EFFECT OF HIGH ROOT TEMPERATURE AND EXCESSIVE INSOLATION UPON GROWTH.

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(With 2 Text-figures.)

In an earlier paper (3) it was demonstrated that the reduction of light due to the over-crowding of barley plants brings about a condition of light starvation which has a harmful effect upon growth, even when an abundance of food and water is supplied to the roots. The suggestion was made that this factor of light competition might be equally or even more important in the case of broad-leaved plants, as greater overshadowing might occur.

To test this water culture experiments were repeated several times with peas at different seasons, 64 plants being closely crowded in a solid square, and 64 others having abundant room to prevent any shading of one another. The nutrient solutions were changed frequently and the tendrils of the peas were cut off as early as possible to prevent damage from one plant clinging to its neighbour when being moved.

Sutton's[1] Harbinger peas were used throughout.

In a test carried on from September 10th to December 21st, 1920, the prevailing conditions were:

Average weekly maximum temperature of house	9–26° C.
,, ,, minimum ,, ,,	2–11° C.
Total hours of sunshine per week	45·9–48

Temperature and sunlight both fell off considerably during the latter half of the experiment.

[1] We are indebted to Mr Martin Sutton for the gift of all the seeds used in these experiments.

From a comparatively early date the advantage seemed to be with the spaced plants, and became more marked as growth proceeded and the intensity of light decreased with the waning season. The difference in shoot growth was not noticeable for several weeks, but the roots of the spaced plants soon became strong and bunchy, being larger than any of the crowded roots. In the latter the roots on the outside were comparatively strong, but decreased steadily in size towards the middle of the square, where they were fairly long but very thin. At harvest-time the spaced plants were strong and healthy, well branched, bearing plenty of long well-filled pods, while the roots were very strong. In the crowded square, on the other hand, the middle plants were obviously smaller in all respects than the outer, the difference being now as noticeable in the shoots as in the roots. Most of the pods were thin and distorted, and the seeds had not developed properly.

Table I.

Dry Weights. (Mean figures.)

	Shoot	Root	Total	Efficiency index
Spaced plants:	3·488 ± ·081	·474 ± ·016	3·962 ± ·095	2·253 ± ·024
Crowded plants:				
Outer rank	2·478 ± ·057	·332 ± ·009	2·810 ± ·066	1·953 ± ·022
2nd	1·726 ± ·093	·236 ± ·011	1·962 ± ·102	1·609 ± ·046
3rd	1·348 ± ·055	·173 ± ·010	1·521 ± ·065	1·402 ± ·041
Inner	1·574 ± ·061	·207 ± ·012	1·781 ± ·072	1·556 ± ·039

The above table shows how seriously the reduction of light due to overcrowding affected the growth of peas. A large reduction in dry weight and efficiency index occurred at the outer edge of the square, although one side of each plant was free from light competition, and this reduction was intensified inside the square, where shading came on all sides. Apart from the outer row the differences between the plants were not very marked, showing how effective is the shading of pea plants by their neighbours when in close proximity. Broadly speaking, these results are comparable with those obtained for barley, and indicate a similar reaction of broad- and narrow-leaved plants to light deficiency. The percentage of nitrogen in the spaced plants was lower than in the crowded ones, being only 3·62 per cent. against 4·15 per cent. As with barley this probably shows that peas utilise less nitrogen in the production of each unit of dry matter when adequate illumination is available.

When, however, the above experiment was carried on under conditions of very high temperature and prolonged intense sunshine, certain differences in behaviour manifested themselves which demanded closer investigation.

Between May 7th and June 25th, 1920, the following conditions prevailed:

Average weekly maximum temperature	27–35° C.
„ „ minimum „	8–13° C.
Total hours of sunshine (per week) ...	49·3–65·7
Daily average hours of sunshine ...	8·4

It was soon evident that the crowded plants were making the better growth; they were larger and greener than the spaced plants, some of the latter becoming yellowish, with leaves that inclined to shrivel. The crowded peas maintained their apparent lead, and when cut were mostly healthy and green, with only four casualties, whereas many of the spaced plants were pale in colour and 15 out of the 64 had succumbed.

The effect of competition was evident in the crowded square, as the outer plants averaged 2·127 ± ·065 gm. and the average of the inner ranks varied from 1·523 ± ·185 to 1·686 ± ·058. The spaced plants, however, failed to demonstrate the advantage of the extra light they had received, as their mean weight was only 1·912 ± ·042 gm., less than the outer rank of the crowded set.

