THE EFFECT OF AERATION ON GROWTH OF THE TOMATO IN NUTRIENT SOLUTION[1]

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(WITH NINE FIGURES)

Introduction

It has long been recognized among plant physiologists that the air relations of roots have an extremely important bearing on both the vegetative and the reproductive phases of plant growth. It has been shown many times that on submerged soils and soils impermeable to air, most plants develop poorly or die early. The most common illustration of this fact is the "drowning out" of wheat in the Spring when water collects in small depressions of the ground.

The consensus of opinion among experimenters is that the air relations of roots have a direct influence on the absorption of water and on the absorption of nutrient ions from the soil solution, as well as on the more direct respiratory requirements of the roots as needed for the continual proliferation of new root tissue and root hairs.

Experimentation has shown that it is not the excess of water itself which is injurious, since plants develop perfectly in water cultures. It is, rather, a lack of aeration resulting from root-submersion which is harmful. Many plants grown in a nutrient solution will develop successfully only when the roots have direct access to sufficient oxygen in solution, as when the solution is thoroughly aerated, or when air is carried into the solution by means of continuous solution renewal.

SACHS (**12**), in his early work with nutrient solutions, discovered that the aeration of some of his cultures resulted in increased growth. After his work in 1860, the subject was given attention by various workers from 1901 to date, and it has been repeatedly shown that lack of aeration of the nutrient medium is an extremely important limiting factor in plant growth.

ARKER (**3**), working with lupines, found that root growth was accelerated by passing air through both soil and water cultures. HALL, BRENCHLEY, and UNDERWOOD (**8**), using lupines and barley, found that aeration of the nutrient medium resulted in a 50 per cent. increase in total dry weight of plants. PEMBER (**11**), found that barley plants did not respond to aeration when grown in solutions renewed periodically every two weeks. FREE (**7**), working with buckwheat in solutions which were renewed every two weeks found that bubbling air, oxygen, or nitrogen through the culture solutions produced neither beneficial nor injurious effects, but that the same treatment with carbon dioxide caused injury within a few hours, and death after a few days.

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ALLISON (**1**) and ALLISON and SHIVE (**2**), showed that continuously renewed solutions produced soybean plants which were superior in all respects to those grown in periodically renewed solutions. Aeration of periodically renewed solutions resulted only in an increased root development. Aeration of continuously renewed solutions resulted in a marked increase of both tops and roots.

KNIGHT (**9**), using maize plants in soil cultures, found that aeration of the roots brought about a definite increase in dry weight. In water cultures, the maize plants failed to respond to aeration. It is noted here, however, that *Elodea canadensis* was used to aerate the solution, and that the quantity of oxygen liberated into the solution by this method may well have been too little to affect the growth of maize. Wallflowers and *Chenopodium album* on the other hand, showed considerable increase in dry weight when aerated by this method. KNIGHT also found that the root growth of maize was correlated inversely with the carbon dioxide content of the solution, rather than directly with the oxygen content.

CLARK and SHIVE (**5**), showed that aeration of continuously renewed solutions produced a marked increase in growth of both tops and roots of the tomato. The influence of aeration upon top growth was more pronounced than it was upon root growth. Although the plants in the non-aerated solution were much smaller, they started to blossom and fruit earlier than did those in aerated cultures. At the time of harvest (81 days) the aerated plants, however, showed evidence of yielding a much larger crop of fruit than the non-aerated plants.

LOEHWING (**10**), working with the sunflower and soybean in soil and sand cultures, found that aeration, providing less than 10 liters of air per kilogram of soil or sand per day caused early rapid growth and produced taller and heavier plants; it also resulted in larger root systems, more rapid nutrient absorption, and a much increased total weight. When more than 10 liters of air per kilogram of soil or sand was used, however, the plants were injured and retarded to a point even below that of the controls. This work suggests the possibility, under certain conditions, of reaching a point of excessive aeration which might have an adverse effect on plant growth. There is a possibility that LOEHWING's results might not apply to the aeration of a nutrient solution, where there would be no possibility of mechanical drying out of the roots.

