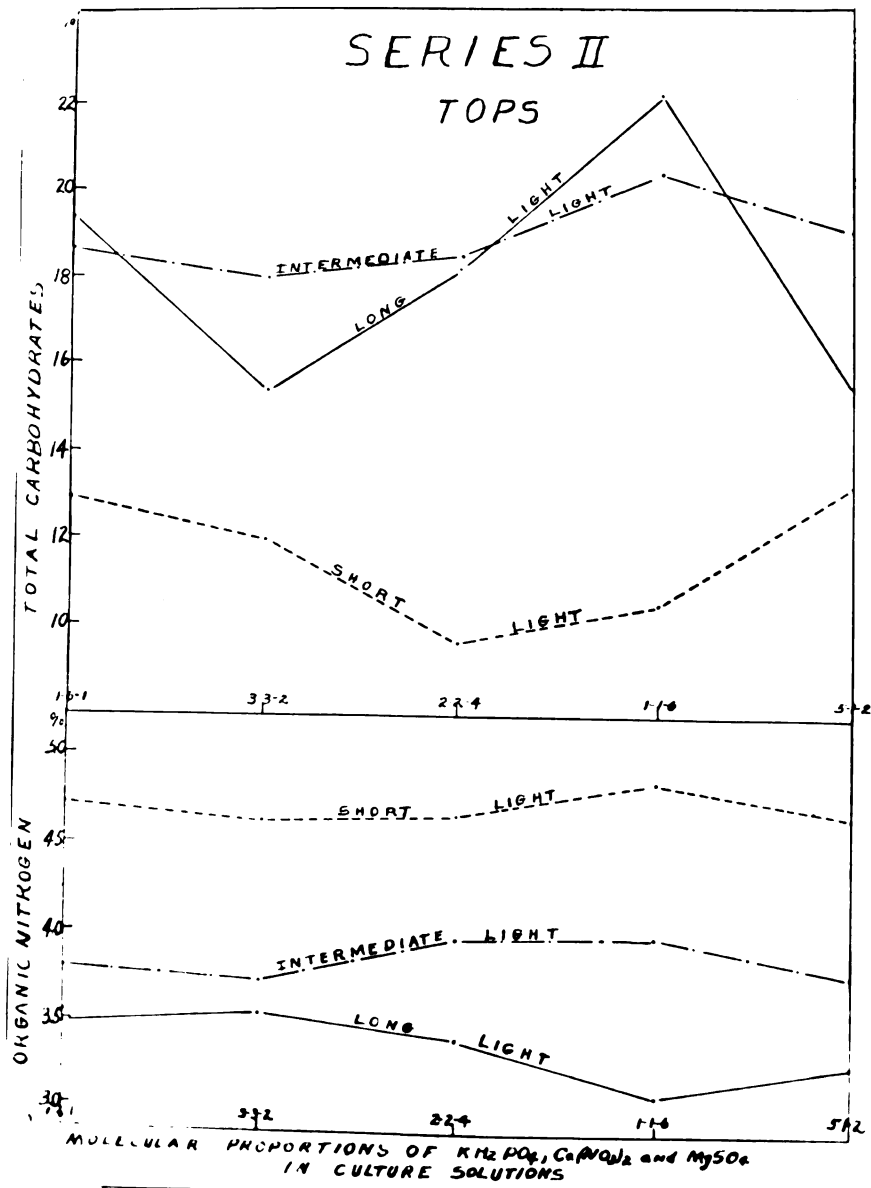


Figure 3. The relationship between molecular proportions of K_2HPO_4 , $Ca(NO_3)_2$ and $MgSO_4$ in culture solutions and the total carbohydrate and organic nitrogen content of tops in Series II.

The lowest content of polysaccharides was found in the highest magnesium treatment, if the values of the three light treatments are averaged. However it is hardly safe to conclude that this is a fixed relation, as the cultures varied widely in this respect.

No one treatment was greatly superior in total carbohydrate accumulation, altho the high magnesium treatment led in this respect in long and intermediate light. The very high percentages found with all treatments tended to mask any effects due to nutrients.

The nitrogen data showed almost no differences between nutrient treatments at any light duration. The light effect, per se, was again distinctly shown.

In the third series it was decided to grow the plants only until the first blossoms appeared, in order to find if the differences could be observed before the plants were mature. It was also decided to limit the light durations to 10 and 15 hours, as the greater differences had been found between these durations. Triplicate cultures, involving the growth of 120 plants under any one condition, were used, instead of the duplicate cultures in the former series.

Analytical results on this series are presented in Table 8, and a graphic representation in Figure 4. In this table, the column "acid-hydrolyzable carbohydrates"

represents only one analytical step, no attempt being made to separate starch from hemicellulose.

The level of carbohydrate accumulation at this stage of the plant's growth was distinctly lower in 13 hours light than was the case when the plants were grown to maturity. With 10 hours light, the final level was more nearly that found in Series I.