A marked difference was noticeable between the plants in the spaced set. Those which were green and healthy had good stiff roots studded with rather outstanding sturdy laterals, whereas in those in which the upper leaves were turning pale the roots looked unhealthy and brown, and were flabby and inclined to be slimy. The worse the shoot the worse the root. The green healthy plants were of the normal type, with one tall shoot and large dark green leaves, whereas those with pale shoots were bushy at the base, owing to the development of axillary buds. This was apparently due to an effort to overcome some detrimental factor acting upon the spaced peas and preventing them from developing normally, for in the earlier experiments with barley the crowded plants also appeared to make the larger growth on the whole, but were not so heavy as the spaced plants when cut. Even the outer rank of the crowded plants showed the influence of this adverse factor to some extent, as the mean weight was not very much above that of the inner plants which were under the influence of more light competition. As in the first experiment described the plants within the square were all very similar in growth and weight.

The harmful effect was obviously due to the prevailing high temperatures or the excessive power of the sun's rays, or both, but the relative importance of these two factors was by no means clear. For several years it has been noticed that plants fail to do well in the greenhouse in hot summer weather, whereas the same species flourish outdoors at the same time, and it was suspected that the high temperatures reached by the culture solutions had some connection with this phenomenon (4). An examination into temperature conditions was therefore undertaken.

In the last experiment described (p. 199), temperature readings of the nutrient solutions taken on various occasions on hot days showed very considerable differences according to the situation of the plants. Two typical records were as follows:

	Air temperature (shade)	Crowded plants		Spaced plants
June 7th, 2.30 p.m.	23° C.	Outer rank	19° C.	25·5° C.
		2nd „	16° C.	
		3rd „	15·5° C.	
		Inner „	15·5° C.	
June 25th, 10 a.m.	24·5° C.	Outer rank	20° C.	22·5° C.
		2nd „	18·5° C.	
		3rd „	18·5° C.	
		Inner „	18·5° C.	

On hot sunny days, therefore, the spaced plants were liable to be subjected to very high temperatures at the root, on occasion exceeding that of the air. In the crowded square, however, the outer ranks received a partial shelter from their neighbours and the solutions never became so hot, while within the square all the temperatures were usually very even, within a very few degrees, and were somewhat lower than the others. Under these conditions the crowding apparently served as a measure of protection either by keeping down the root temperature or by the reduction it effected in the amount of sunlight reaching the leaves. It is obvious that beyond a certain limit the effect of high root temperatures and of abundant sunlight became directly harmful and inhibited growth, but the extent to which each factor was responsible was not shown by the data obtained.

Further knowledge on this point was gained from a similar experiment carried on in the abnormally hot autumn of 1921, when readings were made of the daily maximum and minimum temperatures of the solutions of specified plants. No shading was applied to the greenhouse, and the sun's rays struck through the sloping roof directly on to the crowded square and some of the spaced plants, while the rest of the latter were on a side bench under a higher roof at a different angle, from which the concentration of the sun's rays seemed to be considerably less, though the light intensity was apparently not affected. The environmental conditions were as follows:

Average weekly maximum temperature of house	23·6–31° C.
,, ,, minimum ,, ,,	10·0–15·3° C.
Total hours of sunshine (per week)	21–52
Daily average hours of sunshine	5·8

In this case the crowded plants showed less difference among themselves than usual, the outer ones averaging 1·681 gm. against 1·339 gm. for the inner. The spaced plants alongside were seriously harmed, and only produced 1·055 gm. dry matter.

The temperature records of the solutions were:

	Highest max.	Lowest max.	Mean max.	Highest min.	Lowest min.	Mean min.	Diff. between daily max. and min.
A. Spaced (under sloping roof)	29·5° C.	16° C.	26° C.	17° C.	8° C.	13·5° C.	21–2° C.
B. Corner of square	29·5° C.	15° C.	22° C.	17° C.	8·5° C.	13·5° C.	15·5–1·5° C.
C. Middle of square	23·5° C.	14° C.	18·5° C.	20° C.	12° C.	16° C.	6·5–0·5° C.