ARRINGTON and SHIVE (**4**), using the tomato, showed that aeration of a continuously renewed nutrient solution produced a marked increase in the absorption rates of cation, anion, and total nitrogen over the corresponding rates from a non-aerated solution. Yields produced by aerated cultures were approximately double the yields produced by the non-aerated cultures. Carbon dioxide accumulation in the culture solutions was found to be without effect on growth, rate of nitrogen absorption, or oxygen content of the solutions. This work of ARRINGTON and SHIVE demonstrated that lack of dissolved oxygen in the culture solution is a limiting factor in the growth of the tomato, rather than the carbon dioxide content, as suggested by FREE (**7**), and by KNIGHT (**9**).

It will be seen from this review of experiments on lupines, barley, buckwheat, soybeans, and tomatoes, that there is much evidence to indicate that aeration of the nutrient solution produces plants superior in vegetative growth to those grown in unaerated solutions. It is also apparent that past investigators have used a number of widely different methods for supplying the nutrient solution to the plant. Some of these methods have undoubtedly resulted in efficient aeration of the solution; others have resulted in varying degrees of insufficient aeration. These various methods might be outlined as follows:

1. Unaerated, unrenewed solutions, where the plant is allowed to complete its growth without the solution's being changed, renewed, agitated, or aerated.
2. Unaerated solutions replaced periodically by removing all the old solution and refilling to volume with new.
3. Unaerated solutions renewed periodically by adding new solution to volume.
4. Unaerated solutions renewed continuously with fresh solution, added by means of a drip.
5. Unaerated solutions renewed periodically by analysis and replacement of water and absorbed salts.
6. Unrenewed solutions aerated by bubbling air through the solution.
7. Periodically renewed solutions aerated by bubbling air through the solution.
8. Continuously renewed solutions aerated by air which is carried in along with the new solution.
9. Solutions periodically renewed but continuously circulated, and aerated by air which is forced in by the circulation mechanism.

As far as is known, no quantitative study has been made concerning the effects on plant growth of different degrees of aeration of the nutrient solution; nor has any optimum point been found, with regard to degree of aeration, for either vegetative growth or fruit production. As stated by ALLISON and SHIVE (**2**), it is impossible, on the basis of our present knowledge, to specify optimum conditions as regards oxygen requirements for plants in general, since these requirements have been shown to be distinctly variable among different species and even different varieties. It should be entirely possible, however, to specify through experimentation, the optimum conditions regarding oxygen requirements for a particular variety of plant in a given nutrient medium under controlled conditions.

It is evident that there is need for more knowledge concerning the effects of aeration on plant growth. Until we can discover the optimum air requirements of roots for certain plants under controlled conditions, and until we can standardize our treatment of such plants, our conclusions in the field of plant nutrition must necessarily be incomplete.

In view of the dearth of experimental information regarding quantitative aeration requirements of plants such as the tomato, and in view of the many existing commercial greenhouse installations for the use of nutrient solution cultures in producing crops of various plants, and of the distinct future commercial possibilities in this direction, it seemed advisable to set up an experiment with the following aims in view:

1. To determine, if possible, the optimum aeration for both vegetative and reproductive growth of the tomato plant.
2. To determine, if possible, the effect of varying amounts of aeration on total fruit production and on speed of fruit production as well as on dry weight of leaves, stems, and roots.

Procedure

The plant of the experiment involved a study of the tomato plant, variety Louisiana Red, as grown in nutrient solution, receiving five different treatments as regards aeration of the roots.

Seeds were planted in flats of clean sand, and the seedlings grown there for approximately three weeks, receiving frequent watering with the same nutrient solution that was used later in the experiment. When about 7 cm. high, the young plants were transferred to their permanent locations in the excelsior screens.

The nutrient solution used for all cultures was that found by SHIVE and ROBBINS (**13**), to produce excellent growth of tomatoes under average greenhouse conditions. It was composed as follows:

Salts	KH_2PO_4	$Ca(NO_3)_2 \cdot 4H_2O$	$MgSO_4 \cdot 7H_2O$	$(NH_4)_2SO_4$
Molar concentration	0.0023	0.0045	0.0023	0.0007

In order to supply the necessary trace elements, a supplementary solution which had proved beneficial in previous experiments at the University of Kansas was added to the nutrient solution in the following amounts:

Salts	H_3BO_3	$MnSO_4 \cdot 7H_2O$	$ZnSO_4 \cdot 7H_2O$	$CuSO_4 \cdot 5H_2O$
Parts per million	0.5	0.5	0.2	0.1

As a source of iron, iron tartrate in 0.5 per cent. solution was added regularly to the nutrient solution to give a concentration approximating 0.5 parts per million. Throughout the experiment, chlorosis was entirely prevented by the addition of iron tartrate in combination with carefully controlled acidity of the solution. Daily titrations were made, and the hydrogen-ion concentration of the solutions was carefully kept within a range of pH 5.0 to 6.0, which was shown by CLARK and SHIVE (**6**), to include the point of maximum nitrate nitrogen absorption.

