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ON THE RELATIONS BETWEEN GROWTH AND THE ENVIRONMENTAL CONDITIONS OF TEMPERATURE AND BRIGHT SUNSHINE.

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(With 13 Text-figures.)

IT is fully recognised that the amount of growth made by any crop in the field and the rate at which maturity is reached is influenced by many factors such as temperature, rainfall, season, sunlight, soil conditions and available plant food. There is, however, little definite information as to the influence of each of these factors on a plant at various stages of growth nor with regard to the changes in the actual rate of growth at different periods from the seedling to the mature plant.

It is difficult or even impossible to gain this information from crops growing under normal conditions in the field, because some of the factors cannot even be measured with any degree of accuracy and all are so intimately associated that the action of one or other can hardly be disentangled from the rest. Simplification is therefore essential and some method must be adopted whereby certain of the factors are controlled and kept as constant as possible, thereby reducing the number of the variable influences to be observed. The method of water culture was therefore used, as it enables a strict control to be placed on the food and water supplied, it permits of the roots being observed and weighed with far greater accuracy than in soil experiments, and its compactness allows of a large number of plants to be given individual treatment at the same time. It is also possible to keep a close watch on the temperature variations to which the plants are subjected and to observe the effect of these variations on a number of individuals at different stages of growth.

ENVIRONMENTAL CONDITIONS.

The experiments were carried out in a roof greenhouse specially constructed for water culture work and extended over a period of sixteen months from September 1915 to January 1917. As Rothamsted is situated in a country district away from the fogs that are common to urban areas the light conditions were good for any given period of the year. This is an important point, as Gregory[1], in experiments on cucumbers at Cheshunt, near London, has shown that with high temperatures light becomes a limiting factor, *i.e.* although other conditions are favourable the growth is limited by the deficiency of light. Artificial heating was installed and the minimum temperatures were kept above freezing point throughout the winter months so that the results, so far as they refer to the effect of minimum temperatures, are only applicable in cases where the latter do not fall below 32° F. Throughout the period the maximum and minimum temperatures were recorded daily except on Sundays, but as the thermometers were read at 9 a.m., the Monday readings included those for both the preceding days, thus insuring that a high maximum or low minimum on Sunday was not lost. The weekly numbers of hours of bright sunshine cover the seven days as they are taken from the daily records made at Rothamsted.

For the whole period of sixteen months the prevailing conditions of temperature and light, as indicated by the weekly means of maximum and minimum temperatures (Fig. 1), and the weekly hours of bright sunshine (Fig. 2), are summarised in the following table:

		Mean	Standard deviation
C.	Mean maximum temperature	66·5° F.	11·7° F.
D.	Mean minimum temperature	45·9° F.	4·66° F.
E.	Hours of bright sunshine	20·3	16·6

The mean maximum temperature is naturally greatly influenced by the amount of sunshine, thus partly accounting for the large standard deviation. The minimum is much less variable, as during the winter months special care was taken to keep the night temperatures at a reasonably high level by means of artificial heating.

There is a close correlation between these three environmental conditions. The effect of each on the others depends upon the individual characteristics of the house, such as aspect and ventilation and artificial heating, and the extent of these effects can be measured by the correlation, as follows:

$$r_{CD} = + \cdot 6284 \pm \cdot 0384$$
$$r_{CE} = + \cdot 7560 \pm \cdot 0271$$
$$r_{DE} = + \cdot 2895 \pm \cdot 0595$$

[1] 1917. *Third Annual Report of Experimental and Research Station, Cheshunt, Herts,* p. 22.

The close association of hours of sunshine with maximum temperature is to be expected; nevertheless, taking into consideration that the mere total of weekly sunshine ignores its distribution between the several days of the week and the hours of its incidence on individual days, the

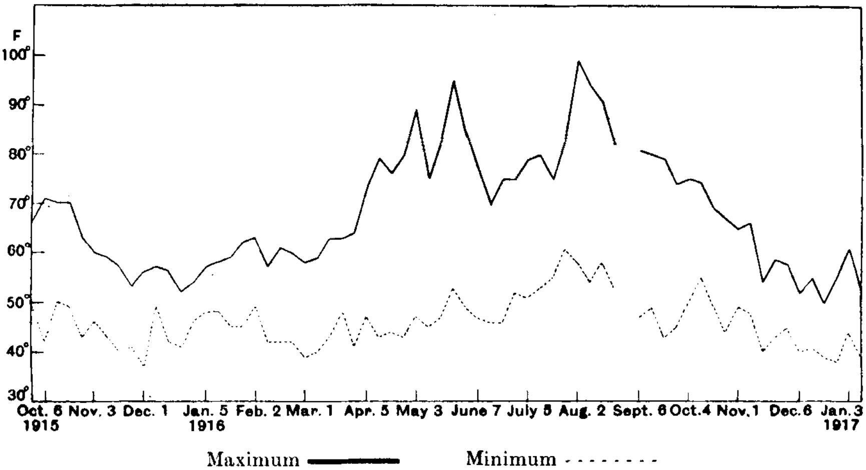


Fig. 1. Average weekly temperatures in roof water-culture house, Sept. 29th, 1915—Jan. 10th, 1917.

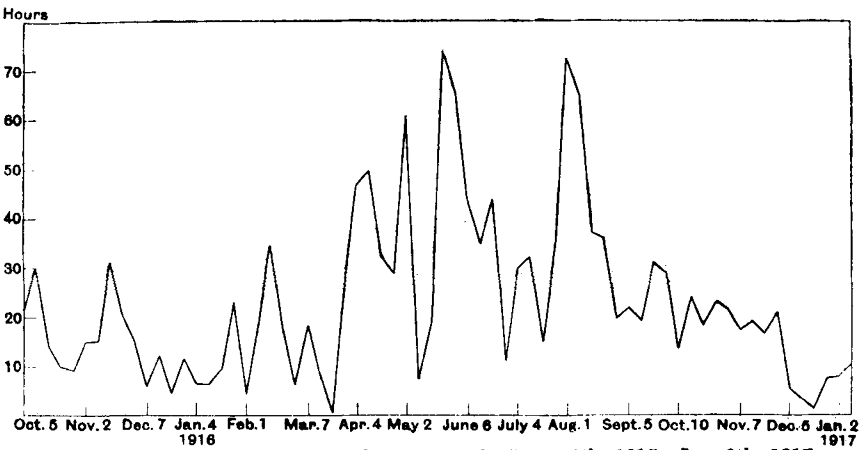


Fig. 2. Total hours of bright sunshine per week, Sept. 28th, 1915—Jan. 9th, 1917.

value obtained, ·7560, is remarkably high. The correlation between mean maximum and mean minimum temperatures is also high, as is naturally the case; but the correlation between bright sunshine and mean minimum temperature would be higher, owing to the close association of both with the mean maximum, if some contrary tendency were not in operation. This is brought out by the partial correlations

$$_{E}r_{CD} = + \cdot 6534$$
$$_{D}r_{CE} = + \cdot 7709$$
$$_{C}r_{DE} = - \cdot 3638$$

The correlation between mean maximum and mean minimum for constant sunlight is + ·6534, slightly greater than before, showing that variations in sunlight affect these two variables in opposite directions; the correlation between mean maximum and sunlight for constant mean minimum is also greater, showing that the variations in mean minimum have tended to obscure this high correlation, a high mean minimum tending to occur with high mean maximum but with *low* sunlight. The third partial correlation, that between mean minimum and sunlight for constant mean maximum is strongly negative, and explains how the other two correlations have been obscured. The weeks of high sunshine are evidently the weeks of much radiation and night cooling; this partially counteracts the effect of high day temperatures produced by sunlight.

The small effect of sunshine on the range of mean minimum temperatures is brought out in Fig. 3, which shows that with considerable increase in total sunshine for a specified period (11 weeks) the highest mean minimum temperature is very little raised and the total range of weekly mean minima is little affected, at the same time that the highest mean maximum is pushed up many degrees and its total weekly range is greatly extended. It will be shown later that this relatively constant range of mean minimum temperature over prolonged periods is of great importance to the healthy growth of plants under these conditions of life, and that a comparatively slight increase above a certain level is very detrimental, but fortunately does not often occur.

METHOD.