In these spaced plants the mean maximum temperature was very high, and for a period of seven successive days the solutions ran up to above 29·7° C., the highest reading of the thermometer. The differences between the day and night readings were therefore often large, although the mean minimum did not fall below that of the outer crowded square. A surprising difference was evident with the spaced plants on the side bench. These grew well and strongly, looked better than any of the crowded plants, and when cut averaged 2·171 gm. dry matter against the 1·055 gm. of the spaced set under the more sloping roof, *i.e.* they were twice as heavy. Daily temperature records were not taken for this set, but on several occasions readings were made of all the solutions, and they were always approximately the same for both sets of spaced plants.

	Oct. 5th, 2 p.m.	Oct. 6th, 2 p.m.	Oct. 11th 12 noon
Spaced, on side bench	31° C.	28·5° C.	24° C.
Spaced, under sloping roof	31° C.	28·5° C.	25° C.
Air temperature	28·5° C.	28° C.	26·5° C.

The relation of temperature to growth has been considered by various workers, but generally in connection with the rate of growth of the roots of seedlings during short periods covering a few hours at most. Under these conditions Leitch (7) found that for peas 30° C. is a critical temperature above which growth is adversely affected, 28–30° C. being the optimum, considered as the highest temperature at which no time factor is operating. Lehenbauer (6), working with maize i water cultures, showed that the optimum temperature varied with the period of exposure, and that with prolonged exposure to the initial optimum the rate of growth falls off rapidly. It may therefore be concluded that the higher temperatures near the optimum for short exposures exercise an adverse influence when they continue to act throughout the life of the plant. Balls (2) attributed the decrease and ultimate cessation of growth at high temperatures to the accumulation of katabolic products in the cells, prolonged exposures to submaximal temperatures favouring the rapid production of these substances.

In the experiments under consideration the initial optimum of 30° C. for peas was exceeded on nine occasions, most within a single week, the highest maximum reaching 34° C. These air temperatures were only maintained for a short time, at the hottest time of the day, the period of exposure being thus very short and rare in occurrence. The average maximum temperature ruled several degrees lower, except for the one week. Furthermore the diurnal fall to the minimum temperature was considerable, 10–15° C. or more, and, as Askenasy (1) and Leitch (7) have both demonstrated that the rate of growth follows immediately and accurately any considerable change of temperature, the slowing off of growth would permit of the reduction of accumulated katabolic products and mitigate the effects of exposure to high temperatures. It would seem, therefore, unlikely that the temperatures, *per se*, were high enough to be harmful to growth, as almost the whole of the air temperature curve fell below 31° C., the initial optimum for short period exposures, especially as the root temperatures during the same period were on the whole rather lower, though they followed the air temperatures fairly closely. The adverse factor is to be sought in the intensity of the sun's rays —much depression of growth occurring where they were focussed on the leaves under the sloping roof. The different angle of incidence of the rays on to the side bench prevented such undue concentration on the leaves, and growth was correspondingly better under similar temperature conditions. This is further corroborated by comparison with the May–June (1920) experiment. In both cases the mean weekly temperatures were very similar, as the higher summer maxima were almost compensated for by higher autumn minima. The May–June plants received far more sunshine—411 hours against 262 hours, but showed less signs of distress throughout their growth, and produced 1·913 gm. dry matter as against 1·055 gm.[1] In the summer, however, the greenhouse was shaded and the

[1] For fair comparison only those plants growing in the same situation under the sloping roof are here taken into consideration though it happens that for May–June the mean of these is the same as that of the whole series (p. 199).

leaves did not receive the full force of the sun's rays, the harmful action of excessive insolation being thus mitigated, enabling the plants to make better growth than when they were exposed to the full power of the sun, although acting over a much shorter total period in the latter case. It would appear, therefore, that a high degree of insolation (excessive power of the sun's rays) is a more potent factor for harm than either high temperature or the actual total duration of sunshine.

Further experiments were undertaken to ascertain whether the harmful effects of excessive insolation could be reduced by alteration in temperature conditions. As has been already indicated, the difference between the day and night temperatures of water culture solutions is often considerable, especially in hot weather, when it may be 22·5° C. on occasion. This is considerably greater than the fluctuation occurring under soil conditions in the open, where the minimum soil temperature remains considerably above the air minimum, especially in the summer (5), and the maximum does not rise so high as in the water culture solution under glass. In dull weather the maximum and minimum temperatures approximate more closely, as there is less heating up during the day and a less marked fall in the temperature of the glasshouse at night. A method was therefore devised whereby the plants were subjected to a more even temperature at the roots, in order to ascertain whether this affected growth to any appreciable extent at different seasons of the year. The whole of the practical work in connection with this experiment was carried through by Professor Kharak Singh, of Lyallpur, India.