The culture tanks (4 feet by 10 feet by 6 inches) were made of heavy-gauge black iron, welded, and coated on the inside with hot asphalt.

Four snugly-fitting frames were constructed out of 2- by 4-inch lumber for each tank. One-inch-mesh iron wire screening was attached to the bottom of each frame, and the whole unit coated heavily with hot asphalt. Clean white pine excelsior was then placed in each screen to a depth of four inches to form a permeable supporting medium for the plants.

Asphalt covered heating cable was installed in the bottom of each tank and the entire installation regulated thermostatically to keep the solutions at a temperature ranging between 75° and 80° F.

Seedlings selected for uniformity were placed in the screens, sixteen to a tank, so that their roots were immersed in the solution which was two inches below the screen.

Tank no. 1 was filled with a mixture of one-third well-rotted cow manure and two-thirds sandy loam, as is practised in the commercial growing of tomatoes. This tank was furnished with several drainage outlets at the bottom, had no excelsior screen, and was watered regularly with water only. This tank was instituted here to compare the results of normal plant growth in soil with the others of the series.

Tank no. 2, in addition to the excelsior screen covering the solution, was fitted with a layer of heavy asphalt and sisal-bonded paper so that the plant stems projected through small holes. This was arranged in order to prevent, as much as possible, any diffusion of air into the solution. This treatment was instituted as a control to determine the results of growth in a solution lacking aeration.

All other treatments were set up to furnish varying degrees of aeration of the solution and to determine its effect on growth. In tank no. 3, as in nos. 4, 5, and 6, the excelsior screen was left uncovered and open to maximum diffusion of air through the screen into the solution.

Tank no. 4 was set up with a continuous drip-bubble apparatus after the method of SHIVE and STAHL (**14**). A 50-gallon accessory tank of nutrient solution was connected with a length of rubber tubing, and the solution fed into a Pyrex capillary feed-tube drop by drop, each drop carrying with it into the solution a definite amount of trapped air. At no time was there any overflow from this tank. A series of pinch-clamps regulated the flow of solution, and only enough was supplied to keep the level of the solution at a point corresponding with that of all other tanks. As the plants in this tank matured, it was necessary to increase the rate of flow of solution, and consequently, the amount of air supplied to the solution. Weekly checks were made, however, on the amount of air supplied, and the calculation of 2.5 ml. of air per plant per minute for tank no. 4 is based on the average of these observations.

Tank no. 5 was furnished with a supply of compressed air giving 37.5 ml. of air per plant per minute. The air was supplied at this rate continuously, and was broken up by means of an aspirator into extremely small bubbles when making contact with the solution.

In tank no. 6, the solution level was slightly lower than in the others. The excess solution was led by gravity through an overflow pipe into a small covered tank. As the solution accumulated in this small tank, it actuated a centrifugal pump, thus pumping the excess solution into an overhead tank. From this tank, the solution flowed by gravity again into the main no. 6 tank, providing a continual circulation of the solution. The overhead tank supplied enough pressure that the solution could be squirted through Pyrex nozzles with some force into the main no. 6 tank in which the plants were growing. The average amount of air delivered into the solution, along with the returning solution, was calculated to be 250 ml. per plant per minute. The amounts of air used here were not planned as ideal quantities, but were rather the uncalculated results of efficiently functioning equipment. While not ideal for their purpose, it was felt that they would give useful indications of the effects of greatly differing amounts of aeration.

It should be noted here that the plants in all tanks but no. 1 received similar treatment except as to aeration of the nutrient medium. Daytime air temperature was kept between 65° and 70° F. and at night between 60° and 65° F. The temperature (75°–80° F.) of the nutrient medium was in all cases the same. All plants received the same solution and all received the same amount of new solution per plant per day, as well as the same amount of total solution per plant.

Tanks no. 2, 3, 5, and 6, were given a supply of new solution to volume every 48 hours. Tank no. 4 differed only in that it received its supply of new solution to volume continuously, drop by drop.

