# EFFECT OF THE ROOT SYSTEM ON TOMATO STEM GROWTH

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(WITH TWO FIGURES)

A long succession of observers have found a correlation between elongation of internodes of the stem axis and the presence of the stem tip. Botanists are in general agreement at present that this correlation may be attributed to the formation of auxin in the stem tip and its transmission through the stem to the elongating regions. Shoot growth is also dependent upon factors supplied by the root system. Vigorously growing branches soon suspend growth in length after they have been cut and placed in a vase. This root influence on shoot elongation is not due to the better known functions of the root system, namely water and salt uptake, for no set of conditions insuring adequate water and salt supply of the cut shoot can replace the loss of the root systems. In several papers (**14, 15, 17**) this effect of the root system on growth has been investigated in some detail and definite indications of the substantial nature of this effect have been presented. An analysis of the distribution of growth rates in the Avena coleoptile also led to the assumption of a second growth factor in addition to auxin required for stem elongation. In earlier papers this factor was non-committally named "food factor" (**12, 13**), but later when it became evident that sugar was not identical with this "food factor" (**9, 10, 17**) a special name, caulocaline, was used for this second factor without any commitments as to its nature.

In experiments with pea seedlings the root system was found to exert its specific effect on shoot growth even when it did not have to take up nutrients, and the effect was most pronounced when the roots were in contact with the minimum amount of water. If the roots were submerged too far in the non-aerated tap water, shoot growth was much decreased (**15, 17**). BONNER and AXTMAN (**3**) and SKOOG (**11**) found that in excised embryos the presence of growing roots increased shoot growth. This is remarkable because one would rather expect the shoots to be in food competition with the roots.

All this evidence leads us to the hypothesis that under proper conditions the root system produces a hormone, caulocaline, which is required for stem growth in conjunction with auxin and sugar (**17**). In the present paper the conditions under which the root system exerts its influence on stem growth was studied. All work was done with tomatoes grown in the greenhouse.

## Methods and results

To analyze the different functions of the root system, young tomato plants, San José Canner variety, were grown in sand. When they had reached a length of 10 to 15 cm. the root system was washed free of the adhering sand, and the stem below the cotyledons was split lengthwise so that on one

plant two separate root systems were obtained, each attached to one half of the stem base. The plants were then placed over two adjoining containers with HOAGLAND nutrient solution (**6**) so that half of the root system dipped into each container. The nutrient solution in each container was aerated, and within two weeks the root systems were well developed. Then the two halves of the root system could be subjected to different conditions in an attempt to separate its various functions. As an example, one of the first experiments will be described.

The plants were divided into three groups of 5 to 10 plants each. Group A remained with both portions of the root systems in nutrient solution. Group B consisted of plants in which one-half of the root system was killed, so that they had only one-half of the functional root system in the culture solution. In group C the nutrient solution around the one-half root system was left, but around the other half it was exchanged for peat, which was kept moist with tap water.

Figure 1 indicates the rate of stem elongation of the three groups. Be-

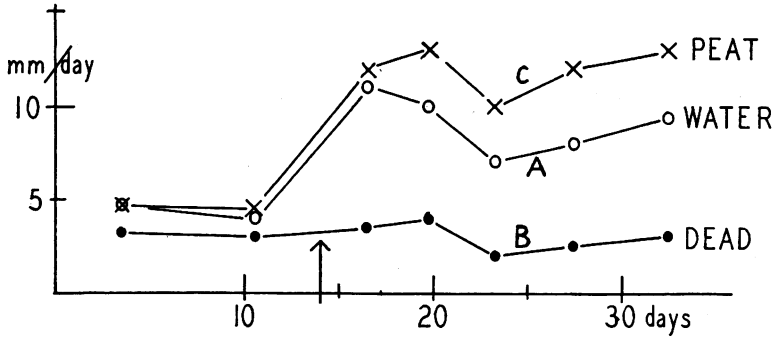


FIG. 1. Growth rate (ordinate, mm./day) of stems of tomato plants with split stem bases and root systems. Both halved root systems of each plant are submerged in nutrient solution, until the 14th day (arrow), when one half is left in the solution, and the other half is either transferred to peat (C), or is left in solution (A), or is dead (B).

fore transfer of roots of C, groups A and C had the same growth rate. In those plants the root system was already close to limiting the growth rate, for plants with only one-half living root system grew less (group B).