Two 100 gallon tanks were set up, with an outlet pipe from below the rim running down inside to within an inch of the bottom of the tank. Water was admitted from above at the other end of the tank and kept running day and night, so that a continuous slow circulation was maintained. A platform weighted with bricks to carry the water culture bottles was so arranged as to bring the necks to the rim of the tank, just above the constant level of the water. To exclude the light from the roots black cotton covers were fastened round each bottle, as the ordinary paper coats are useless when submerged, and the necks were painted with black enamel in addition. A platform of similar height and size was placed close by to carry a set of bottles in which the variation of temperature was not controlled by a water jacket, both tanks and table being under the sloping roof of the glasshouse. Under these conditions the shoots of the peas were subjected to similar insolation and air temperature, but the temperature at the roots varied with the situation. Twenty-four plants were grown in each case, spaced far enough apart to avoid any overshadowing. Maximum and minimum thermometers were placed in several of the bottles and readings taken daily, and the nutrient solutions were changed frequently. Two experiments were carried through:

(1) In spring, during the most favourable period for growth under greenhouse conditions;

(2) In summer, during the time that premature death of the plants usually occurs.

(1) Spring Experiment.

Sutton's Harbinger Peas—April 18th to June 16th.

Growth proceeded satisfactorily with all the plants, and for some time little difference was manifest; eventually the plants on the table began to draw slightly ahead of those in the tanks, and they came into flower somewhat earlier. When cut most of the plants showed incipient signs of dying, as the upper leaves were turning yellow, indicating completion of growth, but comparatively little difference was noticeable between the two sets. The mean dry weights proved to be

	Shoot gm.	Root gm.	Total gm.	Ratio shoot/root
On table	4·284 ± ·109	·885 ± ·028	5·169 ± ·132	5·121 ± ·168
On tank	3·808 ± ·055	·753 ± ·020	4·561 ± ·056	5·215 ± ·143

The mean weekly temperatures (Fig. 1) show a difference of about 8–11° C. between the maximum of table and tank, and 3–5·5° C. between the minima. In all cases the tank maxima were below those of the table, and the minima above, as the surrounding water prevented extreme fluctuations in either direction. On the table the mean maxima ranged 15·5–22° C. above the minima, whereas in the tank the difference was only 3–5° C. Nevertheless, in spite of these considerable differences in root temperature, both as regards the actual temperature reached and the daily fluctuations between maximum and minimum, the growth of the plants was much less affected than might have been anticipated, those on the table being somewhat the heavier. The improvement in the latter case may be attributable to the higher average mean temperatures prevailing throughout the experiment, while it was also probably influenced by the rather low temperatures at the beginning, when the warmer conditions on the table gave the plants the advantage of a better start by enabling them to grow more rapidly at first. This early start was very important, as by the working of the compound interest law it gave these plants a lead which those in the tank were never able to overtake. The ratio of shoot to root was the same in each set, within experimental

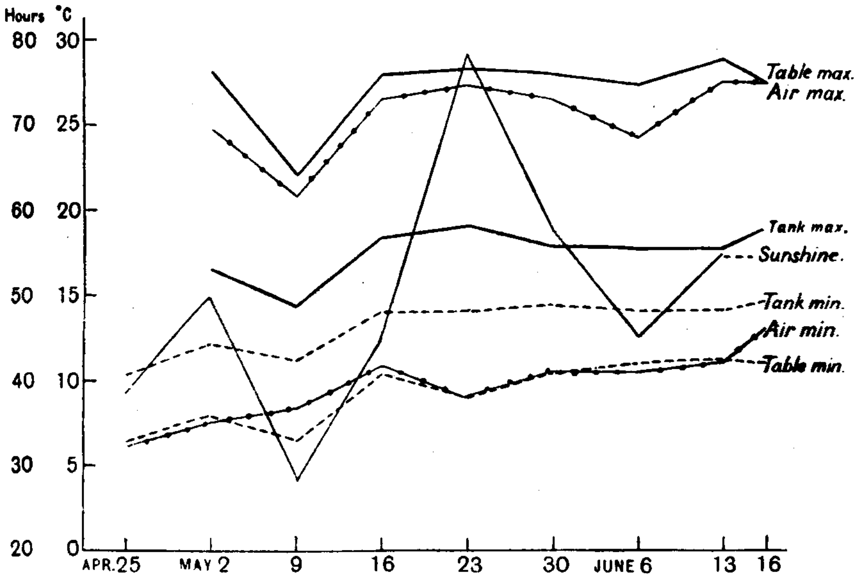

Fig. 1. Temperature records and hours of sunshine, April 19th–June 16th, 1921.