It was necessary to select a species of plant for experiment that would grow under water culture conditions throughout the year and would not show too great a variation in the growth of individuals of the same age from a single sowing. Several years experience had shown that barley and peas are among the most satisfactory subjects for treatment by this method. In many respects barley is the better of the two, as if a pure line is used and the seeds are graded, very even growth can be obtained. Unfortunately during the winter months, in the "dead" season of the year, it is often impossible to get satisfactory germination of barley, as root development is usually inhibited, and even if seedlings are obtained the young plants make very little growth. Consequently

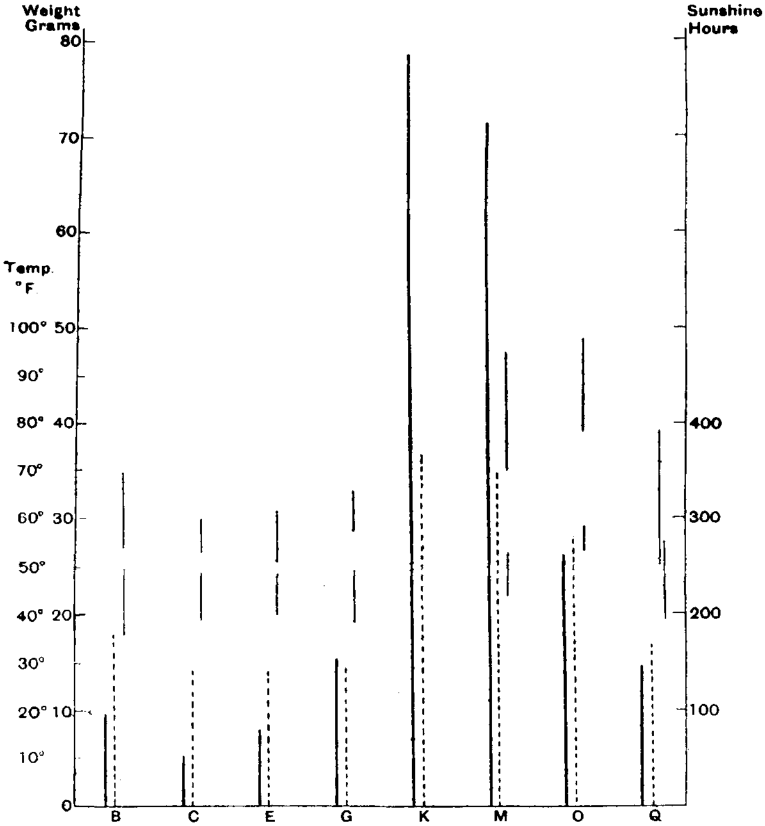


Fig. 3. Graph showing relations between total growth, total hours of sunshine and the range of mean maximum and minimum temperatures for several series of pea plants grown in water culture at different times of the year. All series were grown for 11 weeks except O, in which the plants died prematurely at the end of seven weeks.

Nutrient solutions changed weekly.

Heavy line = total growth.
Dotted line = total hours of sunshine.
Upper light line = range of maximum temperatures.
Lower light line = range of minimum temperatures.

peas were selected, for although the individuality of the plants is rather more marked, seedlings can be obtained throughout the winter, and a certain amount of growth can be relied on at whatever time the experiments are started. A dwarf variety, "Sutton's Harbinger," were used for the majority of the tests, but as unfortunately the stock ran out and could not be replaced the last four tests had to be carried out with Sutton's "King of the Dwarfs[1]."

The seeds were graded and ranged between ·25–·3 gms. or ·3–·35 gms. for "Harbinger," and ·3–·35 gms. or ·35–·4 gms. for "King of the Dwarfs," only one range of weights being used in each test. At intervals of a few weeks sets of 160 pea seedlings were put into water cultures. Usually two parallel tests were carried out, in one of which the nutrient solution[2] was changed weekly and in the other the original solution was retained throughout the experiment. The same day that the water cultures were set up ten extra seedlings were prepared for drying, in order to obtain the initial dry weight of the plants. In addition 10 seeds of the grade used were weighed, to give the relation between seed and seedling after germination. At regular weekly intervals 10 plants from each set were removed from their solutions and the roots carefully washed two or three times in clean water to remove adherent food salts. The roots and shoots were separated before drying, and when the plants were in the fruiting stage the pods were removed, and dried and weighed separately. The 10 plants taken each week were selected at random from the whole group, and may be considered to represent more or less accurately the average growth of any similar number of plants at the time. The figures thus obtained were graphed, and the data yield valuable information as to the rate of growth of the pea plant and its relation to certain environmental conditions.

A. Nutrient Solutions changed weekly

The constant change of the nutrient solution ensured that a plentiful supply of food was always available and that starvation effects did not manifest themselves. The supply of water was maintained by replacing that which was lost from the bottles by transpiration from the leaves, and as the tests were carried out in the greenhouse the plants were not

[1] Our thanks are due to Mr Martin Sutton for the gift of all the seeds used throughout these experiments.

[2] Nutrient solution:

Potassium nitrate	... ...	1 gm.
Magnesium sulphate	... ...	·5 „
Calcium sulphate	... ...	·5 „
Sodium chloride	... ...	·5 „
Potassium di-hydrogen phosphate		·5 „
Ferric chloride	... ...	·04 „

Distilled water to make up 1 litre.

subjected to rain or wind. Under these conditions the chief variable factors influencing growth were probably

(1) temperature (maximum and minimum),
(2) bright sunshine and light intensity,
(3) humidity of the air.

Of these factors temperature records are available throughout. The sunshine figures give a very incomplete idea of the amount of available light or of the intensity of light but unfortunately no apparatus for automatically recording the changes in actual light intensity was available, and this part of the investigation is therefore incomplete. The humidity was not measured as at the time the possible significance of change in this respect was not realised, but readings taken during 1919 show that the range of humidity within the house is considerable. The results of the investigation are therefore chiefly of use in indicating the relationship of temperature and sunshine to the rate of growth at different periods of the life of the plant.

Eight series of peas were grown during these observations, the seedlings being placed in water cultures on the following dates:

"*Harbinger.*"

Series B.	September 28th, 1915.	Series G.	January 4th, 1916.
C.	October 28th, 1915.	K.	March 10th, 1916.
E.	December 2nd, 1915.	M.	April 26th, 1916.

"*King of the Dwarfs.*"

O.	July 3rd, 1916.	Q.	October 3rd, 1916.

When seeds are germinated a loss in dry weight occurs owing to the fact that respiration goes on steadily from the beginning of growth, with a consequent loss of material by oxidation that at this stage is not balanced by the manufacture of fresh plant material. After the seedlings are set up in water culture this loss continues, for the same reason, over a period which varies in length according to the time of year (Figs. 4 and 5). Assimilation, which results in the building up of new substances from the air and the absorbed food salts cannot begin till the green leaves have appeared, and even then some little time elapses before the gain from assimilation balances the loss from respiration. Furthermore, the weights obtained show that the gain is at first very slow, as the leaf surface is initially small, and it is often several weeks before the young plant is again as heavy as the seedling was when first put into the culture solution. For the sake of convenience growth is divided into two periods which will be considered separately.

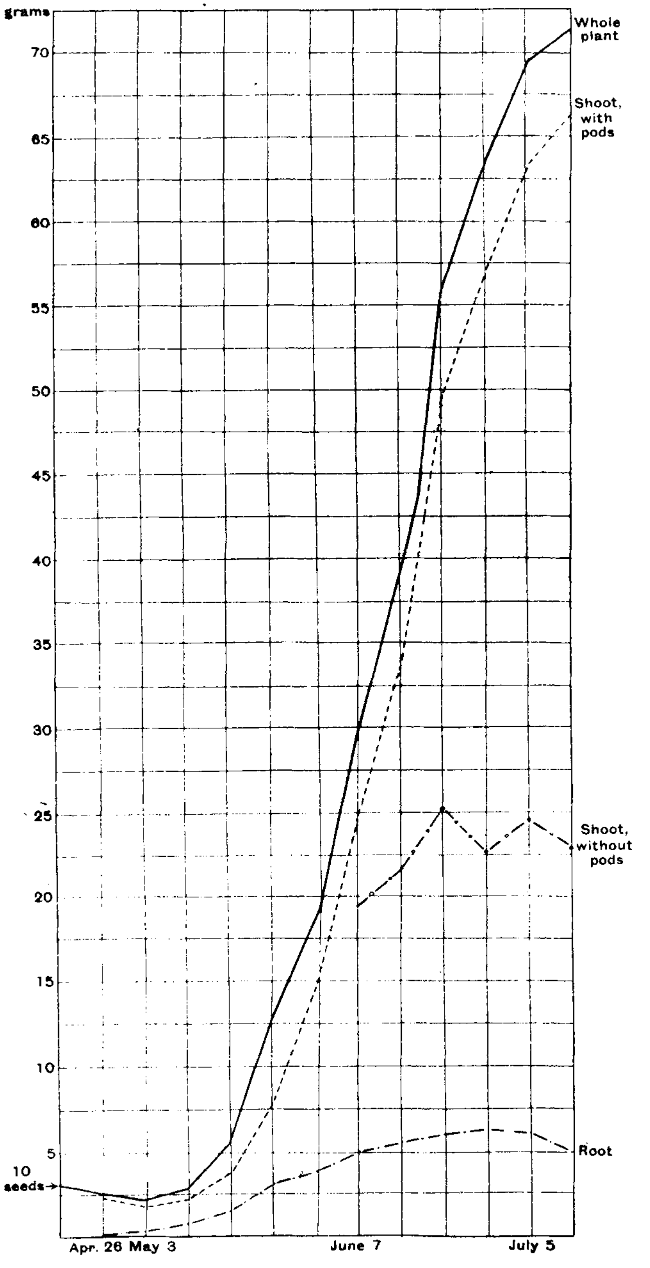


Fig. 4. *Summer Growth.* Dry weights of 10 pea plants, series M, grown from April 26th—July 12th, 1916. Nutrient solutions changed weekly.

(1) *1st period* from the seedling stage till the time that the plant regains its initial weight after the loss by respiration—*i.e.* the time during which a casual observer would say that the plant "makes no growth."

(2) *2nd period,* succeeding the former, during most of which the plant is obviously making growth, and which continues to the end of the experiment.

1st period of growth.