Four days after transfer of group C its growth rate was still approximately the same as that of A, but in subsequent periods the growth of the former became and remained significantly above that of A in spite of the fact that the root system effective in taking up salts and water was reduced to one-half. The increase in growth rate followed the appearance of many new roots with abundant root hairs on the root system in peat. Observation showed that relatively little water was taken up from the peat, the bulk coming from the nutrient solution.

In this and later experiments it was noted that even with abundant aeration of the nutrient solution, chlorosis developed in the tomato plants having all roots submerged in the solution. This chlorosis became especially

severe when the pH of the nutrient solution was approximately 7, and it was less pronounced at pH 5 to 6; even at this lower pH the plants were only light green. Even the severest chlorosis disappeared, however, as soon as roots developed in the peat, or above the nutrient solution. This might have been due to improved uptake of iron from the peat, since iron humates are known to be present in peat and to be an excellent source of iron for the plant. For this reason, an inorganic inert medium was compared with peat. For this inorganic medium $\frac{1}{8}$- to $\frac{1}{4}$-inch-mesh haydite was chosen, a pumice-like, light-weight, inert, burned-shale, sharp-edged, material which can hold a considerable amount of water and gives aeration as good or better than peat. Four groups of 5 tomato plants each were set up with halved root systems. The growth rate of the groups was comparable and almost constant for a period of two weeks as shown in table I. After transfer of one-half the root system to the solid medium, the growth rate of these plants almost doubled one week after the transfer whereas the growth rate of the plants with both root systems in solution fell off to a very low rate.

This same type of experiment was repeated at least ten times, always with the same results. When the pH of the nutrient solution was kept at 5, the growth of the plants with both root systems in solution was better than at a higher pH, but it was always exceeded by the plants with one portion of their root systems not submerged in solution. This fact is stressed by the experiment shown in table II, where the growth rate of the plants with one portion of the root system in silica gravel failed to increase above that of the control plants. This was due to the fact that for the first 13 days after transfer to gravel the water level was kept up to the surface of the gravel. Upon draining of the gravel the growth rate immediately increased. In this case, a pure quartz gravel washed for 5 hours with strong $H_2SO_4$, then leached with rain water for 24 hours was used. Its color did not indicate the presence of any iron. Still the plants with half of their roots in this material, watered with rain water, became dark green. When half of the root system of these plants was cut off, only those plants having roots left in the gravel continued to develop green leaves even though they had no roots left in the nutrient solution. All of these experiments show that the effect of roots growing outside the nutrient solution upon the formation of the green color of the leaves is neither through iron uptake nor the iron uptake of the other roots, but by making iron (and other elements) available for chlorophyll formation. These roots can even offset the bad effect of high pH in the nutrient solution.

A summary of the data on the growth of the stem from 7 experiments, involving 140 plants, and all giving the same qualitative results, is presented in table III. The growth rate of the control plants remained constant or dropped over a 25-day growing period. The growth rate of the treated plants rose immediately after transfer of a portion of their root system to a solid moist medium.

The problem was also attacked with a slightly different technique. In-

## TABLE I

GROWTH RATE IN MM./DAY OF TOMATO PLANTS (3 TO 5 PER GROUP) WITH SPLIT ROOT SYSTEM, THE HALVES SUBMERGED IN DIFFERENT CONTAINERS WITH NUTRIENT SOLUTION*

| GROUP | ROOTS IN CONTAINER NO. | LENGTH IN MM. MARCH 19, 1940 | MARCH 19–25 | MARCH 25 TO APRIL 2 | APRIL 2, 1940 HALF ROOT SYSTEM IN NUTRIENT OTHER HALF IN | APRIL, 1940 | | | | | | | LENGTH IN MM. APRIL 25, 1940 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 2–5 | 5–8 | 8–11 | 11–15 | 15–18 | 18–22 | 22–25 | |
| A | 1<br>2 | 100 | 7.8 | 7.0 | Peat | 5.7 | 9.0 | 7.7 | 10.0 | 10.0 | 7.5 | 15.7 | 417 |
| B | 2<br>3 | 98 | 7.0 | 8.0 | Nutrient | 6.7 | 8.0 | 4.7 | 1.5 | 3.3 | 2.0 | 2.0 | 292 |
| C | 5<br>4 | 104 | 7.7 | 6.0 | Haydite | 6.7 | 7.7 | 14.7 | 15.0 | 12.0 | 12.5 | 14.7 | 497 |
| D | 4<br>3 | 104 | 6.0 | 6.5 | Nutrient | 6.7 | 9.3 | 6.7 | 3.0 | 1.7 | 1.2 | 0.7 | 294 |

* The second column shows that, *e.g.*, each of groups B and D had one-half of their root system in container 3.