For purposes of clarity in discussing experimental results, use will be made of the following descriptive terms: Treatment no. 1 will designate treatment of plants growing in tank no. 1, treatment no. 2 will designate treatment of plants growing in tank no. 2, etc.

Results

The cultures described here were started on January 1, 1939, and all plants were harvested on May 21, 1939. Fruit was picked and weighed as it ripened, and an accurate account was kept of the daily production of plants receiving different treatments. Leaves and petioles fallen by abscission were kept at the base of each plant for inclusion in the harvest. The dry weights quoted were obtained by storing the material in a hot dry room for several months, then drying it further in a vacuum oven at 80°.

Fruit production

The average fruit production per plant for each treatment based on the unit of aeration is shown in figure 1.

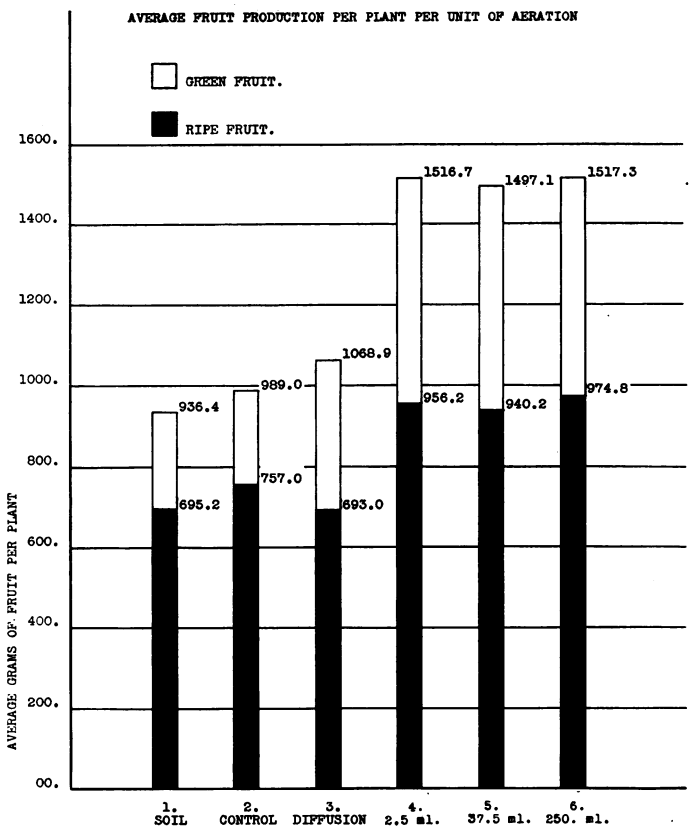

FIG. 1. Average fruit production per plant per unit of aeration.

The increase in both ripe fruit and total fruit production, due to aeration of the nutrient solution, is clearly illustrated by this table. The difference in results between treatments 3 and 4 is highly significant. The differences, however, between treatments 1, 2, and 3, and the differences between treatments 4, 5, and 6, are not considered significant, as the percentage variation is less than 10 per cent. The average speed of ripe fruit production per plant for each treatment, based on the number of days of growth, is shown in figure 2.

An interpretation of these results indicates that an extremely small amount of aeration of the nutrient medium, such as that of treatment no. 3, has a beneficial effect on the speed of ripe fruit production only in the early stages of growth. Plants receiving treatment no. 3, however, show a distinct lag in speed of ripe fruit production, especially in the later period of growth, behind plants given treatments no. 4, 5, and 6, all of which received a greater amount of air than those given treatment no. 3.