In the division of the plant into root and shoot the remains of the seed are associated with the shoot. From the very first the root increases steadily, though slowly, in weight even while the total weight of the plant is diminishing. This increased root substance is therefore obtained at first at the expense of the shoot and must consist of material transferred from the seed or of the earlier products of assimilation or possibly

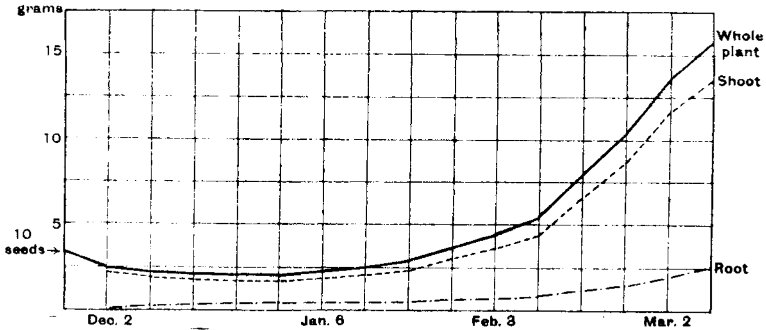


Fig. 5. *Winter Growth.* Dry weights of 10 pea plants, series E, grown from Dec. 2nd, 1915—March 9th, 1916. Nutrient solutions changed weekly.

of both. As the root thus increases in weight all the time, the loss of weight in the whole plant is less marked than in the shoot alone, and it therefore happens that the whole plant regains the initial seedling weight earlier than the shoot does. The length of time taken by the shoot to pass through the first period of growth varied with the time of year according to the prevailing temperatures as follows:

	Experiment started:	Length of first period for shoot	Max. weekly temp. ° F.	Min. weekly temp. ° F.
B.	Sept. 28th, 1915	3 weeks	70, 69, 70	42, 50, 49
C.	Oct. 28th, 1915	6 ,,	59, 60, 56, 54, 56, 58	46, 43, 40, 41, 37, 49
E.	Dec. 2nd, 1915	7 ,,	58, 55, 53, 56, 58, 59, 59	49, 42, 41, 46, 48, 48, 45
G.	Jan. 4th, 1916	4 ,,	58, 58, 62, 64	48, 45, 45, 49
K.	March 10th, 1916	3 ,,	64, 62, 66	43, 48, 41
M.	April 26th, 1916	2 ,,	89, 75	47, 45
O.	July 3rd, 1916	1 ,,	81	53
Q.	Oct. 3rd, 1916	2 ,,	74, 70	55, 49

If these figures are appropriately grouped it is seen that the length of the first period bears a direct relationship to the range of the mean weekly maximum temperatures, the time decreasing with the rise of the mean maxima. On the other hand the range of the mean minimum temperature seems of little significance as the variations are very irregular and do not run parallel with the length of the first period of growth.

Length of period Weeks	Series	Range of Mean Max. temp.	Range of Mean Min. temp.
1	O	81 °F.	53 °F.
2	M	75–89	45–47
	Q	70–74	49–55
3	B	69–70	42–50
	K	62–66	41–48
4	G	58–64	45–49
6	C	54–60	37–49
7	E	53–59	41–49

It is thus evident that the rate at which assimilation is able to make good the loss by respiration increases directly with rise of temperature; at the lower temperatures a very small increase will reduce the period by a week or more, but higher up the scale a slowing off in the time reduction is noticed. It is probable that this is really a temperature effect rather than one due to light intensity, for with similar temperatures the same length of 1st period growth occurred at different times in the year, *e.g.* in series M started on April 26th the period of two weeks was the same as in series Q started on October 3rd, though the light intensity in the first case would probably be greater than in the second, while 68·2 hours of bright sunshine were recorded in the April period and only 42·1 hours in the October period.

The initial stage of growth, therefore, is represented by a period during which the weight lost by respiration is made up by a gain due to the beginning of assimilation, the rate at which this compensation occurs depending on the maximum temperature.

2nd period of growth.

All the series behaved in a similar way during the first period except with regard to the length of time that this persisted. The second period, that of active growth, is very different, and each series presents its own individual characteristics. Analysis of the results obtained, however, show that these characteristics bear a clear relation to the variable factors at work, and that the plant responds definitely and not arbitrarily to change in the environmental conditions.

(a) Relation of total growth to sunshine and temperature.

Under ordinary field conditions of cultivation the amount of water supplied as rain and the action of wind in drying out the soil and causing rapid alterations of temperature would influence the direct effect of temperature and sunlight. Under greenhouse conditions the first two factors are eliminated and the enquiry can therefore be narrowed down. In order to work out the relationship of total growth to sunshine and temperature it is essential that the growth should have occurred over equal periods, and for this reason only the first eleven weeks of each series are considered. One series, O, died after seven weeks, and this will be specially considered later on. The results are most clearly demonstrated by Fig. 3, in which are graphed for each series the total growth of the plant, the total number of hours of sunshine over the 11 week period, and the ranges of the mean weekly maximum and minimum temperatures over the same period. As would naturally be expected the total growth in summer was much in advance of that in winter. The three series C, E, G, started in October, December and January, show a steady increase in the total growth, G being more than twice as heavy as C. The available sunshine in all three cases was the same, but the range of maximum temperature was successively rather higher, though the greatest difference was only six degrees (60°–66° F.). In the dead season of the year, therefore, slight differences in maximum temperature are very important in determining the amount of growth and they act independently of the available sunshine. The ranges of minimum temperatures were similar in all three cases and therefore did not influence the result.

The optimum time for growth under the experimental conditions was spring and early summer. In the presence of an abundant and unstinted food supply series K, started in March, made five times as much growth as G, started two months earlier. Double the amount of sunshine was available and the temperature ran up steadily from a rather low level until it almost reached the maximum weekly mean attained during the season. The series M, started a month later, did not do quite as well, but this may have been due to the fact that though the highest mean temperature was the same as K the means for the last three weeks were comparatively low.

A striking point emerged when an attempt was made to grow a series O at the beginning of July. The weather was bright and sunny throughout, the seedlings were started at 80° F., for only one week did the mean temperature fall as low as 75°, and for three weeks the average maximum was above 90° F. The plants were unable to stand the strain and after seven weeks growth they were dead, having made only 28 gms. dry matter compared with 39 gms. produced during a similar period in series M more than two months earlier. The mean minimum temperatures were comparatively high, the lowest mean being equal to the highest recorded at any other period. Evidently constant high temperature combined with excessive insolation under glass are inhibitory to growth, the best results being obtained with rather less sunshine and a greater range of temperature.

Autumn plants started in September and October resembled those grown in the winter, with a certain amount of extra growth due to a rather more generous supply of sun and heat.

It is thus seen that the possible amount of growth depends directly upon the sunshine and temperature at all periods of the year, but that beyond a certain point these beneficial factors become harmful and result in the premature death of the plants. Usually the two factors work together but when one factor, sunshine, remains constant, temperature is able to act independently in influencing growth. The converse of this may also be true but has not been demonstrated in these experiments.

(*b*) *Relation of the efficiency index to the time of year and the age of the plant.*

The "efficiency index" represents the rate per cent. at which fresh material is continuously added to the plant over a definite period[1], and it provides a very useful means of indicating the rate of growth at different periods of the life of a plant. In Fig. 6 the efficiency indices are plotted for weekly periods for all the series. As has already been stated during germination the seedlings lose weight by respiration, so that at the very beginning they weigh less than the seeds from which they came, and during the early part of the first growth period a further loss occurs until assimilation is in full play. At these stages the efficiency indices are negative, but when growth has fairly set in they are always positive, except occasionally at the very end after active growth has ceased but respiration is still continuing.

The curve shows at a glance that during the summer months, while growth is rapid, the efficiency indices reach a high level; in the spring and autumn they are medium, whereas in the depth of the winter they are very low and indicate that little more growth is made than will provide material to keep the plant alive and progressing very slowly.