## TABLE II

ROOT SYSTEM OF TOMATO PLANTS SPLIT ON MARCH 18, 1941. BOTH HALVES WERE AT FIRST IN NUTRIENT SOLUTION WITH ADDED IRON; pH OF SOLUTIONS WAS KEPT BETWEEN 5.2 AND 6.0. ON MARCH 29 ONE HALF OF THE ROOT SYSTEM OF 10 PLANTS WAS TRANSFERRED TO SILICA GRAVEL. UNTIL APRIL 11 THE GRAVEL WAS COVERED WITH RAIN WATER, WHICH WAS DRAINED OFF ON THAT DATE, LEAVING THE GRAVEL MOIST, WITH EXCELLENT AERATION

| ROOT SYSTEMS | GROUP | GROWTH RATE IN MM./DAY | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | MARCH, 1941 | | | APRIL, 1941 | | | | |
| | | 21–28 | | 28–3 | 3–11 | | 11–14 | 14–18 | 18–21 |
| | | *mm.* | | *mm.* | *mm.* | | *mm.* | *mm.* | *mm.* |
| Both in nutrient solution | A | 4.8 | | 5.9 | 11.2 | | 7.7 | 10.6 | 7.0 |
| One in nutrient solution, the other transferred to gravel on March 29 | B | 5.0 | One half root system in gravel | 10.7 | 10.6 | Water drained off gravel | 10.7 | 13.1 | 8.3 |
| Growth of group B in percentage of group A | | 104.0 | | 95.0 | 95.0 | | 139.0 | 124.0 | 119.0 |

## TABLE III

A SUMMARY OF STEM GROWTH (FOR 3.5-DAY PERIODS IN MM./DAY) OF TOMATOES GROWN WITH BOTH PORTIONS OF THEIR HALVED ROOT SYSTEMS IN NUTRIENT SOLUTION (TOP ROW). MEAN OF SEVEN EXPERIMENTS, EACH COMPRISING 20 PLANTS

| | OBSERVATION PERIOD IN DAYS | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3.5 | 3.5 | 3.5 | 3.5 | 3.5 | 3.5 | 3.5 |
| Both portions of the root system in nutrient* | 8.8 | 8.5 | 8.0 | 8.8 | 9.0 | 6.3 | 6.4 |
| One half root system in nutrient, other half transferred to solid medium after 3rd period | 8.6 | 8.3 | 7.7 | 11.1 | 12.4 | 10.8 | 9.9 |
| Growth of treated group in percentage of control group | 98 | 98 | 97 | 129 | 138 | 170 | 154 |

* Figures in second row refer to plants 10.5 days before and 14 days after one portion of their root system was transferred from nutrient solution to either moist peat, haydite, silica gravel, or glass wool.

stead of mechanically dividing the root system into two parts, tomato plants were induced to develop a root system outside the nutrient solution in addition to the roots in the nutrient. This was done by growing tomatoes in wire baskets containing a layer of about 3 cm. of peat, haydite, gravel, sand, or soil, which was kept wet with tap water. These baskets were suspended

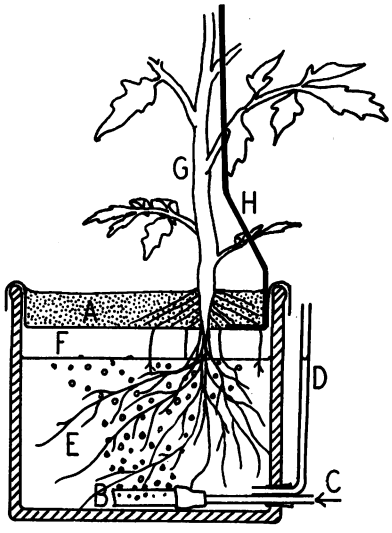


FIG. 2. Cross section through a two gallon earthenware crock, two-thirds filled with nutrient solution (E), through which air (C) is finely divided with aerator (B). The water level can be read at D. On top of the crock is attached a wire basket, filled with peat (A). In this peat a tomato plant (G), tied to support (H), develops a root crown, and in the solution the feeder roots branch out. F is air space between peat and nutrient solution.

from the edge of two-gallon crocks, two-thirds filled with nutrient solution, which was well aerated (fig. 2). The stems of tomatoes, germinated in sand and transplanted into the baskets, extended through the wire basket so that all roots dipped into the nutrient solution, and within two weeks from planting, a second root system developed in the medium in the basket. In general, those roots remained short and had many root hairs, but occasionally some of them grew down into the nutrient solution and then elongated very much.