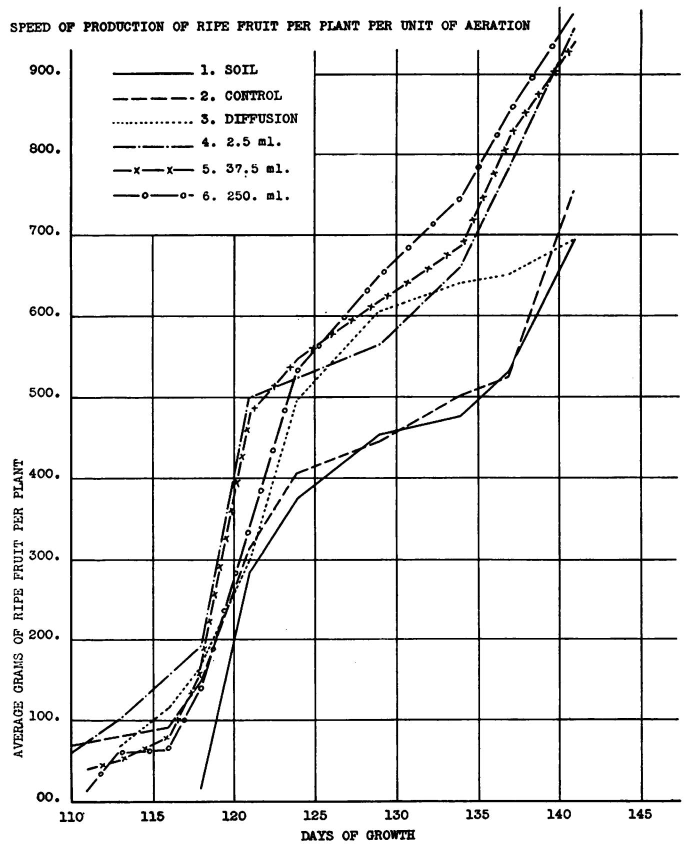

FIG. 2. Speed of production of ripe fruit per plant per unit of aeration.

On the other hand, a greater degree of aeration, as represented by treatments no. 4, 5, and 6, had a much more beneficial effect on both total fruit production and speed of ripe fruit production.

The most pronounced feature of these results, however, is the fact that the aeration requirements for optimum fruit production are low. Amounts of air greater than 2.5 ml. per plant per minute have very little effect on either total fruit production or speed of ripe fruit production. This can perhaps best be noted in figure 3, where the results of treatments 2, 4, 5, and 6, supplying no air, 2.5 ml., 37.5 ml., and 250.0 ml. of air, respectively, per plant per minute are plotted in a curve based on amount of air per plant per minute.

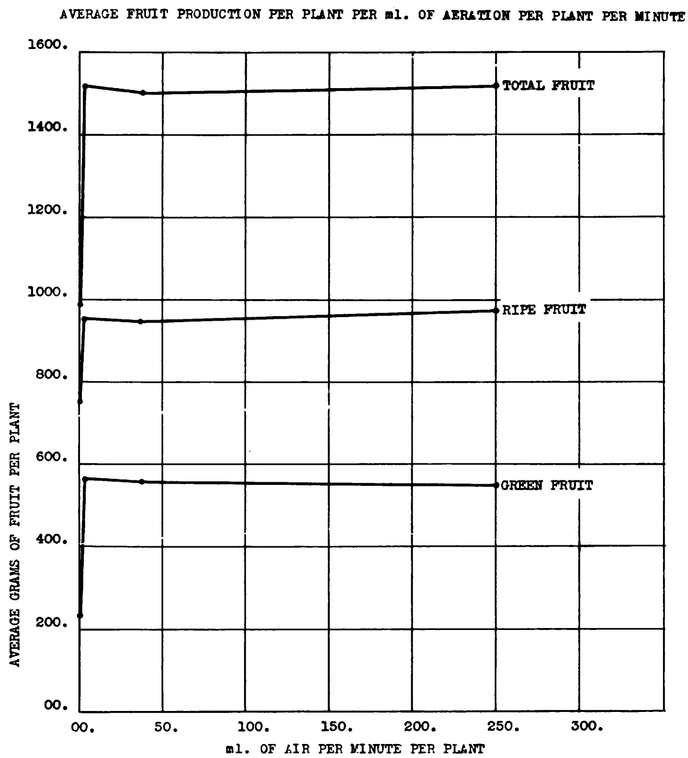

FIG. 3. Average fruit production per plant per ml. of aeration per plant per minute.

The slight superiority of treatment no. 2 over the soil grown plants of no. 1 is not significant; it might possibly be due to a stimulus of the reproductive phase of the plant, brought about by a lack of oxygen. This conclusion is apparently borne out by the fact that treatment no. 2 produced less vegetative growth than any one of the other treatments including no. 1.

VEGETATIVE GROWTH

The average dry weight of roots per plant, based on the unit of aeration is illustrated in figure 4.