The highest level of sugar accumulation was found with treatment 2-2-4, as an average of both light durations. Treatment 1-1-6 was unaccountably low in these fractions, while the high potassium treatment was very good in the short light. The last treatment was again conducive to non-sugar formation in this series, altho not superior to treatment 2-2-4. These two treatments were also best in total carbohydrates.

The content of organic nitrogen was the highest in each case in the high magnesium treatment. The differences were only a few hundredths of a percent and are hardly worthy of mention. The light effect on the level of protein elaboration was noticeable at even this stage of growth.

A general summation of the results of these studies, and a consideration of average ratios, shows that the culture solutions might be ranked as follows with respect to production of sugars: 1-1-6, 2-2-4, 3-3-2,

Table 8

CONTENT OF CARBOHYDRATE AND NITROGEN IN HILLOCK PLANTS

Series III

Treatment	Sample sugars %	Sucrose %	Total sugars ratio	Acid-hydrolyzable carbohydrates %	ratio	Total Car- bohydrates %	ratio	Organic nitrogen %	Nitrate Nitrogen %
1-1-6	3.07	0.45	.68	5.73	.83	6.61	.81	4.811	.079
1-1-1	3.46	0.29	.70	5.73	.83	6.15	.77	4.759	.339
5-1-2	3.59	0.77	.77	5.73	.83	6.66	.82	4.714	.150
3-1-2	7.61	0.27	1.00	6.49	1.00	10.53	1.00	4.745	.130
2-1-4	2.87	0.11	.79	6.45	.93	9.28	.88	4.359	.039
1-1-6	2.04	0.63	.77	5.73	.73	7.29	.76	5.008	.351
1-1-1	3.21	0.53	.74	5.77	.86	8.17	.85	5.034	.427
5-1-2	3.07	0.71	.68	3.13	1.00	9.57	1.00	4.742	.189
3-1-2	9.39	0.03	.69	4.44	.71	6.84	.71	4.661	.399
2-1-4	3.25	0.27	1.00	5.81	.93	9.41	.93	4.005	.261

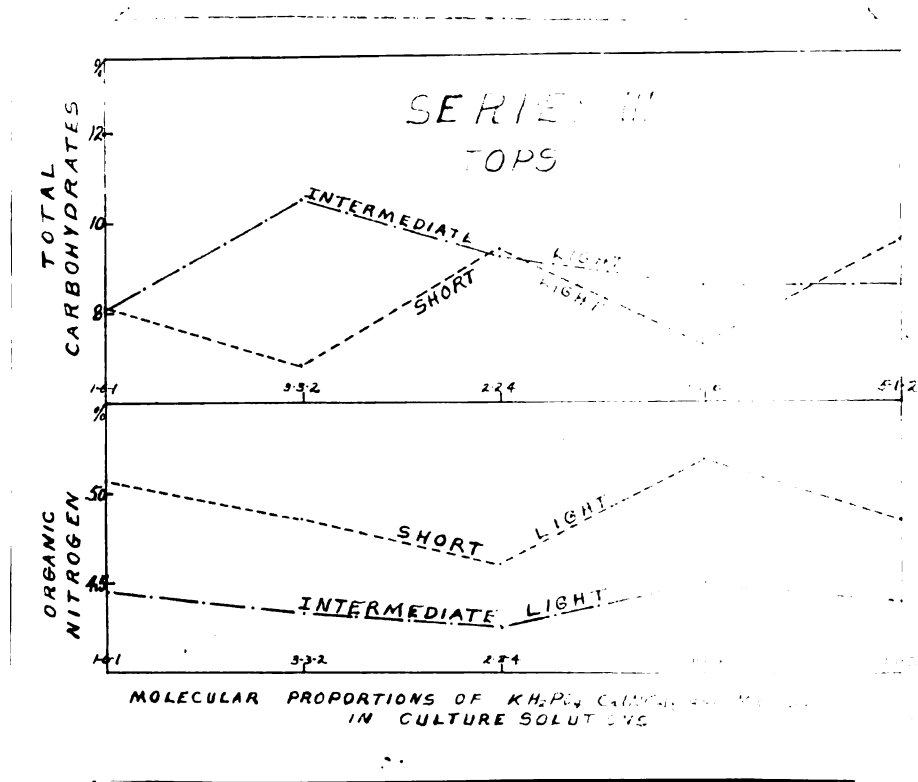


Figure 4. Graph showing carbohydrate and nitrogen content of tops in Series III.

5-1-2, 1-6-1. This indicates that the proportion of magnesium sulphate in the culture solution, indicated by the third figure in each group, bears considerable relation to sugar content. The treatment high in calcium nitrate was rather consistently low in these fractions, while high potassium occupied an intermediate position.

With respect to polysaccharides, the following ranking seems justified: 5-1-2, 1-6-1, 2-2-4, 3-3-2, 1-1-6. Only in the case of the high potassium treatment was there a sharp distinction, as it was greatly superior in nearly all cases.