1 Blackman, V. H. (1919). "Compound Interest Law." *Ann. Bot.* XXXIII, pp. 353–360.

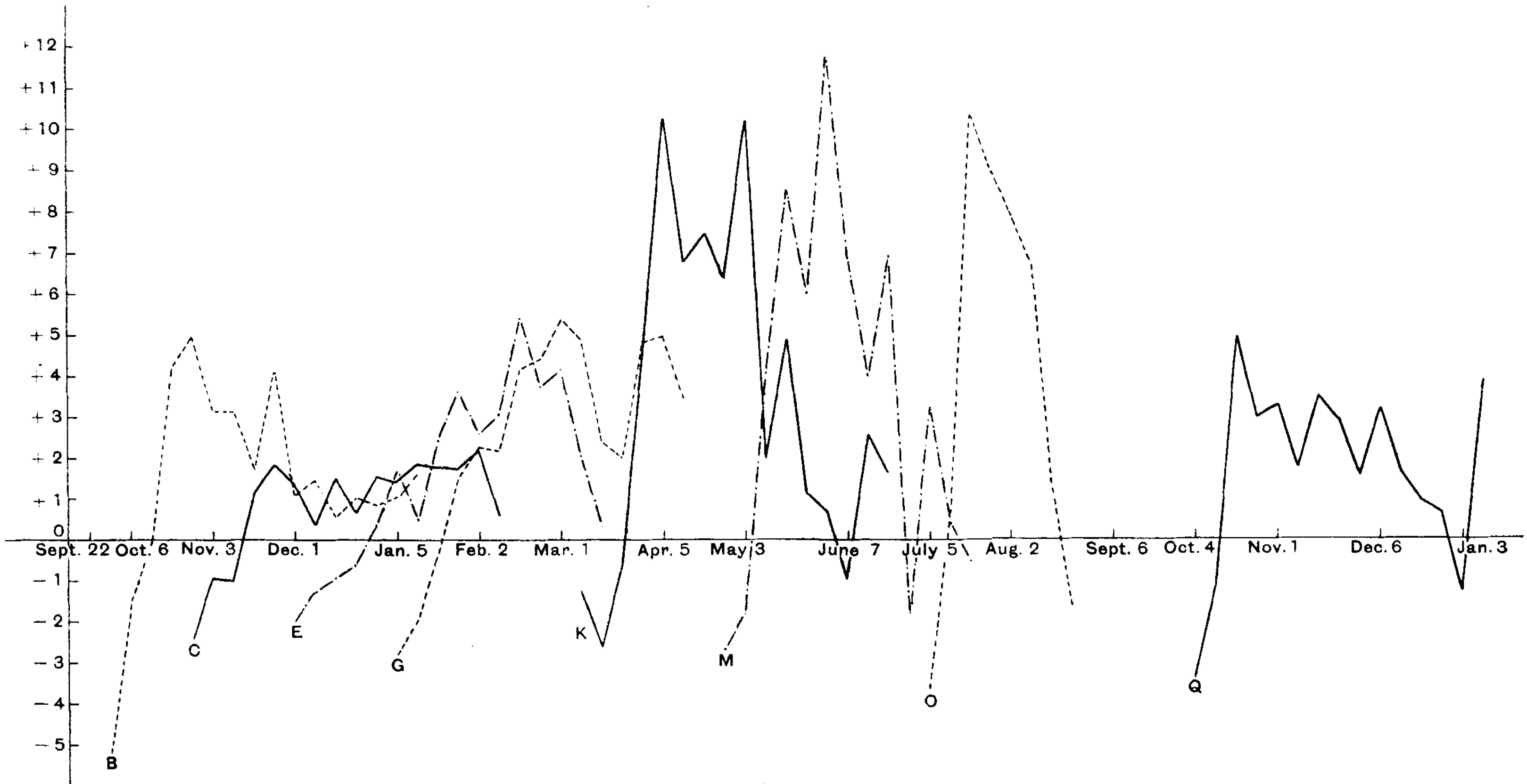


Fig. 6. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions changed weekly.

Low efficiency indices were the rule from September to April[1], nearly all being below 5. During this period practically all the maximum temperatures were below 65° F. (see Fig. 1) and although the sunshine curve was much less regular than that of temperature all the weekly sunshine totals were below 35 hours, seven being below 7½ hours (see Fig. 2). During December the efficiency indices were very low and only varied within small limits, being much the same in series of different ages, which is not usually the case. This is evidently connected with the fact that during December occurred the lowest group of maximum temperatures for the whole year, and the period also embraced the largest group of low sunshine records. A rise in the indices began in January coinciding with an improvement in both temperature and sunshine. From March to August[2] high efficiency indices, much over 5, were obtained. Throughout this period the maximum temperatures were above 65° F. except during the first four weeks when they were slightly lower. Fifty per cent. of the weekly sunshine totals exceeded 35 hours, the excess often being considerable, six totals being 50 or more hours, while none ran below 7½ hours as happened earlier in the year. Thus broadly speaking high efficiency indices are associated with high temperatures and plenty of sun, while low indices occur in cold weather with deficient light.

Within this generalisation, however, more detailed information can be worked out.

An examination of the curves (Fig. 6) shows that during the greater part of the year, from March to November, the efficiency indices rise to their maximum very early in the life of the plant, usually within one or two weeks from the close of the first period of growth. In spring and autumn this maximum efficiency index is not very great, in summer it is much larger, but, given a moderate or plentiful supply of heat and sunshine, the impulse of the plant is to attain its maximum rate of growth as early in life as possible. This, of course, tends to the production of larger plants, as rapid growth at the beginning provides a large leaf surface at an early date so that more assimilation and increase of material can take place. When plants are started in the winter, in December or January, this rapid rise to the maximum does not occur, but the efficiency indices slowly climb up, taking about five weeks from the end of the first growth period to attain their maximum. This is associated with low maximum temperatures and low sunshine totals extending over the whole life of

[1] First series started in September, last series ended in April.

[2] First series started in March, last series ended in August.

the plant, so that at no time is the growth encouraged by a spell of greater heat or more abundant sunshine. As soon as the rate of growth reaches its maximum in the spring and autumn it begins to fall off slowly and irregularly but as at these times of the year growth was not completed within the period of experiment it is not certain what the behaviour would be at the end of growth. In the summer the rate of growth tends to fall away from the maximum but remains very high for several weeks. During this period the plants probably reach their maximum efficiency, making the fullest use of the food supplied under favourable conditions of temperature and sunshine. Growth is so rapid that it draws to a close towards the end of the experimental period and this is indicated by a sudden drop in the efficiency index, which occasionally becomes negative at the very end, indicating the continuance of respiration after assimilation has ceased, possibly combined with some degree of desiccation. The maintenance of a high rate of growth for several weeks during the summer combined with a sudden later drop is in marked contrast to the slow steady fall in the earlier part of the year, and explains fully why the later sown plants are so much more weighty than the rest. The later fall in the indices is not determined by either temperature or sunshine, but is a characteristic feature in the physiology of the plant occurring towards the end of growth, but the degree in which the fall is marked does depend to some extent upon the environmental conditions, as it is more obvious when favourable circumstances have kept up a rapid rate of growth until late in the life of the plant. The importance of the rapid rise to the maximum rate of growth is well shown by series K and M, both grown in the summer months. M reached a considerably higher maximum efficiency index than K, but whereas in K the rate of growth was at its maximum within a week of the 1st period, in M three weeks elapsed before this point was reached. Consequently, in spite of the ultimate rate being higher in M, the total growth was only 71 gms. against 91 gms. in K.

In the July series O the effect of the excessive heat and insolation was not manifest at first, as the maximum rate of growth was reached at the usual time, one week after the end of the first period. The rate fell off steadily though not abnormally quickly for another three weeks, but by that time the energy of the plants was exhausted and during the next fortnight the efficiency index fell rapidly until at the end the plants were prematurely dead.

An examination of the data by statistical methods shows a remarkable agreement with the results deduced by observation during growth and comparisons of the figures and curves for the individual series.

Of the factors which affect the relative rate of increase of growth age, maximum and minimum temperatures and hours of sunshine can be investigated from the available data. The relation between age and rate of increase over the whole life is far from linear, so that the simple formulae of partial correlation cannot be applied, but the series of mean relative rates of increase may be divided into two satisfactorily linear series by separating the young plants (mean age up to four weeks old) from the old plants (mean age over four weeks). During the first period the mean efficiency indices rise to a maximum and during the second they fall from the maximum. This result bears out the observations that growth is divided into two distinct periods and that the tendency is for the maximum rate of growth to be attained at the beginning of the second period and to fall off afterwards.

When allowance is thus made for age the effect of environment upon the young and old plants must be considered separately.

The actual correlations between relative rates of increase (efficiency index) and the four other variates, age and the three environmental measurements, are

	Young plants	Old plants
Age	$+\cdot6995\pm\cdot063$	$-\cdot3498\pm\cdot065$
Mean maximum temperature	$+\cdot4444\pm\cdot097$	$+\cdot3907\pm\cdot063$
Mean minimum temperature	$+\cdot3958\pm\cdot104$	$-\cdot0588\pm\cdot074$
Bright sunshine	$-\cdot0132\pm\cdot123$	$+\cdot5177\pm\cdot056$

The quantities measure the extent to which the variables concerned are actually associated; growth in young plants is thus associated with relatively warm days and nights but not significantly with sunshine, in the older plants it is associated strongly with sunshine and warm days but not significantly with the night temperatures.

The combined effect of the independent variation of these four quantities may be expressed by regression formulae, the coefficients of which can be calculated from the correlations. If A stand for the age measured from a mean value of 2·5 weeks and 10 weeks for young and old plants respectively, C the mean maximum temperature measured from 67° F., D the mean minimum temperature measured from 46° F. and E the hours of bright sunshine in excess of 21 per week, then the relative rate of increase of young plants has the regression formula

$$\cdot03 + 1\cdot9544A + \cdot3586C - \cdot0190D - \cdot1551E,$$

while for the old plants it is

$$2\cdot91 - \cdot2121A + \cdot07515C - \cdot2320D + \cdot0619E.$$

In interpreting these formulae it should be remembered that as *C*, *D* and *E* are closely associated the alteration of any one of them without the other is to some extent an unnatural process. Thus the fact that in both formulae the coefficient of *D* is negative, in the first to an insignificant extent but in the second significantly, shows that the greater growth has in general been made with the lower night temperatures *after allowance has been made* for the cooler days and less sunshine which are in fact associated with cooler nights. In the same way sunshine is detrimental to the seedlings *after allowance has been made* for its beneficial effect upon the day temperatures. Once the average effect of the environmental conditions is ascertained it is possible to obtain a truer representation of the relative rate of growth at different ages. For this purpose the average of the relative rates of increase for any age is corrected by means of the regression formula to its probable value under standard environmental conditions. The result of so doing is shown by comparing Figs. 7 and 8. The falling off of growth with age is more gradual after allowance has been made for changing environment; the points lie closer to the regression line for the older series, but the four first series are distinctly less linear. The whole series so corrected is likely to give a much truer picture of the normal history of the plant than when no correction is made. On the other hand, it is clear that irregularities are still present though they are smaller, and the three measures which have been used evidently do not give a complete picture of the plant's environmental experience during the week to which they refer. Among the other factors of environment that cause these irregularities are probably the distribution of the hours of sunshine over the day and week, the variation in the actual intensity of light apart from bright sunshine and the humidity of the surrounding air.

The abrupt rise in the relative rate of increase for the mean 9th period may possibly be mere coincidence but is more likely to have a physiological significance. Examination of the actual curves of efficiency indices show that somewhere in the neighbourhood of this period a real or secondary maximum efficiency index occurs, and in several cases the data show that just at this time the plants were in their first flush of flowering. This rise may therefore be real and connected with the initiation of sexual reproduction. If this be so it affords an interesting parallel to the increase in growth occurring at the time of puberty in human beings[1].