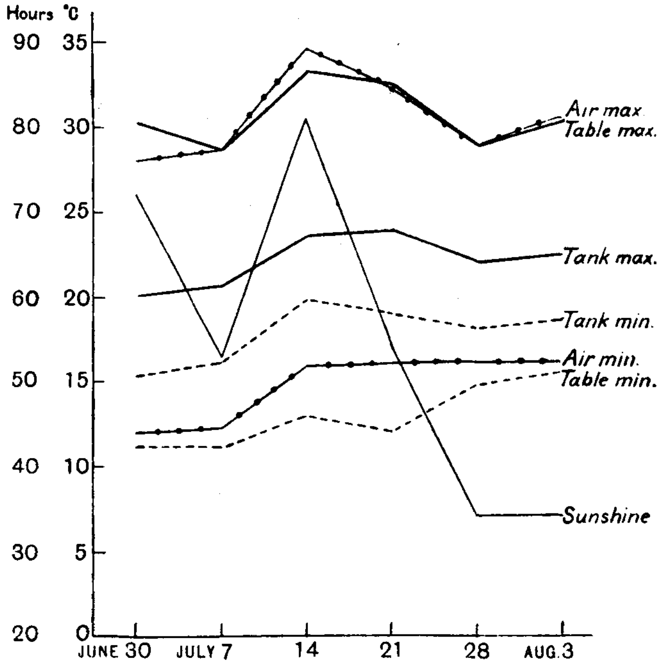

Fig. 2. Temperature records and hours of sunshine, June 24th–Aug. 3rd, 1921.

error, showing that the variable temperature had not caused any change in the development of the roots compared with that of the shoots.

The daily average of sunshine over the whole period was seven hours. During the first month the total hours per week were somewhat low, but May 16th–23rd was a very sunny week, ten to fourteen hours being registered on each of five days. After this no further period of excessive sunshine was recorded. At first the temperatures fluctuated to some degree with the amount of sunshine, but later were independent of it, for when the total sunshine dropped during the last five weeks, the mean temperature remained very constant and high, 27–28·5° C.

It would thus appear that under similar conditions of light and provided no inhibiting factor such as excessive insolation comes into play, the amount of daily fluctuation of root temperature has comparatively little effect on the growth of peas within a total mean range of 7–29° C., provided that the mean temperatures do not vary considerably. These are the limits in the experiment under consideration and possibly might be extended to some degree in either direction. Within those limits a large variation in maxima, up to 11° C., will permit of much the same amount of growth as measured by dry weight, though a low mean maximum (below 16° C.) in the early stages may cause some retardation. Growth proceeds equally well whether the temperatures at the roots are fairly even, varying within 5° C., or whether they fluctuate as much as 22° C., on the average, *i.e.* within certain limits high maximum temperatures associated with low minima have the same ultimate effect on growth as low maxima and high minima.

(2) Summer Experiment.

Sutton's Harbinger Peas—June 24th to August 3rd.

The experiment was begun in hot sunny weather when temperatures ruled very high and the number of hours of sunshine was excessive. Very soon many of the unprotected plants on the table began to show signs of distress, turning pale and wilting, and within eighteen days many were dead. In six weeks there were only four survivors, and these were small and distinctly unhappy. The plants in the tank grew well from the beginning and remained green and healthy to the end, only one failing. At the time of cutting the upper leaves were just beginning to turn yellow, showing growth was finished. The mean dry weights were:

	Shoot gm.	Root gm.	Total gm.	Ratio shoot/root
Table (4 plants only)	1·157 ± ·091	·214 ± ·026	1·371 ± ·109	5·63 ± ·478
Tank (23 plants)	1·839 ± ·007	·227 ± ·075	2·066 ± ·078	8·26 ± ·289

The plants in which the roots were protected from excessively high temperatures made therefore about half as much growth again as the unprotected survivors on the table. The increase was chiefly due to shoot growth as the roots weighed much the same in both cases, thus suggesting that the injurious action of combined strong insolation and high temperature is more marked on the assimilatory tissues than on the roots, the organs of absorption, the ratio of shoot to root being thus reduced. This is in contrast to what happens when growth is adversely affected by overcrowding, in which case the shoot root ratio increases (3), probably owing to an attempt on the part of the plant to increase its assimilatory surface in view of the decreased illumination.