Total carbohydrates, as mentioned previously, tended to be at about the same level whether the solution was high in potassium or magnesium. They were clearly lower in the high calcium treatment, excepting in Series II, where an excessively high level prevailed under all conditions.

SHIV'S TRANSLATOR FIELD EXPERIMENT

Shiv's Translator field plants were grown in selected water cultures, Shiv's 1 at sea level, type 1. Analyses of tops and pods for carbohydrate fractions, organic nitrogen and nitrate nitrogen are reported. The effect of light duration on the relative amounts of carbohydrates and nitrogen was also studied. Physical measurements are given in all cases.

Results of physical measurements indicate that the highest average top length, dry weight of tops and dry weight of entire plants exclusive of fruit were found with solutions high in calcium nitrate. With respect to the last measure, i.e., whole-plant treatment was more effective than high calcium treatments.

Highest content of total sugars (simple sugars and sucrose) was found with solutions high in potassium. Polysaccharides (starch and hemicellulose) were markedly high with an abundant supply of potassium.

Total carbohydrates were maintained at a fairly high level by all treatments except the one high in calcium.

Under the conditions of these experiments, the duration of light determined the general level of carbohydrate and nitrogen assimilation. Organic nitrogen was always highest with short light and nearly always higher with intermediate light than with long light. Total

carbohydrates were lowest with short light when the plants were young to maturity, but did not differ greatly from intermediate light in plants grown four weeks. Between intermediate and long light (Series I and II) the differences were not consistently in favor of higher total carbohydrates in long light, but the average of all treatments showed a uniform trend in that direction.

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GROWTH OF BEANS IN WATER CULTURE UNDER
VARIOUS LIGHT EXPOSURES

II Base element relationships

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Introduction

The response of plants to the supply of various nutrient elements and the positive correlation between the amount supplied and the percentage found in the plant have been the subjects of numerous investigations. The degree of response is largely governed by environmental factors, which may even nullify the effect of varying treatments. Soil as a medium of growth is apt to be much more inflexible than a less dynamic material such as quartz sand, which in turn is a less flexible medium than water cultures. It is possible to obtain significant differences in growth and composition of plants in water cultures where the differences in nutrient supply are rather small. Although the intake of any one element may be a function of the relative supply of other elements as well as the one in question, an intake proportionate to the supply will obtain

(1) The writer wishes to express his appreciation to Dr. P. J. Anderson for permission to perform the analyses herein reported in the laboratory of the Tobacco Substation, Connecticut Agricultural Experiment Station.

under optimum conditions.

In connection with cooperative research studies on salt requirements, attempts have been made to control many of the governing factors, especially with plants growing in water cultures. Factors such as the degree of acidity of the culture solution and its effect on the composition of the plant have been quite thoroughly evaluated.

As a continuation of the study of the growth of peas in water cultures, it was decided to investigate the effect of light duration on the intake of base elements by the plant. Such problems as the effect of the season on the composition of the plant are perhaps related to light duration.

Historical

Gilbert and Hardin (8) working with a variety of crops under field conditions conclude as follows "In general the current concentrations of mineral elements in the solutions of crop plants were found to correlate directly with the applications of chemical fertilizers." Earlier work by McCool (15) shows the same relation in the expressed sap of corn, beets and onions.

Among the fertilizer elements applied to the soil that cause a marked response in the plant, potassium is usually foremost. Otryganjew (18) raised the potassium content of tobacco from 0.45 to 7.22 per cent K_2O on a poor sandy soil. Anderson, Swanback and Street (2) reported a range of 4.07 to 6.69 per cent K_2O on field tobacco, while greenhouse tobacco ranged from 1.48 to 6.78 per cent K_2O in soil cultures and 1.16 to 5.36 per cent in sand cultures, with fertilization varying from 0 to 300 pounds per acre of K_2O . On the other hand Haley, Lonconecker and Olson (10) growing tobacco on a calcareous soil were able to increase the percentage of potash to only 3.27 per cent by the addition of 450 pounds K_2O per acre, as compared with 1.74 per cent with no potash. Similar results are reported by Bartholomew and Janssen (4) for several legumes and grasses. Fonder (7) has noted consistent differences in potash content of alfalfa grown

on several soil types.

In water cultures an extremely wide range of potash content has been reported by Sayre (19), working with canning peas. With $\text{CaO}/\text{K}_2\text{O}$ ratios varying from 0.029 to 18.3, he obtained potash percentages ranging from 0.87 to 8.70 per cent in leaves and from 0.68 to 7.60 per cent in stems.

Responses to calcium and magnesium applications in soil are usually related to the relative abundance of these elements as compared with the potash supply. A relative abundance of potash depresses the intake of either or both, as shown by Morgan (16 p. 905) and Haas (9).