[1] Hall, G. S. (1908). *Adolescence*, Vol. I, pp. 59, 84, 93, 99.

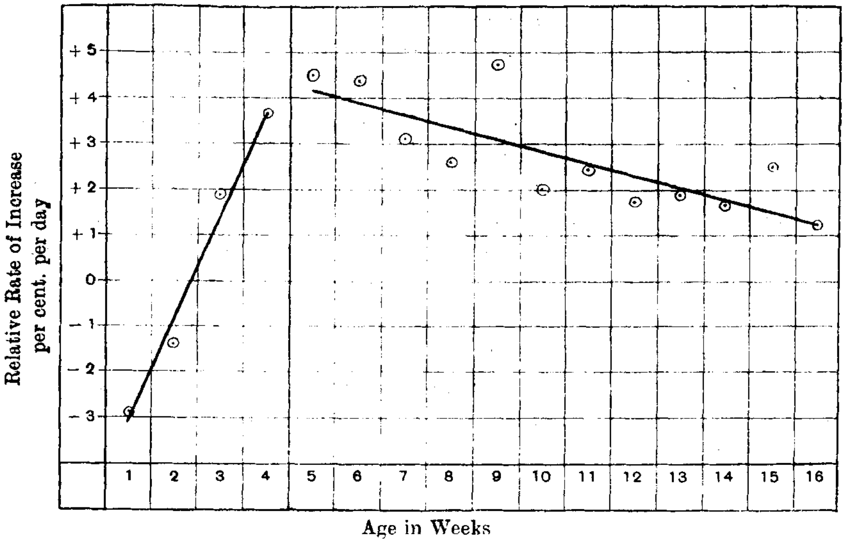


Fig. 7. Mean relative rate of increase at each age, with regression lines for young and old plants.

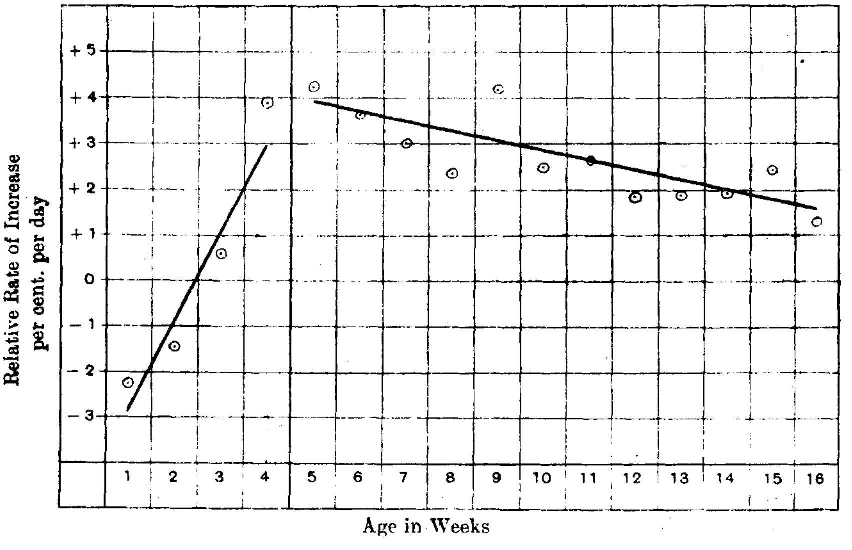


Fig. 8. Mean relative rate of increase at each age reduced to standard conditions, with regression lines for young and old plants.

{ Mean Maximum Temperature—67° F.
Mean Minimum Temperature—46° F.
Bright Sunshine—21 hours.

B. NUTRIENT SOLUTIONS NEVER CHANGED.

1st period of growth.

The series in which the solutions were never changed were set up to correspond in time as closely as possible with those in which the food was renewed. The following table shows how exactly the two sets correspond with regard to the length of the first period of growth.

Solutions never changed			Solutions changed		
	Series started	Length of first period of growth for shoot Weeks		Series started	Length of first period of growth for shoot Weeks
A	*Sept. 23rd*, 1915	2	B	*Sept. 28th*, 1915	3
D	Oct. 29th	6	C	Oct. 28th	6
F	Dec. 4th	7	E	Dec. 2nd	7
H	Jan. 5th, 1916	4	G	Jan. 4th, 1916	4
I	Feb. 19th	4	No corresponding set		
L	March 10th	3	K	March 10th	3
N	April 26th	2	M	April 26th	2
P	July 3rd	1	O	July 3rd	1
R	Oct. 3rd	2	Q	Oct. 3rd	2

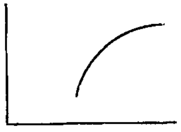
The only instance in which the first period varied by even a week was when there was five days difference in the date of beginning the experiment. At that time of year, in September, both temperature and sunlight were falling and the difference of nearly a week would fully account for the prolongation of the first period of growth in the later started plants. This series is therefore left out of consideration in drawing up comparisons. The close correspondence shows that during the first period of the plant's development under the experimental conditions the presence of an excess of nutrients, below toxic limits, has no effect upon growth. Very little mineral matter is sufficient to supply the needs of the seedling and the fresh quantity given when the solutions are changed is disregarded and exercises neither a beneficial nor harmful action. As a matter of fact, so little food salt is withdrawn from the solution at this time that the fresh solution added weekly closely resembles the old, and it is probable that no difference is detected by the plant.

2nd period of growth.

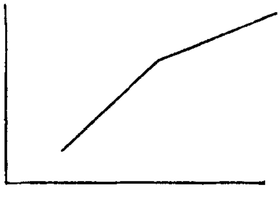
As the series with changed and unchanged food solutions were carried on together the conditions of sunlight and temperature were identical in each case, the only different factor being that in one set an unlimited supply of food was available and in the other a very limited quantity was at the disposal of the plants.

(a) Effect of restricted food supply on total growth.

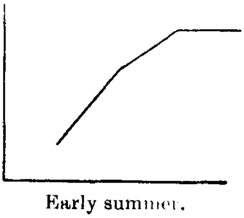
It was to be expected that the unchanged set would make less growth than the others, but the comparative relations of the amount of growth at different periods of the life of the plant are not altogether what were anticipated. As the plant grows and steadily draws on the limited food supply, the available amount of nutrient in the solution correspondingly decreases, and it might have been expected that with this decrease in available food a gradual decrease in growth would occur, giving a curve of the form



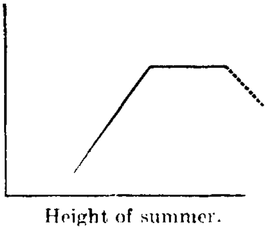
This, however, did not occur in any case. At all seasons of the year the growth in the earlier part of the second period showed a steady rise. In winter when growth was very slow the rise continued throughout the experiment; as the temperature and sunshine increased the time got shorter until eventually the rise reached its maximum in about three weeks. Then, quite abruptly, the growth changed and the curve flattened to a greater or less degree, but when once the change had occurred steady increase was again made, so that in most cases the curve took the form



In the early summer months growth ceased before the end of the experiment, causing a second flattening in the curve, whereas in the height of the summer no further growth was made after the first rise and a later drop often took place on account of loss due to respiration and desiccation.



Early summer.



Height of summer.

It is difficult to suggest an explanation as to why the abrupt changes followed by a period of steady growth should be the rule, instead of a gradual decrease in growth parallel with the gradual decrease in food. A comparison of these series (Figs. 9 and 10), with the corresponding sets with unlimited food supply (Figs. 4 and 5), shows that except during

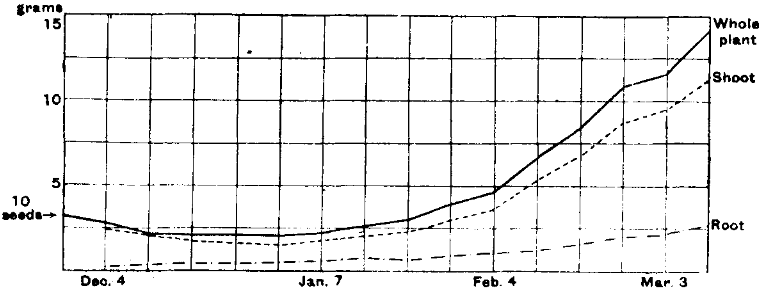


Fig. 9. *Winter Growth.* Dry weights of 10 pea plants, series F, grown from Dec. 4th, 1915 –March 10th, 1916. Nutrient solutions never changed.

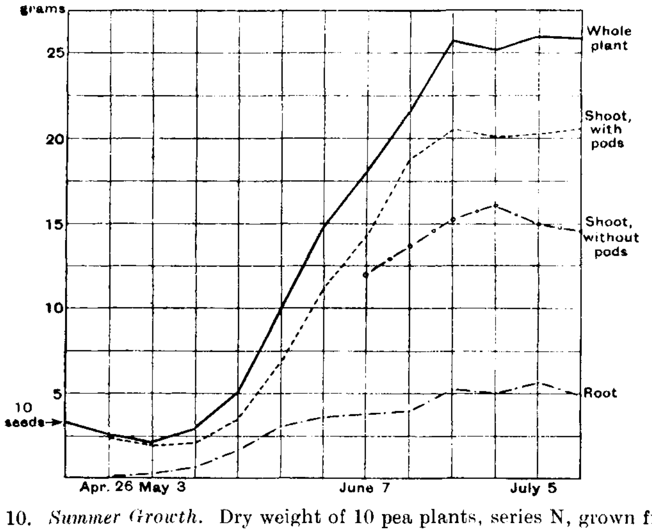


Fig. 10. *Summer Growth.* Dry weight of 10 pea plants, series N, grown from April 26th—July 12th, 1916. Nutrient solutions never changed.

the summer period of very rapid growth the amount of dry matter produced with limited and unlimited food supply is much the same or even identical for several weeks after the end of the first period, showing that the gradual reduction in food material does not always immediately affect growth. Eventually the well-supplied plants continue their steady increase but the restricted ones fall off in the manner indicated above. In the summer with optimum conditions the extra food supply is beneficial from the first as the plants have a very high efficiency index and are able to utilise the nutrients to much better advantage, but though the restricted plants cannot keep pace with the others they rise in weight quite steadily for several weeks before depression sets in. It is only in series grown inclusively from March to June that the changed series pull ahead immediately the first period closes, while during the rest of the year the plants either do not begin to take advantage of the full supply in the one case or else they do not feel the lack of the full supply in the other till a later date.