Under these conditions the tomatoes grew slowly until the roots in the basket were well developed, then their growth increased to approximately the same rate as that of tomatoes grown in sand and watered with nutrient. The following growth rates in mm. per day were measured for plants approximately 300 mm. tall in a humid greenhouse (70 to 80 per cent. humidity, 26.5° C.); 14.6 with haydite in basket; 14.3 with peat in basket; and 16.1 in ordinary sand culture. In the dry greenhouse (30 to 40 per cent. humidity, 26.5° C.) 11.6 with haydite and 10.2 with peat. In other instances growth rates as high as 27.2 mm. per day were measured, which compared with 26.9 for similar tomatoes grown in gravel with sub-irrigation (both with day temperatures of 26.5° C. and night temperatures of 20° C.). The aeration of the solution is of no importance for the growth of the tomato plants as soon as roots have developed in the basket. In some experiments it was even found that aeration decreased the growth rate in direct proportion to the amount of air passed through the solution. In 16 non-aerated plants the growth rate was 11.1 mm. per day. With an air stream of 0.5 to 2.5 ml. per minute the growth rate was 9.0; from 16 to 17 ml. per minute it was 8.6; from 25 to 60 ml. per minute it was 8.4, and from 100 to 180 ml. per minute it was 7.1. In another experiment 18 tomato plants with their roots in an aerated nutrient solution grew at a rate of $22.9 \pm 1.6$ mm. per day over a two-week period, whereas 16 comparable plants, in unaerated solution, grew $26.3 \pm 1.0$ mm. per day. This same difference was maintained in following weeks. The standard deviation in the aerated plants was in every case higher than in non-aerated plants. This was due to a much greater number of plants with extreme growth rates, mainly with extremely low rates.

In the plants in the baskets chlorosis also developed when the pH of the culture solution was above 6 and when no roots had developed in the medium in the basket. As soon as the roots grew out in this medium chlorosis disappeared. Sometimes only half of the plant became green and in these cases it was found that roots had developed only at the side of the stem below the green sector. This localized effect was also observed in the tomatoes with the halved root system described before. Here also the sector of the tomato plant above the root system in the solid medium turned green and only much later the whole plant changed color. Another indication that the nutrient solution as such is not responsible for the chlorosis was found in the observation that two plants in the same basket with their roots

## TABLE IV

GROWTH RATES IN MM./DAY OF PLANTS GROWING UNDER DIFFERENT CONDITIONS, AND THE GROWTH RATES OF THESE SAME PLANTS AFTER THE ROOTS DEVELOPED IN HAYDITE OR SOIL IN THE BASKET HAD BEEN CUT OFF

| | Basket filled with | Growth rate in mm./day | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Original length April 18 | April | | | | May | | | |
| | | | 18–21 | 21–25 | 25–28 | 28–5 | 5–9 | 9–12 | 12–16 | 16–19 |
| Solution aerated | haydite | 24.1 | 5.2 | 7.9 | 10.5 | 16.0 | 20.7 | 19.7 | 18.7<br>11.2* | 18.7<br>10.0 |
| Solution not aerated | haydite | 28.5 | 4.7 | 9.7 | 19.7 | 20.4 | 27.2 | 28.3 | 21.6 | 21.6 |
| Solution not aerated | soil | 25.0 | 5.7 | 9.6 | 24.1 | 24.1 | 29.2<br>27.0† | 27.3<br>18.3 | 26.9<br>19.2 | 26.9<br>17.7 |

* Roots in basket cut off May 12.
† Roots in basket cut off May 7.

in the same solution might be very different. The one with roots in the peat, sand, gravel, or haydite was dark green and grew rapidly, whereas the one without a root system outside the nutrient solution was yellowish green and remained stunted.