The use of hydrated magnesian lime containing 57 per cent CaO and 29 per cent MgO might be expected to increase both the calcium and magnesium, but such was not the case, as is shown in the following table from the work of Anderson, Swanback and Street (2).

Table 1

EFFECT OF MAGNESIAN LIME ON PERCENTAGE OF CALCIUM,
MAGNESIUM AND POTASSIUM IN TOBACCO.

(Air dry basis on unfermented leaves)

Pounds magnesia applied per acre	Percentage found in cured leaves		
	K ₂ O	CaO	MgO
None	4.83	6.75	1.32
100	3.98	6.22	2.47
200	3.12	5.63	3.13
400	3.09	5.26	3.83
600	2.40	4.95	4.59

It may be seen that the potash was notably depressed and the calcium quite strongly reduced. The reciprocal repression affects all three bases, as has been noted by Fonder (5), (7), for alfalfa.

It is only where both potash and magnesia are available in relatively small amounts that the plant is able to take up calcium freely, as has been shown by Morgan (16, p 905) and Haley, Longenecker and Olson (10) working on tobacco in soils and Sayre (19) with peas in water cultures. Fonder (6) did not find as great differences on peas grown in several soils in the greenhouse, but the differences in calcium content of the various soils was not great and no fertilizer was added. Nightingale, Addoms, Robbins and Schermerhorn (17) in a study of calcium deficiency in tomato plants obtained results that clearly indicate mutual calcium and potassium repression. The

absence of calcium permitted an intake of as high as 10.62 per cent potassium, as compared with as low as 2.23 per cent in its presence. Calcium varied from a trace to 3.84 per cent.

References to the effect of light on the intake of bases are not numerous in the literature. Bartholomew and Jannsen (4) by means of analyses at different times of the day, conclude that potassium is taken up as freely at night as during the day. Tyson (20) grew sugar beets in shaded compartments having from one to four layers of cheesecloth, and one group under two layers of cheesecloth and one of black calico. He found that the ash content of the leaves increased with a decrease of light. Calcium and magnesium content of leaves was inversely proportional to the intensity of light while potassium content was decreased with one and two layers of cloth, but increased with greater shading until it was about the same as in leaves grown in full sunlight. This would indicate a greater base absorption in weak light. Nightingale et al (17) in the studies previously noted, found that plants grown in a calcium deficient medium, when placed in darkness showed the presence of "uncombined" calcium, i.e., calcium that could be detected microchemically by the usual treatment with oxalic acid, and that the presence of calcium in this form permitted growth and perhaps protein elaboration.

Plan of Experiment

The material for this work was the oven dried samples of the peas used in Part 1 for determination of nitrate and total nitrogen. Analyses were made for crude ash, potassium, calcium, and magnesium on the tops of all three series. No analyses of pods were made, as previous results had shown no consistent trend. The reader is referred to Part 1 for details of treatment and physical measurements of the plants.

Chemical Methods

Crude ash and calcium were determined by the official methods of the I. O. A. C. (3). Magnesium was determined by the volumetric method of Handy (11). Potassium determinations of the first series were made by the sodium cobalti-nitrite method of Idie and Hood (1). A comparison of this method with the official chloroplatinate procedure showed that the former method did not give consistent results, most of the percentages being too high. Series I was therefore repeated and all potassium figures reported are by the official method.

Experimental Results

Data on crude ash for all series are given in

Table 2.

Table 2

PERCENTAGE OF CRUDE ASH IN PMA PLANTS

Treatment*	Percentage crude ash		
	Series I	Series II	Series III
	<u>17 hours light</u>		
1-1-6	12.71	15.35	
1-6-1	12.76	15.91	
5-1-2	15.47	18.05	
3-3-2	14.59	17.37	
2-2-4	14.83	16.85	
	<u>13 hours light</u>		
1-1-6	13.41	12.80	11.80
1-6-1	15.43	15.00	16.43
5-1-2	15.21	15.85	17.08
3-3-2	16.43	14.12	14.09
2-2-4	16.55	14.71	13.20
	<u>10 hours light</u>		
1-1-6	14.95	14.93	15.31
1-6-1	16.32	16.71	16.09
5-1-2	16.10	13.22	14.38
3-3-2	15.05	15.77	15.12
2-2-4	15.97	14.97	15.25

The average amount of crude ash was greater under short light than intermediate light in every case. Long light was not consistent being the lowest in Series I and the highest in Series II. No plants were grown under long light in Series III.

*Culture solution, Shive's 1.00 atmosphere, 1st figure KH_2PO_4 , 2nd figure $Ca(NO_3)_2$, 3rd figure $MgSO_4$.

The effect of nutrient materials on the crude ash was quite clearly shown. In every case except one, the lowest figure was found with the high magnesium treatment 1-1-6. The highest percentage of crude ash was noted with the high potassium treatment in five out of eight groups, and with high calcium treatment, or a combination of the two, in the other groups. This is in accordance with the relative percentages of the three elements commonly found in plants.