The maximum amount of growth that can be made with a given constant supply of nutrients before growth ceases varies with the time of year, *i.e.* with the environmental conditions. Plants grown during May and June averaged 26 gms. dry matter and the total ranged down to 14 or 15 gms. in plants grown in spring or autumn. The winter grown plants did not reach the stage of ceasing to grow, but judging by the trend of the efficiency index curve it is probable that the dry weight would have been below that of the spring and autumn plants. The reason for this variation in dry matter produced is probably that growth is not only dependent upon the mineral food supplied to the root but also on the quantity of carbohydrates produced by assimilation. Under favourable conditions of temperature and sunlight when assimilation is greatly encouraged the formation of carbohydrate is very rapid and the amount of other constituents of dry matter become proportionately though not actually less. This is illustrated in an exaggerated form by those plants which store up starch or sugar, as potato and beet, but it holds good in other green plants as well. When conditions are less favourable to assimilation less carbohydrate is produced in proportion to the amount of food material absorbed, and with a limited supply of the latter a lower total growth is produced.

One curious discrepancy between the changed and unchanged series is noticeable. The maximum growth with unlimited food supply was made in a series grown from March to May, but in another grown from May to July there was a decided falling off which was attributed to less favourable environmental conditions. With limited food, however, the maximum growth was made in the second set, from May to July, so that apparently the environmental conditions that are optimum for dry weight production in the presence of plenty of food are not necessarily the optimum when a restricted supply is available.

Dry Weight per plant in grams.

	Unlimited food supply	Restricted food supply
March—May	K. 9·2	L. 1·85
May—July	M. 7·2	N. 2·6

(*b*) *Effect of restricted food supply on efficiency indices.*

The general form of the curves (Fig. 11) of the efficiency indices for the various series throughout the year is much the same whether the food supply is abundant or restricted, showing that on the whole there is a similar response to the environmental conditions that are common to both sets. In detail the correspondence is less close, indicating the influence exerted by the variable factor of food. In most cases during the earlier weeks the rates of growth go up or down together in both cases, as at this stage the environmental conditions of temperature and light common to both are more potent than the variation in food supply. Later on, when food begins to be much restricted in the one set, the efficiency index curves no longer run together, and they become much more irregular and erratic in the starved series. Under the conditions of restricted food supply, therefore, changes in the common environmental conditions produce exaggerated effects on the rate of growth. The foregoing applies more particularly to the spring and autumn months, but matters are rather different during the period of most rapid growth in the summer. At this time the conditions of light and heat are so favourable to growth that the plants can take advantage of a very large supply of food, and any restriction in this respect is felt more severely than when growth conditions are less good. Both sets of plants make the most of the available food immediately the first period of growth is over, and rise almost at once to a maximum efficiency index. This greatly depletes the food store, and when no more is supplied the rate of growth cannot be kept up and a rapid fall occurs, in contrast to the prolonged period during which a high rate of growth is maintained in the presence of abundant nutrients. In some cases the restricted plants never attain such a high efficiency index as the unrestricted, and the fall in the rate is less sharp, but in others the maximum index is as high or even higher and then an exceedingly sharp fall occurs, on one occasion (set P) the drop being from 11 to zero in three weeks.

A statistical comparison of the figures relating to the "changed" and "unchanged" series bears out the results obtained from observation of the curves of total growth, but shows more clearly the course of events in the later part of the life of the plant. The mean differences between

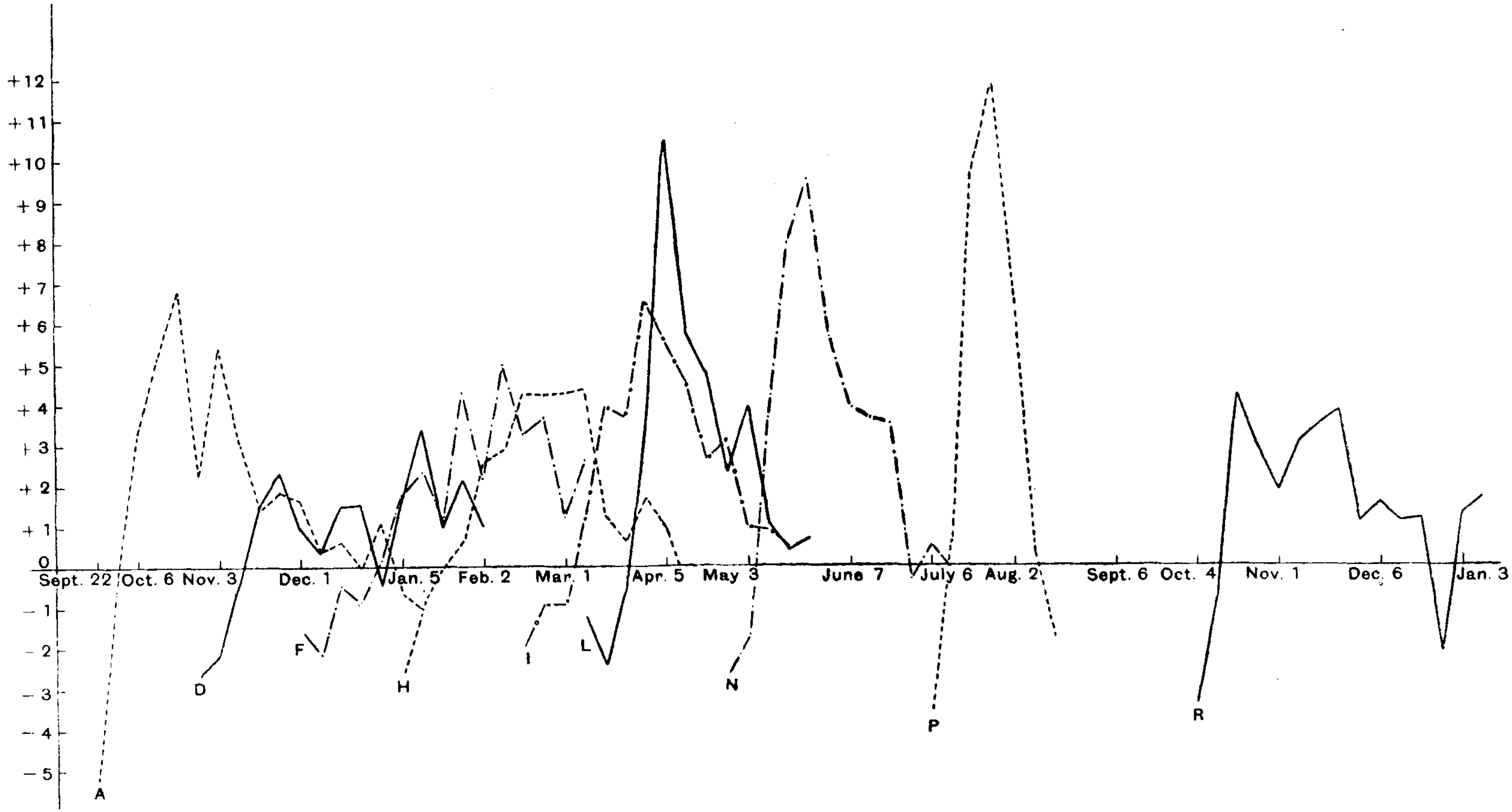


Fig. 11. Mean efficiency indices (per cent. rate of increase) per day over weekly periods. Nutrient solutions never changed.

the relative rates of increase (efficiency indices) week by week are shown in the following table, and are seen to fall into two distinct groups:

Week	Mean difference in efficiency indices of "changed" and "unchanged" series	
1	− ·109 ± ·18	
2	+ ·110	− ·07 ± ·15. Difference insignificant.
3	− ·106	
4	− ·062	
5	− ·220	
6	+ 1·647	+ 1·19 ± ·20. Difference definitely significant.
7	+ 1·119	
8	+ ·993	
9	+ 1·768	
10	+ ·667	
11	+ 1·116	
12	+ ·455	
13	+ 1·700	
14	+ ·997	
15	+ 1·707	

The insignificant differences obtained in the early weeks emphasize the fact that during the first period of growth and for perhaps a short time longer the plant gains no benefit from the constant renewal of the nutrient solutions, probably because during this time the demands on the external sources of nutrition are comparatively small, as some supply is still available in the seed and the manufacture of fresh food by assimilation is not yet in full swing. When once this period is over the variation in food supply makes itself felt at once, and this continues throughout the life-history. No constant change in the difference of the rate of increase is observable, but the variations are irregular throughout. This is somewhat contrary to expectation, as it was surmised that the drop in the efficiency indices in the unchanged series in late life would be far greater than that in the changed sets where no starvation effects were manifest. Apparently the natural fall in the indices that occurs late in life in all cases was more or less parallel to that induced in the semi-starved plants.