Throughout the period the mean temperatures in the solutions were from 4–5·5° C. higher than during the earlier test, all being above the highest means previously registered, but the differences between the table and tank maxima and minima were very much the same in both cases. The table maxima, however, ruled very high, ranging from 28·6–33·3° C., *i.e.* at temperatures above the initial optimum, which would cause a depression in the rate of growth during their period of operation. Added to this, there was a great deal of strong sunshine during the first and third weeks, and this association of excessive insolation with high root temperatures wrought havoc among the plants on the table, and gave them a very bad start. During the last three weeks there was a great drop in the amount of sunshine, but the temperatures remained high, so that at the end of the period the temperature effect was the more marked. The same amount of sunshine, however, had far less detrimental effect when the roots were kept cooler, and not only did nearly all the plants in the tanks survive, but they made much greater individual growth.

Nevertheless, a comparison of the dry weights shows that the conditions in the later test were less favourable even in the tank, though the depreciation was not nearly so great as on the table.

Total dry weights.

	April—June gm.	July—Aug. gm.
Tank	4·561	2·066
Table	5·169	1·371

Growth in the second experiment was practically finished in six weeks instead of in eight, but with the speeding up less than half as much dry weight was produced. This may possibly be attributed to the excessive insolation rather than to the high root temperatures, as the tank maxima were much lower than the table maxima of the spring experiment and so were under the limits at which growth is adversely affected. On the other hand, the mean minima ranged several degrees (4–8·5° C.) higher than in the earlier test. Previous experiments with peas (3) have shown that with high maximum temperatures a rise in minima is disadvantageous and checks growth considerably. Temperatures of 13–15·5° C. are distinctly harmful when associated with 26·5–35° C. as maxima. In the present case the mean minima were higher and ranged from 15·5–20° C., being above 18·5° C. for most of the time, and may have exercised a harmful effect even though the associated mean maxima only reached 20–24° C. The total growth in the tank in summer may therefore have been depressed by the high minimum temperatures as well as by the excessive insolation, but the influence of these two factors cannot yet be dissociated.

Summary.

1. Under ordinary environmental conditions of temperature and sunlight the growth of peas, as of barley, is seriously hindered by overcrowding, even when each plant receives a similar supply of food and water. Not only is less dry weight produced, but the pods become thin and distorted and fail to develop their seeds properly.

2. Growth tends to be depressed in hot sunny weather when no protection is afforded. The chief detrimental factors concerned appear to be high temperatures at the roots associated with strong and prolonged sunshine, though the two factors acting individually are much less potent for harm. Under these conditions crowding shelters the roots from overheating and the leaves from too much sunlight, and up to a certain point crowded plants make better growth than those spaced well apart. Overcrowding, however, still depresses growth, probably because the light and root temperature reductions are too great.

3. Provided insolation is not excessive the amount of daily fluctuation of root temperature over a total range of about 22° C. (6·7–28·9° C.) has comparatively little influence upon growth; high maxima and low minima give similar results to low maxima and relatively high minima, provided the average mean temperatures are not too dissimilar.

4. With high root temperatures a difference in the degree of insolation or in the angle of incidence of the sun's rays may have a considerable influence on growth, a slight easing off of the solar conditions enabling much better growth to be made.

5. With very strong sunshine reduction of high maximum root temperatures (from 29° C. upwards) allows of satisfactory growth, when unprotected plants are rapidly killed. The inhibitory action of too high temperatures at the roots is thus clearly shown.

Nevertheless, the growth so made is less good than under more normal conditions of insolation, thus demonstrating the harmful action of too powerful sunlight, when all the root temperatures rule high.

6. Root temperatures appear to be of greater importance than atmospheric temperatures, as good growth can be made in hot atmospheres provided the roots are kept relatively cool.

7. There is some reason to believe that the minima are of as much importance as the maxima, *i.e.* that plants can withstand very high maximum temperatures provided there is a considerable drop to the minima, but cannot put up with the constant conditions of heat induced by fairly high maxima and high minima.

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