Table 3 presents the analyses of the three dominant bases in the tops for all series. Tops include all aerial parts of the plants with the exception of pods.

The data for Series I are also presented in graphic form in Figure 1. In this graph the increments of potassium, represented by the first of the three figures, increase from left to right. The increments of calcium, represented by the second figure, and of magnesium, by the third figure decrease from left to right. To more clearly illustrate the repressive effect of potassium on the other two bases, the treatment 5-1-2 was placed at the right of all sections of the graph.

Considering first the correlation between the supply of any one base in the culture solution and the percentage in the plants produced in that solution, it can be seen that a very good agreement existed. In all

Table 3

CONTENT OF POTASSIUM, CALCIUM AND MAGNESIUM IN TOPS OF PEAS

Treatment	Series I			Percentage on air dry basis			Series II			Series III		
	K			K			K			K		
	Ca	Ca	Mg	Ca	Ca	Mg	Ca	Ca	Mg	Ca	Ca	Mg
1-1-6	3.64	.58	1.16	4.25	.76	1.80	17 hours light					
1-6-1	2.75	3.32	.27	4.01	2.81	.40						
5-1-2	5.64	.27	.15	6.50	.24	.27						
3-3-2	4.81	1.45	.41	5.47	.77	.90						
2-2-4	4.69	.54	.30	5.16	1.40	1.37						
1-1-6	4.20	.61	.66	5.05	.29	.92	17 hours light					
1-6-1	3.67	3.61	.33	4.75	2.16	.31						
5-1-2	6.38	.19	.27	7.05	.16	.19						
3-3-2	4.37	1.70	.53	6.37	1.09	.26						
2-2-4	4.83	1.25	1.19	5.48	.63	.43						
1-1-6	4.76	.47	1.00	5.90	.26	.60	10 hours light					
1-6-1	4.20	2.18	.33	5.76	1.36	.30						
5-1-2	7.10	.22	.32	8.10	.16	.23						
3-3-2	6.27	.51	.28	6.96	.37	.35						
2-2-4	5.87	.29	.50	6.51	.28	.52						