That the growth rate of the plants in these baskets is in the first place determined by the roots developing in the medium above the culture solution was indicated by the fact that the growth rate of the plants remained low as long as the roots in the basket had not developed. The complementary experiment in which the roots growing in the basket were being cut off gave the expected result (table IV). In another experiment, within a week after cutting the roots in the basket, the growth rate of the tomatoes had dropped to one-third of that of the controls in spite of the fact that the dry weight of these roots, which were removed, was much less than 10 per cent. of the dry weight of all roots. By cutting off four-fifths of the root system which developed in the solution the growth rate temporarily dropped to about 50 per cent., but soon returned to normal. This indicates that less than ten per cent. of the root system in those tomatoes is responsible for more than 50 per cent. of their growth rate.

It would be expected from the previous experiments that there is a rather close correlation between the growth rate of the tomato stems and the weight of the root system developed in the basket. In an attempt to determine whether this was due to this root system as such or to other factors a number of determinations of the sugar content, auxin content, osmotic concentration of the cell sap, etc., were carried out in two sets of plants which had shown great difference in growth rate. One set of plants had been growing in a green house maintained day and night between 26° and 27.5° C. and 30 to 40 per cent. humidity; the other set was grown under exactly the same conditions except that the humidity was kept between 70 and 80 per cent. Under these conditions tomato plants grown in gravel with sub-irrigation showed exactly the same growth rate (for a weekly period in the dry house 21.5 mm. per day, in the wet house 21.5 mm. per day). The difference in growth rate of the two sets of plants grown in baskets above nutrient solutions, therefore, was not due to the different humidities as such. At the low humidity the peat in the basket dried out more rapidly and therefore had decreased the development of roots. In table V a number of the determined values have been condensed. These figures show a great difference in growth rate of the stems between the tomatoes grown in the dry and in the wet atmospheres. They also show that the difference is not correlated with sugar content of leaves, leaf development, root development in the nutrient solution, osmotic concentration and pH of the roots and stem tissues, auxin content of the green tips, or thiamin content of leaves, tips, and roots, for they all are of the same magnitude in the two groups of tomatoes with the different growth rates. Under wet conditions the stomata were more open, and the suction force was slightly less; but these same differences were found in the plants under sub-irrigation which did not show any differences in

growth rate. The only outstanding difference between the two sets of plants was the weight of the roots in the basket and stem length, weight, and growth.

The root system in some solid, well-aerated medium is not essential for growth. Even when the whole root system is completely submerged in nutrient solution growth takes place, although in the author's experiments at a decreased rate. If the iron content of the nutrient solution is sufficiently high (10 to 100 times more than required when used in sub-irrigation) and when the pH is carefully kept adjusted, chlorosis does not necessarily develop in tomatoes which have their complete root system submerged

## TABLE V

VARIOUS VALUES FOR TOMATOES GROWN IN BASKETS ABOVE NUTRIENT SOLUTIONS AT THE SAME TEMPERATURE AND LIGHT CONDITIONS BUT IN DIFFERENT RELATIVE HUMIDITIES.* EACH VALUE IS THE MEAN OF 3 TO 8 DETERMINATIONS

| | WET HOUSE | DRY HOUSE |
|---|---|---|
| Total length when harvested (mm.) | 362 | 271 |
| Growth rate in mm./day | 24.7 | 13.8 |
| Dry weight of leaves (mg.) | 1518 | 1228 |
| " " per leaf (mg.) | 134 | 123 |
| " " of roots in basket (mg.) | 155 | 72 |
| Wet weight of roots in solution (gm.) | 6.75 | 6.47 |
| " " " stems (gm.) | 20.72 | 11.35 |
| Osmotic concentration of press sap from roots (atm.) | 4.82 | 4.46 |
| " " " " " " stems (atm.) | 8.19 | 8.07 |
| pH of press sap from roots | 5.52 | 5.50 |
| " " " " " stems | 5.20 | 5.20 |
| Auxin content of tops in degrees curvature/gram | 74 | 80 |
| Vitamin $B_1$ in $\gamma$/gram dry weight of tops | 14.3 | 12.0 |
| " " " " " " " leaves | 8.2 | 8.5 |
| " " " " " " " roots in basket | 6.8 | 6.5 |
| Glucose; percentage dry weight of leaves | 0.82 | 0.88 |
| Sucrose " " " " " | 0.61 | 0.79 |
| Suction force (atm.) | 8.71 | 11.1 |
| Opening width of stomata (10 = wide open) | 3.8 | 1.9 |

* Wet house, 75 per cent.; dry house, 35 per cent.

in nutrient solutions. A very small proportion of all roots if outside the nutrient solution and in a healthy condition both offsets unfavorable pH or low iron content of the nutrient solution and greatly increases the growth rate. Even roots which have developed in the saturated atmosphere above a nutrient solution can perform this function.