The beneficial effect of air is clearly shown here by the fact that treatment no. 2, with no aeration, produced the smallest dry weight of roots. Treatments no. 1 (the soil grown plants) and no. 3 (receiving diffused air) each produced significantly larger quantities of roots than did treatment

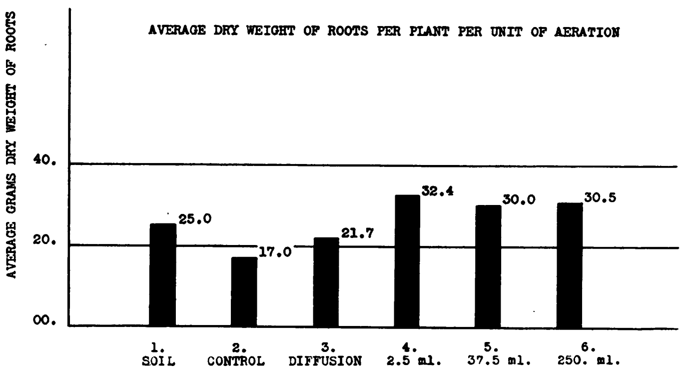

FIG. 4. Average dry weight of roots per plant per unit of aeration.

no. 2; treatments 4, 5, and 6, all receiving an aeration of more than 2.5 ml. per plant per minute each produced much larger quantities of roots than either no. 1, 2, or 3. These results indicate that, as in the case of fruit

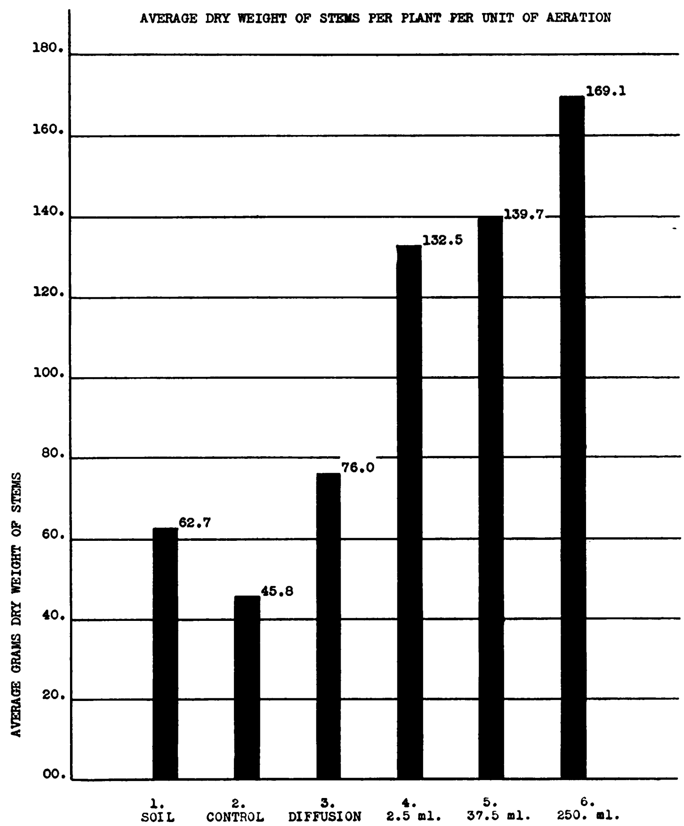

FIG. 5. Average dry weight of stems per plant per unit of aeration.

production, the air requirement for optimum root production is low; amounts of air over 2.5 ml. per plant per minute have very little effect on the production of roots.