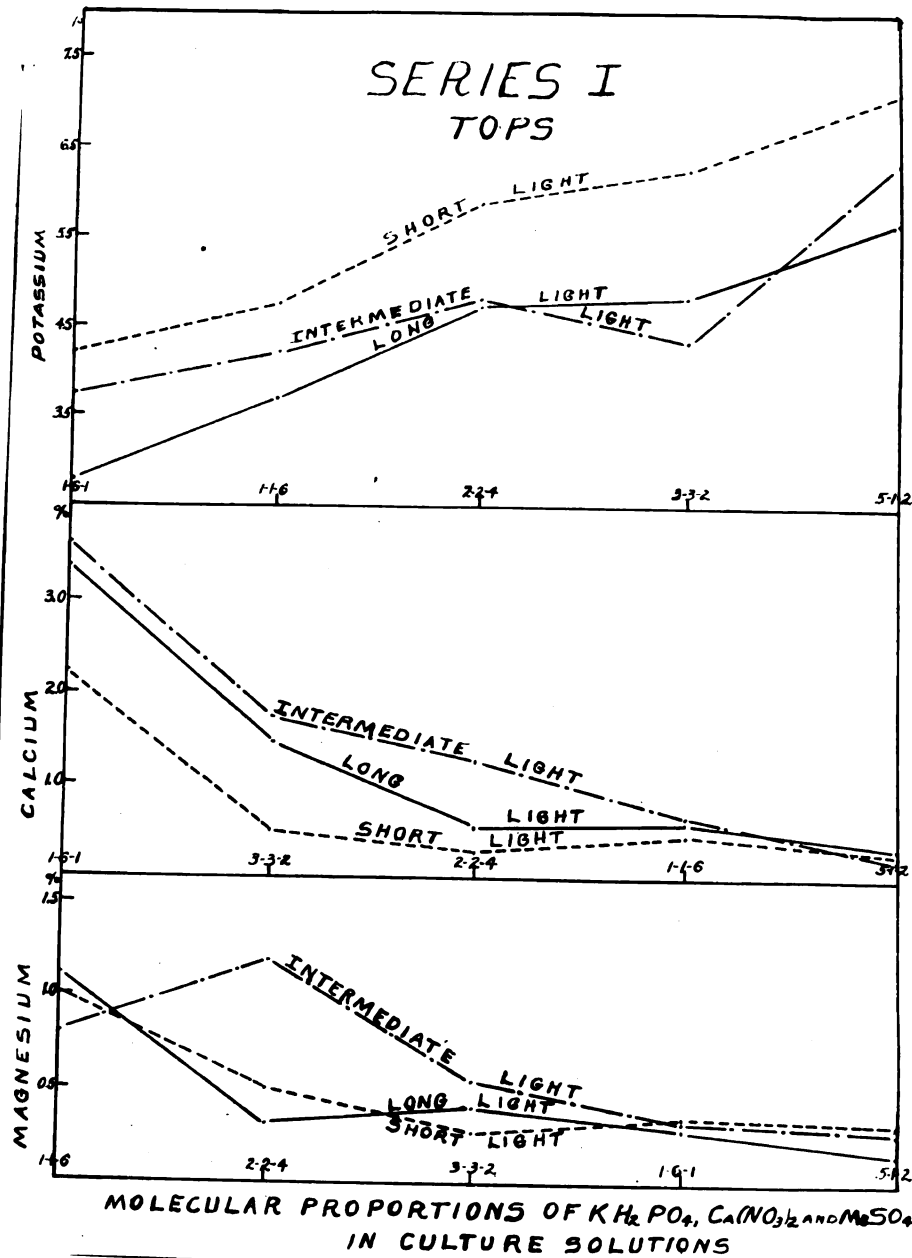


Figure 1. Graph showing intake of base elements under several light exposures in Series I.

but one of the intermediate light treatments a regular increase in percentage of potash was to be found. While calcium did not vary as widely, yet it also showed a higher content in the plant with each increase in amount in the culture solution. The correlation in the case of magnesium was rather poor in the higher treatments grown with 13 hours light, but aside from this group, it displayed a regular increase.

Evidence on the mutually repressive effect of the bases was quite apparent. A large amount of potash in the culture solution (treatment 5-1-2) resulted in a lower calcium intake under all conditions than a high proportion of magnesium (treatment 1-1-6). Furthermore solution 1-1-6 permitted greater calcium intake than solution 2-2-4 in two light durations, failing only in intermediate light. This was perhaps due to the fact that while solution 2-2-4 furnished twice as much calcium as solution 1-1-6, it also supplied twice as much potassium.

The effect of potassium on magnesium intake was quite similar. In every case solution 1-6-1 permitted greater magnesium intake than solution 5-1-2. Between solutions 5-1-2 and 5-3-2, both of which supplied equal amounts of magnesium, but varied in potassium, the intake of magnesium was increased as the potassium supply decreased, except under short light.

Calcium showed a greater repressive effect than magnesium on the intake of potassium. In all cases solution 1-6-1, high in calcium, produced plants lower in potassium content than did solution 1-1-6.

The most marked effect of the duration of light on the absorption of bases was upon the intake of potassium. With 10 hours light the level of potassium intake was significantly higher throughout the range of cultural treatment. Intermediate light gave higher percentages of this element than long light, with the exception of one treatment. Between long and short light an average difference of over one per cent in potassium content was found for all treatments.

Calcium content in reference to duration of light showed the 13 hour day length able to maintain the highest level. Short light was featured by the lowest relative level of calcium absorption, and except in the highest concentration by a rather low absolute content.

With respect to magnesium, the intake was not consistent. Intermediate light duration permitted a greater intake than long light in all but one treatment. Under 10 hour day length the range of magnesium content was narrower, the low magnesium cultures having a slightly higher intake, and the high concentrations somewhat less than under greater light durations.

The data for Series II are also presented in Table 3, and shown graphically in Figure 2. The correlation between the supply present and the absorption was considerably better in most respects. Potassium intake increased regularly with increase in the supply and the magnesium was also consistent. The calcium content of the long light plants grown in solution 3-3-2 was lower than in solution 2-2-4, but this was the only inconsistency in this respect in the series.

The various repressive effects noted in Series I were again evident in this series. The high potassium culture, 5-1-2, was particularly repressive to calcium and magnesium absorption in all cases.

Very definite differences in potassium absorption with respect to light exposure were found. Short light plants were again the highest in potassium content, while intermediate light was clearly more conducive to potassium intake than long light. As might be expected in view of the antagonism of potassium and calcium, the short light plants had the lowest level of calcium intake. The differences between long and intermediate light were not as conclusive, but favored the former in all but one treatment.

Magnesium was considerably higher under long light than in Series I and definitely greater than in the