Only very few experiments were carried out to investigate whether the results obtained with tomatoes applied to other plants as well. With Cosmos very striking effects were observed. When young plants 8 cm. in length were transplanted in the peat baskets with their roots in the well-aerated nutrient solution, some growth occurred; but within 1 to 2 weeks the newly formed leaves were practically white, growth came to a standstill, and the completely etiolated tops started to die. In a few plants this condition im-

proved again, and in all such plants roots were found which had developed above the nutrient solution or in the peat. Increasing the iron and minor elements in the culture solution did not give the slightest improvement, whereas the same solution produced good growth when used to water Cosmos plants growing in sharp washed river sand or pure quartz sand or haydite.

The same effects were noted when Cosmos plants were grown suspended in jars with nutrient solution. The stems were kept in position with a cotton plug, in which no roots developed. Aeration of the culture solution did not give any improvement of the poor growth, and could not offset the chlorosis which developed both in aerated and unaerated solutions. Within one week after lowering the nutrient solution to 6 cm. below the top of the jars the growth became normal again, but only in those plants which had a sufficient number of young roots developed in the air above the nutrient solution. Also in this case the stem growth rate was determined by the extent of root development outside the nutrient solution.

## Discussion

It seems that the previous experiments are sufficient to draw the following conclusions: A tomato plant with all of its roots submerged in a complete nutrient solution will grow slowly and may develop a chlorosis which cannot be cured by increased doses of iron and minor elements, even when sprayed on the leaves. Aeration of the solution improves the development of the roots, but aeration itself cannot cure the condition of stunted growth and chlorosis. This poor growth is *not* a result of insufficient water or salt uptake; at no time was wilting of plants observed. From table V it follows that the sugar and the osmotic concentration of plants growing slow and fast was the same, so that apparently their salt concentration was also the same. This is brought out more clearly by the experiments with divided root systems. The plants do not become normal and healthy before roots develop outside the solution. But then half the root system in solution is sufficient to take up all the water and salt required for good growth, whereas, beforehand double this amount of roots seemed insufficient. The effect is so marked and appears so soon after transfer of the roots that an indirect effect of the roots in air on those in solution seems highly improbable. Effects due to better aeration of the root system in water through oxygen supplied by the roots in air are excluded since (1), aeration of the solution decreases rather than increases top growth; (2), the two portions of the root system are separated by 10 cm. of split hypocotyl, and these halved hypocotyls do not show development of aerenchyma. Therefore, we must conclude that the portion of the root system in solution was perfectly capable of taking up all necessary salts and water, but that the top was unable to utilize them without the help of roots in air. The experiments described above have shown that although the roots in the solid medium are able to take up water, the bulk of the water uptake occurs by the roots in nutrient solution. Since the roots outside the nutrient solution have practically no

salt uptake, and cause increased growth even though they cannot take up organic materials (when grown in haydite, silica gravel, or sand), their effect can only be due to internal secretion of a factor required for satisfactory top growth. This same conclusion has been reached in the case of seedlings (**14, 15**), and this factor was named caulocaline. It is possible that caulocaline is a complex of factors; for further discussion the reader is referred to WENT and BONNER (**17**), where evidence of the chemical nature of caulocaline is produced. If we piece all present knowledge together, we can conclude: Roots supply a factor (or factors) to the growing region of the shoot, indispensable for stem growth, and for convenience sake named caulocaline. In many plants this caulocaline is formed only in roots surrounded by moist air. It travels upward in the stem, apparently under the influence of auxin (**16**), through the living elements of the vascular bundles (**5**) and has not been extracted in large quantities as yet.