The correlations between relative rate of increase (efficiency index) and the three environmental measurements for the "unchanged" series are as follows:

	Young plants	Old plants
Mean maximum temperature ...	+ ·4760	+ ·1695
Mean minimum temperature ...	+ ·4170	− ·0619
Bright sunshine	+ ·0300	+ ·4263

When these figures are compared with those for the "changed" series given on page 226, it is seen that with the young plants little difference occurs, showing that in early life the amount of food supplied in both sets was in excess of requirements and did not therefore act as a limiting factor. With older plants, however, when the food solutions were not renewed the correlation of rate of increase with mean maximum temperature was very much lowered and that with bright sunshine was also reduced to a significant extent. This indicates that when scarcity of food is acting as a limiting factor the plants are unable to take full advantage of the available bright sunshine, while at the same time the beneficial influence of high maximum temperature is reduced to an even greater degree.

Another interesting point can be elucidated from the comparison of seven pairs of changed and unchanged series, each pair being grown under identical conditions for the same length of time. The total variance[1] at any given age, for older plants (in the second period of growth), may be roughly analysed into

37 per cent. fortuitous variation (due to individual difference of seeds etc.).

38 per cent. known environmental factors.

25 per cent. unknown environmental causes (irregularities of temperature and light not affecting the means, humidity etc.).

The percentage of variance (38 per cent.) that can be attributed to the known environmental causes of maximum and minimum temperatures and total sunshine is remarkably high and indicates that these are the most potent of the factors acting upon growth. The causes of fortuitous variation are less clear, and the percentage (37 per cent.) seems rather high considering that it is a mean figure, as under the greenhouse conditions the extremes of individual variation in a number of plants generally reach about the same figure, and the mean variance in the rate of increase might be expected to be less. The extent of individual variation in weight, however, regarded as a percentage difference, must not be confused with the variance of the efficiency index which is to be ascribed to various groups of causes. Further work on this point will be necessary, for if it could be more fully explained it would give more reliable information than is at present available as to the influence of the individuality of plants upon the validity of experimental results.

[1] The mean square deviation of the rate of increase at given age is used as a measure of the variance, and the percentage figures are calculated from this.

GENERAL OBSERVATIONS ON GROWTH.

(1) *Comparison of root and shoot growth.*

Inspection of the growth curves shows that at all stages of growth and at all seasons the dry weight of the root is less than that of the shoot. As the plants get older the shoot becomes rapidly heavier under favourable conditions, but the increase in root weight is by no means parallel to that of the shoot as it is very much slower, with the result that when very heavy growth is ultimately made by any plant the discrepancy in the dry weight of the root and shoot is very marked. This change in the relations between the two parts of the plant is well shown by the ratio between the dry weights of shoot and root for the weekly periods for which figures are available (Figs. 12 and 13).

In the very young seedlings, at the stage at which they are put into the food solutions, only part of the material stored in the seed has been utilised and the roots are as yet very small. Since the seed is included with the shoot the shoot/root ratio at this time is very high, ranging from about 14–32 according to circumstances[1]. From this time more normal relations establish themselves, for the seed store becomes rapidly depleted and the ratio is that between the actual shoot (stem and leaves) and the root. The shoot/root ratio continues to fall at a decreasing rate for a varying period, the lowest ratio corresponding fairly closely with the end of the first period of growth, though it may be reached a week or two earlier or later. From this time onwards, when there is no deficiency of food (Fig. 12), the shoot increases more rapidly than the root in weight, and the shoot/root ratio goes steadily up. The more rapid the growth, the more marked this rise, and in the summer months under optimum conditions of temperature and light the low proportion of root to shoot is most striking. When the food supply is limited (Fig. 13) and less growth is made the figures do not reach such a high level, but exactly the same course of events is noticed, as a rise in the shoot/root ratio occurs from about the end of the first growth period and the largest ratios are obtained in the summer months.

An explanation of this change in the proportion of shoot and root may be found in the different mechanical construction of the two parts. The two main functions of the root are the absorption of water containing dissolved food substances and the fixing of the plant in the substratum. For the efficient performance of the first function a large area

[1] For economy of space this initial high ratio is omitted from Figs. 12 and 13, the first ratio on the curve being that obtained after one week's growth in nutrient solution.

capable of constant renewal is desirable in order that the maximum proportion of root hairs, the actual absorbing organs, may be provided and renewed as they die off. The root, with its multiplicity of long slender

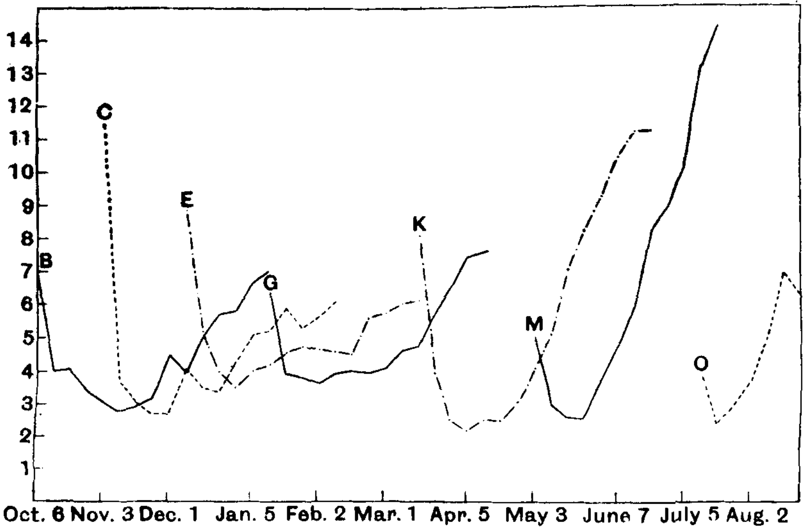


Fig. 12. Shoot/Root Ratios for weekly periods. Oct. 6th, 1915—Aug. 23rd, 1916. Nutrient solutions changed weekly.

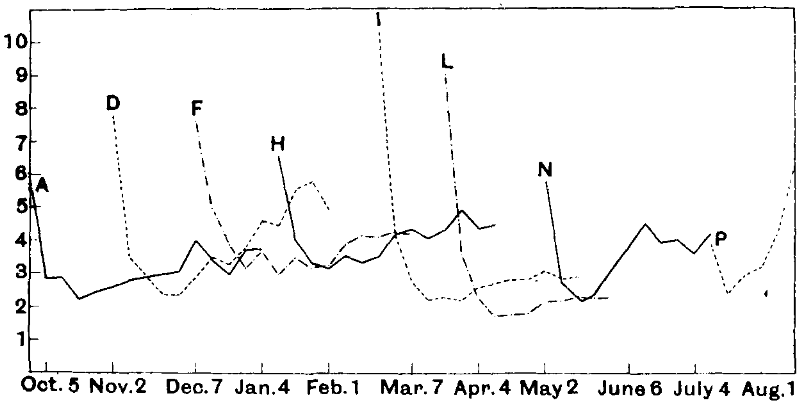


Fig. 13. Shoot/Root Ratios for weekly periods. Sept. 28th, 1915—Aug. 15th, 1916. Nutrient solutions never changed.

branches continually growing in length, fulfils this condition admirably and each addition of an extra rootlet provides an additional absorbing surface out of all proportion to the quantity of plant material used up in the production of the rootlet. In this way a great increase in absorption can be provided for with comparatively little increase in the dry weight of the root. The same structure is also the most economical for the performance of the second function of fixation, as the multitude of fine strands result in a very effective supporting agent. The shoot, on the other hand, is chiefly concerned with the processes of respiration, transpiration and assimilation. For these a considerable bulk of tissue is desirable in order to provide an adequate supply of intercellular spaces, chlorophyll and storage tissue and also that a broad surface may be presented to make the most effective use of sunlight in the elaboration of food material. In order to carry a great expanse of leaf stout stems are necessary, and consequently a large amount of material has to be used in the construction of the shoot. As the plant gets older, the root is increasing its absorbing capacity at the expense of comparatively little new material while the shoot is using up a great deal for growth and may also be acting as a storehouse of reserves, so the relative weights of the two parts tend to diverge more and more. The more rapid the growth, the more rapid the divergence, as is shown graphically by the large shoot/root ratio attained under optimum conditions.

The behaviour of root and shoot with regard to temperature is distinctly different. It has already been shown that during the first period of growth, whatever the season and the temperature, the weight of the shoot falls and then rises again, whereas the root increases steadily in weight from the beginning. After this period the temperature factor is very potent. The shoot weight at all seasons continues to rise, slowly with low mean maximum temperatures, rapidly with high mean maxima. Under no circumstances with the mean maxima attained in this experiment did the increase in dry weight of the shoot cease even for a time until the very end when growth was completed. Up to a certain limit, also, increase in the rate of shoot growth is correlated with rise of temperature. Root growth, on the other hand, is much affected by low mean maximum temperatures, and practically no advance was made in any series, irrespective of the food supply, from mid-November to January, over a period during which the mean maxima were consistently below 60° F. Rise in temperature does not have the same relative beneficial action on the root that it does on the shoot, as no sharp rises in root weight could be detected when temperatures went up. There is some indication that whereas the roots can grow satisfactorily in high temperatures when they are subjected to plenty of heat from an early period of life, root growth is severely checked or even stopped if a sudden and prolonged increase in temperature occurs when the plant is well developed, but this check in root increase does not necessarily imply a corresponding check to the shoot.

Cessation of root increase is a constant phenomenon and always occurs some time before the shoot stops growing. In some cases there is evidence that an actual decrease in weight occurs after this period but as this is most marked in the plants which are grown in constantly changed food solution it is possible that the loss may be partly due to abrasion in the mechanical process of handling, the loss not being made good by growth. Without further information it is impossible to say whether this loss of weight in the roots is of real significance.