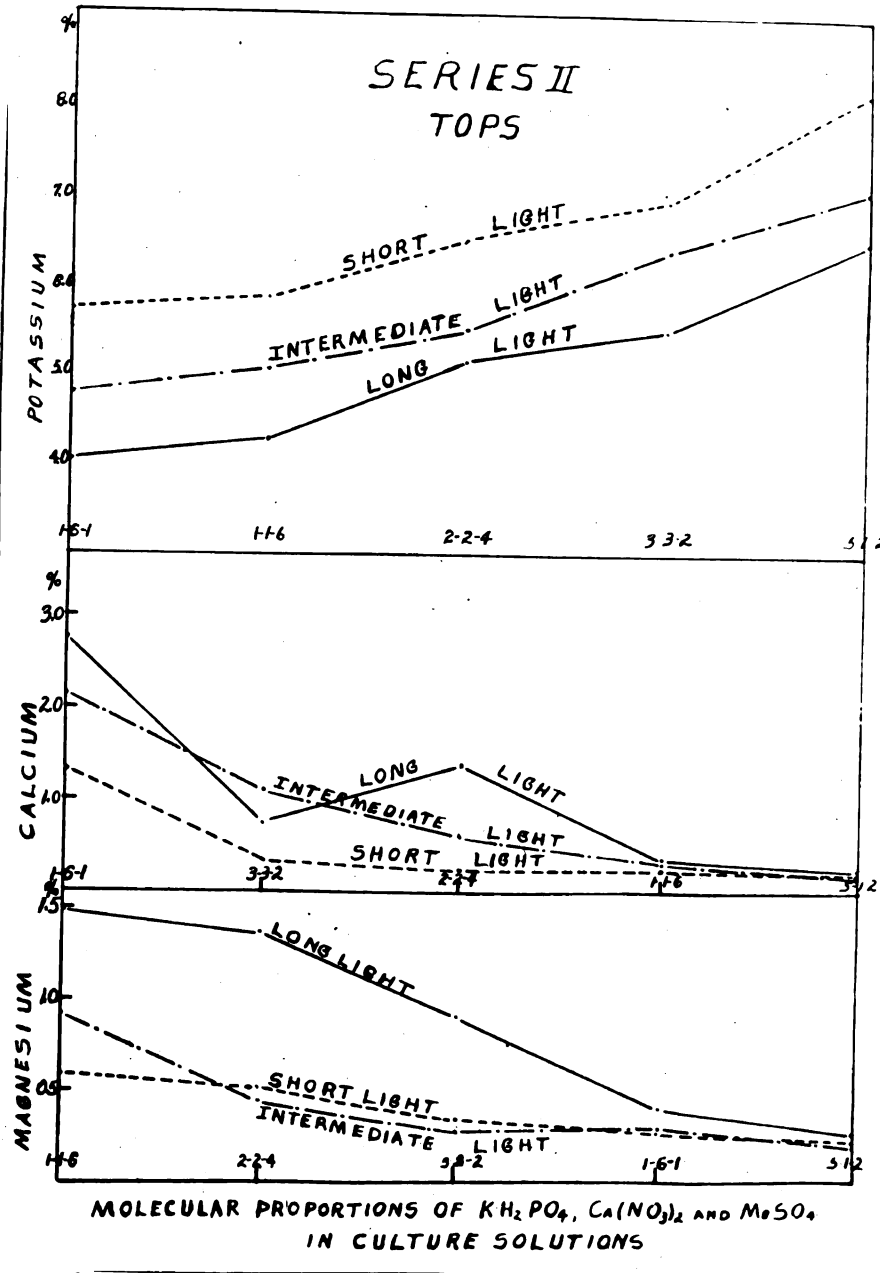


Figure 2. Graph showing intake of base elements under several light exposures in Series II.

shorter light exposures of this series. The differences between intermediate and short light were very slight, as both had a low level of absorption. The average for all treatments of both durations was nearly the same.

Because of the fact that the plants in the third series were grown only to the time of flowering, a period of four weeks, the results as shown in Table 3 and Figure 3, are not entirely comparable to those of the preceding series. The response to high or low supply of the different elements was not as great, consequently the range of percentages was much reduced. A fairly high level of potassium content was reached but calcium and magnesium were very low. The exceedingly low magnesium content of the young leaves was in agreement with results of Latman and Walbridge (14) on potatoes analyzed at several stages of growth. Potassium was somewhat antagonistic to the other bases, but the relatively greater repressive effect of calcium toward potassium had not begun to be evident.

The effect of light duration was more clearly shown in the content of calcium and magnesium than of potassium. Both bases were absorbed in direct relation to the light period. Apparently the absorption of these elements was quite regular during the early stages of growth, and no great accumulation took place in any culture.