Figures 5 and 6 show the average dry weight of stems and leaves per

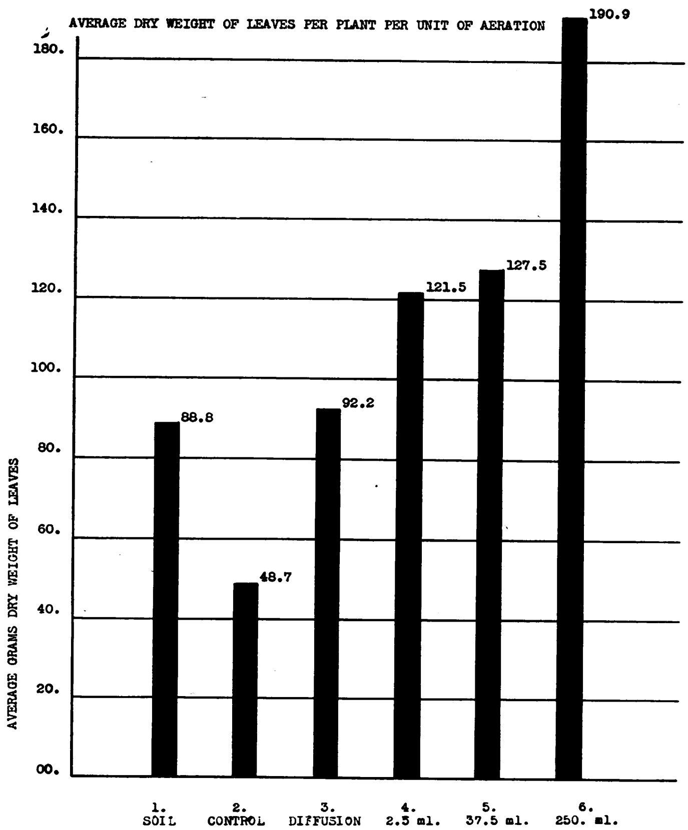

FIG. 6. Average dry weight of leaves per plant per unit of aeration.

plant, based on the unit of aeration. The beneficial effect of aeration is clearly shown in both tables. The smallest average weight of both stems and leaves was produced by plants receiving treatment no. 2, which provided no air, while the dry weights of plants receiving the other treatments are seen to exhibit a proportional response to the amount of aeration per plant per minute.

An interpretation of the results indicates that the aeration requirements for optimum stem and leaf production are high. This is shown by the fact that the greatest amount of both stems and leaves was produced by plants receiving treatment no. 6, which provided the greatest amount of air. It is possible that the optimum amount of aeration for stem and leaf production was not reached in these experiments.

The average, total dry weight per plant including leaves, stems, and roots, based on the unit of aeration is illustrated in figure 7.

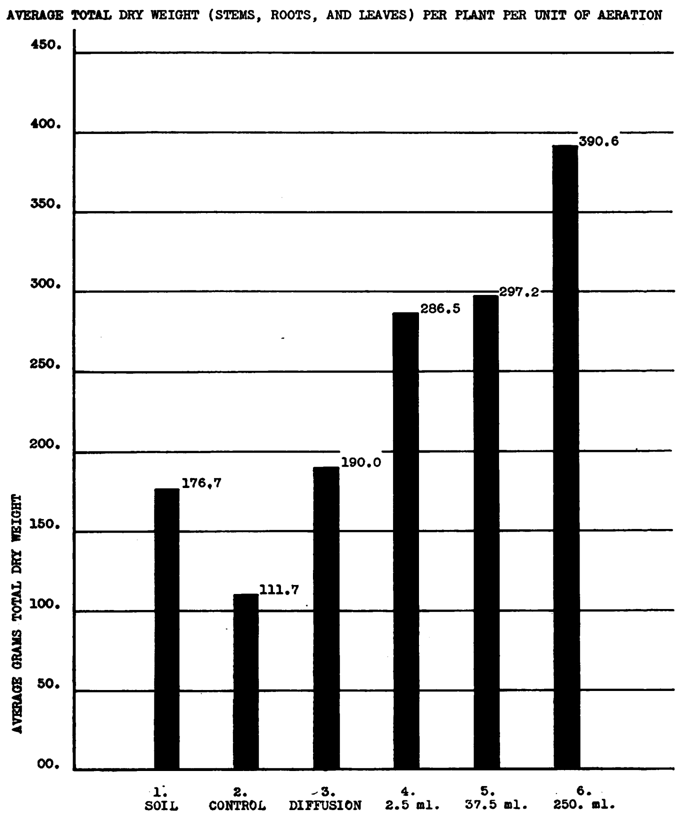

FIG. 7. Average total dry weight (stems, roots, and leaves) per plant per unit of aeration.

Figure 8 shows the effect of increasing amounts of aeration on total dry weight. The rising curve here again indicates, perhaps more clearly, the possibility that the optimum amount of aeration for total vegetative growth was not reached in these experiments. On the other hand, the marked increase in dry weight due to even a small amount of aeration is clearly shown.

No attempt was made to determine the various oxygen tensions of the solutions receiving different air treatments. As shown by figures 6, 7, and 8, however, it is possible that none of the cultures received the amount of dissolved oxygen in the solution which was necessary for optimum vegetative growth. The possibility is clear therefore, that none of the culture solutions was aerated to a point of oxygen saturation.