Let us ask whether this knowledge about the formation of caulocaline is useful in explaining other well-known phenomena. In the first place, we have to bear in mind that the individual differences of various plants are enormous as far as the air requirement around their roots is concerned. Many plants such as rice, *Ranunculus sceleratus,* and *Cyperus alternifolius* (**2**) can grow with all of their roots submerged; but others, like tomato, must have part of their root system in contact with air to produce maximal growth. GERICKE (**4**) specifically mentions that in roses "the root crown should never be immersed in the liquid solution." This excessive aeration of the root crown is *not* required because otherwise no salts and water can be taken up; the oxygen requirement of the roots for salt absorption is much less than that for increasing the growth rate of the stems and for preventing the type of chlorosis described above.

Many plants require a very light and loose top soil. If the upper soil layers are allowed to pack closely together, growth in these plants is stunted. Although in most plants the roots, especially those taking up water and salts, are located deep down in the closely packed soil, still a superficial cultivation of the soil around such a plant will decrease growth if the superficial roots have been injured. This must be due to the necessity of the root crown for growth, because this cultivation does not appreciably change the conditions around the absorbing roots which are in the main below the cultivated portion of the soil.

The knee-roots, or pneumatophores, of the mangrove vegetation have long been considered to serve for air intake and gas exchange in general between the roots down in the mud and the air (**7**). Although it was physically impossible to get any considerable amount of gases exchanged over such a long distance (only through diffusion in the wide intercellular spaces of the pneumatophores) their respiratory function was generally accepted until TROLL and DRAGENDORFF (**8**) proved by direct measurements that no gas exchange of importance occurred through the pneumatophores of Sonneratia. It seems logical, therefore, to assume that these pneumatophores are necessary

for the caulocaline production required for stem growth. This view is strengthened by the observation of KARSTEN (**7**) that in the mangrove vegetation the trees with the largest pneumatophores have the largest growth rates.

In considering the bearing of caulocaline production on the growing of plants in general, water cultures have to be discussed. For 80 years plants have been grown with their roots immersed in nutrient solutions, and in the presence of all necessary inorganic elements satisfactory, although often slow growth was obtained. Proper aeration of the nutrient solution greatly increased growth in many plants. HOAGLAND and ARNON (**6**) have shown that with vigorous aeration tomato plants can grow as rapidly in water cultures as in good soil. GERICKE (**4**) suggested a modification of the water culture method consisting of supporting the plants above the nutrient solution in a seed bed containing some porous material, organic or inorganic. GERICKE'S other improvements over the regular water-culture technique, such as the use of commercial salts and tap water, are adaptations of minor significance. A scientific explanation, however, is lacking for the advantages of hydroponics over the traditional water culture. Probably this is the reason why the importance of the seed bed is not generally recognized. In a pamphlet, BALL (**1**) states that hydroponics was no success in the East and Middle West, giving as the probable reason: "the Gericke plan furnished everything the soil did (see above) except air at the roots."

The experience gained with the foregoing experiments does not support the generally held views as expressed by HOAGLAND and ARNON (**6**): "While the use of a porous bed instead of a perforated cover facilitates aeration of roots, the bed can be dispensed with if provision is made to bubble air through the nutrient solution." This may be true for certain plants, but not for all. In a commercial greenhouse near Pasadena using the water culture method no other provision is made for aeration of the nutrient solution beyond pumping it slowly through the tanks. Since growth of tomatoes in this greenhouse is excellent, it indicates that aeration of the culture solution is not so essential if a proper root system has developed in the seed bed or between seed bed and culture solution.

We thus reach the conclusion that the essential improvement of hydroponics over the old water culture method is to divide the functions of the root system: one root system takes up water and salts; the other, in the seed bed or between solution and seed bed, supplies caulocaline. And this is essentially the same division of labor as we encounter in most trees and perennials. They also develop a long fibrous feeding root system, which penetrates deep into the soil, and in addition they have a root crown which is well aerated, but due to its position, cannot well serve for water and salt uptake.

## Summary

It has been shown that if all the roots of a tomato (or Cosmos) plant be

submerged in a nutrient solution of pH 6 or higher, aeration cannot prevent chlorosis and especially a drop in the growth rate of the stems, although root growth is satisfactory. As soon as a portion of the root system develops in moist air, however, growth of the stem becomes maximal. All experiments point toward the conclusion that the part of the root system which develops in moist air supplies one or more factors (tentatively named caulocaline) required for stem growth and prevention of chlorosis. Thus, in intact plants, the aeration of roots seems to be of relatively greater importance for their caulocaline production than for salt uptake.

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