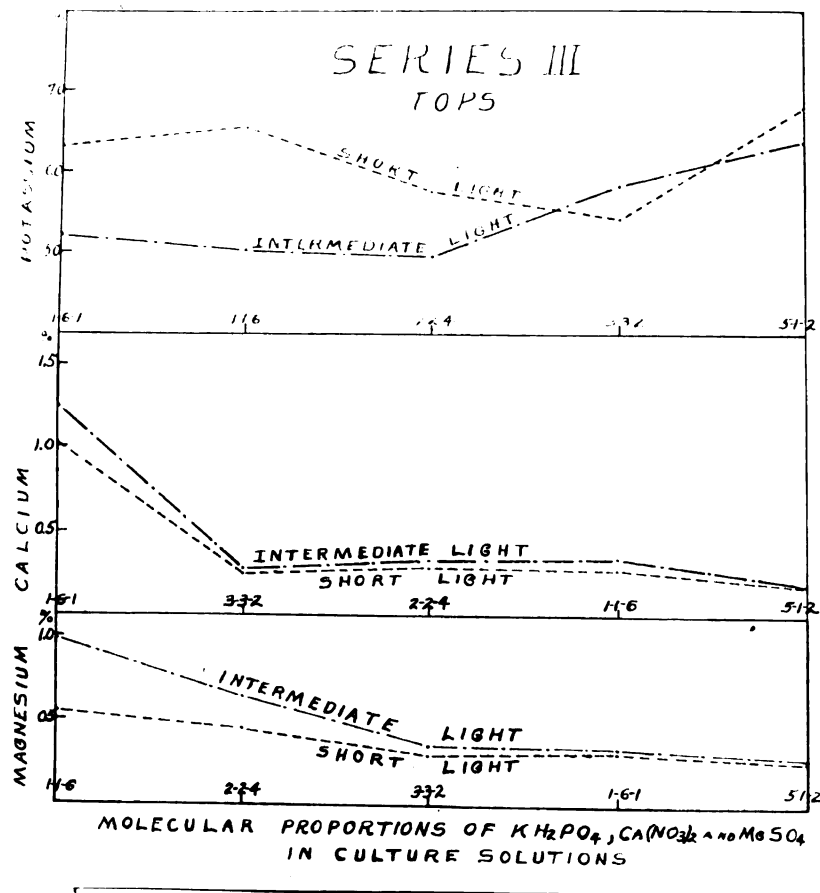


Figure 3. Graph showing intake of base elements under several light exposures in Series III.

The potassium, on the other hand, was not taken up in accordance with the supply, at least in the lower increments. Only in the solution containing the largest amount of potassium, was there an abundant intake. In the other cultures, one part of potash in the solution seemed to permit as great an intake as three. This would indicate that a lower concentration of potash is adequate for young plants.

General Discussion

Considering the evidence of the first two series, it seems conclusive that potassium was most abundant in plants grown to maturity under short light. As the light period was lengthened, the level of potassium intake dropped. In young plants these phenomena were not as well defined.

On the other hand, calcium was most abundant under longer light periods, with 13 or 17 hours about equally efficient in promoting absorption of this element. Magnesium was similarly affected by the photoperiod.

In attempting to explain the results of these experiments, it is well to remember that on these same plants, determinations of organic and total nitrogen showed that the shorter the light period, the higher the percentage of nitrogen. This was in accordance with the findings of many other investigators. Moreover the length of day was practically the only controlling factor, as the plants were able to get an adequate supply of nitrogen from the lowest increments, and therefore failed to respond to increased amounts.

Thus it may be assumed that in a series of culture solutions having the same osmotic concentration, but varying proportions of the three salts, all the plants in the series would have an equal supply of base elements.

It is quite generally agreed that an acid-base equilibrium exists in plants. If light conditions were such as to permit a heavy intake of nitrate, an equivalent amount of one or more bases must also enter the plant. In these experiments, potassium was apparently available in the greatest relative amount, and hence its high level in the short light plants which were all equally high in organic nitrogen. It is also significant that it was only with short light that nitrate nitrogen was present to any amount in these plants. In experiments on the same general theme, Hibberd (12) found an accumulation of nitrogen in the plants grown in short light, proportional to the amount of calcium. In this case, calcium was apparently the most abundant cation, altho no analyses of plants are presented to show whether the plants had absorbed more calcium.

The absorption of calcium, and to a large extent magnesium, seems to bear a reciprocal relation to that of potassium. From the evidence at hand it does not seem safe to arbitrarily state that calcium will increase under short light if the conditions are greatly different from those under which these plants were grown. The statements of Hoagland and Martin (13) in reference to toxicity of salts under various climatic conditions are of interest in connection with these studies. They found that solutions

which stimulated growth under certain conditions might produce marked inhibition of growth at a different time of year.

Conclusions

Crude ash was higher in peas grown in 10 hours light than in 13 hours, but not consistently higher than in plants grown in 17 hours light. A culture solution high in magnesium resulted in the lowest crude ash in all but one case. High potassium or high calcium solutions grew plants which were the highest in crude ash.

The correlation between the relative supply of any one element in a group of cultures, and the relative intake of that element by the plants grown in these cultures, was very clearly marked.

Potassium displayed a strong repressive effect on the intake of calcium and magnesium, often overshadowing other factors where the supply of potassium was high and the supply of the other bases rather low.

Calcium had a somewhat greater repressive effect on potassium than had magnesium, in cultures where these bases were abundant.

Light exposures of 10 hours daily produced plants high in potassium and low in calcium and magnesium.

Light exposures of 13 hours produced plants lower in potash and higher in calcium and magnesium than 10 hour plants. This exposure in Series I had the highest level of calcium intake.

Light exposures of 17 hours resulted in plants markedly low in potassium and usually the highest in calcium and magnesium.

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