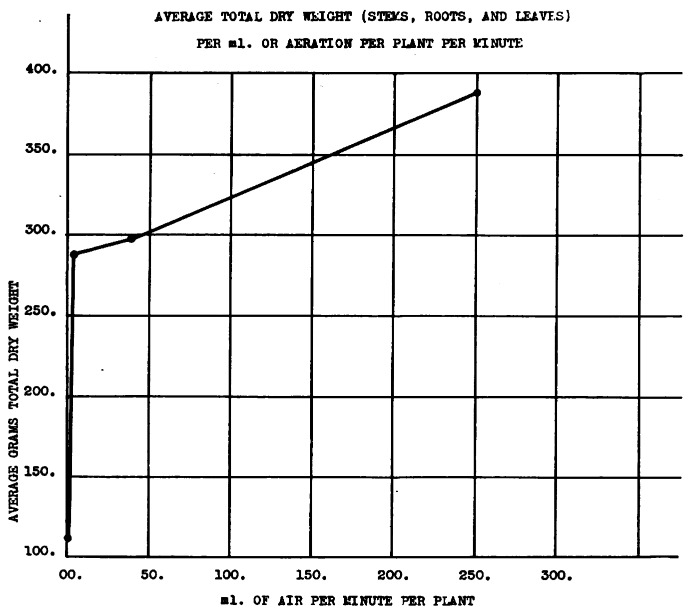

FIG. 8. Average total dry weight (stems, roots, and leaves) per ml. of aeration per plant per minute.

Several interesting observations were made during the course of the experiment.

The roots growing in tank no. 2, unaerated, tended to project their root-tips above the level of the solution, and to produce a large number of long-

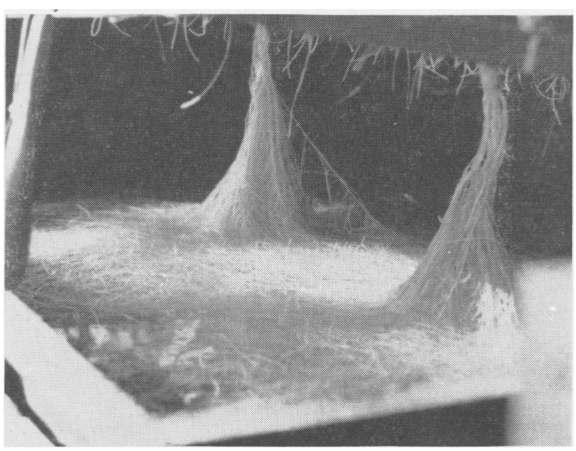

FIG. 9. Root system of mature plants grown in tank no. 2. Several root tips shown projecting above the surface of the solution.

lived root hairs in the damp atmosphere between the solution and the asphalt-paper covering. The roots of the aerated tanks, however, kept their root-tips below the level of the solution and produced a very small number of root-hairs.

The fruit produced by these plants was sampled by several persons, and no noticeable effect of aeration on the quality of the fruit was discovered. The fruit produced by solution-culture plants, however, was definitely firmer and meatier than that produced by the soil-grown plants. This observation was confirmed when some of the fruit was canned.

At the time the plants were harvested, plants receiving treatments number 1, 2, and 3, had slowed down considerably in their rate of vegetative growth; plants in tanks 4, 5, and 6, however, appeared to be continuing their vegetative growth at an unchanged rate.

Summary

In this paper a quantitative study was made of the effects of aeration of the nutrient solution, as related to the fruit production and vegetative growth of the tomato.

1. Aeration was shown to have a decidedly beneficial effect on the production of fruit, as well as on the vegetative growth of roots, stems, and leaves.

2. Aeration of the nutrient medium merely by natural diffusion of air had no significant effect on total fruit production or upon the speed of ripe fruit production, except in the early stages of growth.

3. Aeration of the nutrient medium by artificially supplying the solution with 2.5 ml. of air per plant per minute, or more, greatly increased both total fruit production and the speed of ripe fruit production.

4. Optimum fruit production was obtained when the nutrient solution was supplied with 2.5 ml. of air per plant per minute. Increasing the rate of aeration was without effect.

5. Optimum production of roots was obtained when the nutrient solution was supplied with 2.5 ml. of air per plant per minute. Increasing the rate of aeration was without effect.

6. Optimum production of stems and leaves was probably not obtained in this experiment. Stem and leaf production, within the limits of the experiment, are shown to be proportional to the rate of aeration; the greatest production was obtained with a supply of 250 ml. of air per plant per minute.

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