(2) *Shoot growth and pod formation.*

As the duration of the tests was limited to a certain number of weeks few of the series reached the stage of pod formation. Of these, three received abundant food and one was limited in this respect. As soon as pod formation begins the rate of growth of the stem and leaves, excluding the reproductive organs, falls off immediately and relatively little extra weight is put on, though the increase in weight of the whole shoot is exceedingly rapid (Figs. 4 and 10). Up to the time of flowering the energy of the plant is directed to building up a healthy body capable of bearing the strain of reproduction. When seed formation begins the energy is diverted into this channel, and the shoot (stem and leaves) becomes merely the agent whereby the necessary materials for building up the fruit and seed are supplied. Consequently it is now unnecessary for more food to be expended in the production of a bigger shoot, so little increase takes place and there is evidence that at a later stage still loss of weight occurs owing to the transference of the actual substance of the stem and leaves to the seed. This transference has been proved in the case of certain other plants, among which barley and wheat may be instanced[1]. The most rapid increase in the weight of the pods occurs during the first two or three weeks after they appear, after which the increase slackens off till eventually a drop in weight may occur associated with the onset of maturation and desiccation.

(3) *Relation of nitrogen absorption to dry matter produced.*

A true estimate of the amount of nitrogen taken up can only be obtained by analysis of the plant itself, but labour difficulties during the war rendered it impossible to have the necessary analyses made. In

[1] (*a*) Brenchley, W. E. and Hall, A. D. (1909). "Development of the Grain of Wheat." *Journ. Agric. Sci.* III, pp. 195–217.

(*b*) Brenchley, W. E. (1912). "Development of the Grain of Barley." *Ann. Bot.* XXVI, pp. 913–928.

a few series, however, the water culture solutions were sampled at intervals and the nitrogen present estimated as potassium nitrate. These figures indicate the amount of KNO_3 that had disappeared from the solutions in a given time and enable some idea to be formed of the amount of nitrate taken up and utilised by the plant in the production of varying weights of dry matter. The great objection to this method of estimating the nitrogen absorption is that the amount of nitrogen that is lost by decomposition or denitrification is probably a variable unknown quantity for which it is difficult to devise a method of determination. Tests made at various times with solutions allowed to remain in the bottles for some days or weeks without any plants growing in them seem to show a slight loss of nitrate, though this is not very considerable even after the lapse of some time. The figures obtained in the present experiments are probably sufficiently accurate to give a true indication of the trend of affairs even though the actual quantitative measure they represent cannot be fully accepted.

Analyses of the solutions for KNO_3 were made at various times in the unchanged series L and N and the changed series K and M. When the solutions were unchanged the KNO_3 available throughout the life of the plant was only ·6 gm. per plant and by the time the experiments were finished very little or none of this remained in the solutions. The results obtained in these cases are summarised in Table I, in which the figures apply to the unit of ten plants, grown in six litres of solution.

Table I (Solutions not changed).

Date	After — weeks growth	KNO_3 lost from 6 litres solution	Dry weights of 10 plants produced in period	Ratio of KNO_3 lost to dry matter produced over whole period
Series L		grams	grams	
April 21st	6	4·02	8·044	1 : 2·00
May 12th	9	5·76	14·887	1 : 2·59
May 19th	10	5·76	15·337	1 : 2·63
Series N				
May 10th	2	·96	0·359	1 : 0·37
May 17th	3	1·89	2·520	1 : 1·33
May 24th	4	3·16	7·292	1 : 2·31
June 23rd	8	5·92	23·166	1 : 3·91

The ratio column of Table I shows clearly that as the pea plant gets older the increase in dry matter produced becomes less dependent upon the amount of nitrate absorbed by the roots, and that even when very little intake is possible owing to exhaustion of the food supplies some growth can still occur by means of photosynthesis. It appears that early in life, before the high tide of assimilation is reached, the plant absorbs a relatively large amount of nutrient salts by means of the roots without producing a correspondingly large quantity of dry matter, but as time goes on increasing amounts of dry matter are formed for the same amount of absorbed nitrate. The more favourable the season for assimilation the greater the amount of dry matter ultimately produced per unit of KNO_3, as is seen from the fact that for every gram of KNO_3 3·91 gms. of dry matter were produced in series N in the summer months against 2·63 gms. in series L in late spring.

In the changed series K and M a fresh supply of nitrate was added every week and the results give the measure of absorption and growth for weekly periods, instead of extending over the whole life of the plant to date as in the former case. Under these circumstances it is to be expected that greater irregularity will occur in the figures, as the constant changes in environmental conditions will only be averaged up for a week instead of for the whole time of growth. Even so, however, there is some indication, especially in series M (Table II), that as the plant gets older relatively less nitrate is utilised in the production of dry matter, though the evidence is less conclusive than where semi-starvation occurs.

These results bring out the fact of the relative greater importance of assimilation at the time of heavy growth, when more efficient use is made by the plant of the food material absorbed by the roots. For full information on this point it would be necessary to have a series of analyses of the plant and the nutrient solution at regular intervals in order that the various factors introduced by loss, absorption and assimilation might be examined and correlated.

Table II (Solutions changed).

Date	At end of — week	KNO_3 lost in the week from 6 litres solution	Dry weights of 10 plants produced in the week	Ratio of KNO_3 lost to dry matter produced in the week
Series K		grams	grams	
April 14th	5th	2·34	3·176	1 : 1·36
„ 21st	6th	1·65	5·738	1 : 3·48
May 12th	9th	3·72	6·650	1 : 1·79
„ 19th	10th	4·14	20·984	1 : 5·07
„ 26th	11th	3·52	5·847	1 : 1·66
Series M				
May 10th	2nd	1·29	·737	1 : 0·57
„ 17th	3rd	1·89	2·409	1 : 1·27
„ 24th	4th	2·46	2·792	1 : 1·14
June 23rd	8th	4·44	16·509	1 : 3·72

SUMMARY.

1. Growth may be divided conveniently into two well-marked periods.

(*a*) *1st period*, from the seedling stage till the time that the plant regains its initial weight after the loss by respiration, *i.e.* the time during which a casual observer would say the plant "makes no growth."

(*b*) *2nd period*, succeeding the former, during which the plant is obviously making growth, and which continues till the latter ceases and desiccation sets in.

2. The length of the first period varies inversely with the mean maximum temperature, as the rate at which assimilation is able to make good the loss by respiration increases directly with rise of temperature, up to a certain limit.

3. The possible amount of growth as measured by the dry matter produced depends directly upon the bright sunshine and temperature when the food supply is adequate, but when the latter is limited the total growth is much less owing to the lack of material for building up the tissues. Beyond a certain limit, however, the beneficial factors of heat and bright sunshine become harmful and result in the premature death of the plant.

4. During the first period the rate of growth as shown by the efficiency index was associated with relatively warm days and nights, bright sunshine having little significant effect; the light, however, was good throughout for the season of the year. During the second period the rate was associated strongly with sunshine and warm days, but not significantly with the night temperatures, which did not fall below 32° F.

5. During the greater part of the year the maximum rate of growth (highest efficiency index) is reached early in life, very soon after the second period begins. Under favourable environmental conditions a high rate of increase is then maintained for several weeks, but in less favourable circumstances the efficiency index rapidly falls. In winter, when temperatures rule low and there is little bright sunshine, the maximum rate of growth is not reached till several weeks after the beginning of the second period, and even then the efficiency index is not very great.

6. Plants with a restricted food supply make less total growth than those with abundant food. The falling off in the amount of dry matter produced does not seem to be gradual but is marked by definite periods of which the incidence varies at different seasons.

7. Broadly speaking the response of plants to the environmental conditions is similar whether the food supply is abundant or restricted,

though the mean rate of growth is lower when food is scarce. During the first period the excess of food has no significant effect upon the rate of growth, but during the second period the mean differences in the rate of increase in the presence of abundance and of scarcity of food are strongly significant in favour of the well supplied plants.

8. During the early weeks, corresponding approximately to the first period of growth, the shoot/root ratio falls, owing to the steady increase in root weight which is associated at first with a decrease and later with an increase in shoot weight. During the second period of active growth the shoot increases in weight far more rapidly than the root, and thus the shoot/root ratio rises steadily. Increase in shoot growth is closely associated with rise in temperature, though the lowest mean maximum attained in the experiments did not cause a cessation of growth. Root growth is much affected by low mean maximum temperatures and practically ceased, under the experimental conditions, when they were consistently below 60° F. Rise in maximum temperature had much less beneficial action upon the roots than upon the shoots.

9. In early stages of growth the amount of nitrate absorbed by the plant is relatively large in comparison with the dry matter produced, but later on more dry matter is formed in proportion to the same amount of nitrate, owing to the accumulation of the products of assimilation.

In conclusion I wish to express my indebtedness to Mr R. A. Fisher, who has examined the figures and has furnished me with the statistical information embodied in this paper.

NOTE.

SOME FACTORS IN PLANT COMPETITION

(THIS *JOURNAL*, VOL. VI, NOS. 2 AND 3, 1919.)

By an oversight the weights of the barley and mustard seeds, used in the calculation of the efficiency indices, were omitted.

Mustard.	Tables I—II,	pp. 145—147.	Average wt. per seed	·007 gm.
Barley.	Tables III—VI,	pp. 149—150.	,, ,,	·055 ,,
Barley.	Tables IX—XVI,	pp. 162—167.	,, ,,	·065 ,,

In each case the efficiency indices are per cent. per day.