

Soil Aeration, Hormonal Relationships and Growth of Tomato (*Lycopersicon esculentum* Mill.) Under Different Environments

Ahmed A. Al Masoum

Plant Production Department

Faculty of Agricultural Sciences

UAE University, Al-Ain

Abstract: Greenhouse-grown tomato plants (*Lycopersicon esculentum* Mill.) were used in studying the effect of aeration, flooding, and exogenously applied benzyladenine (BA) on growth and cytokinins production at different growth stages. Fresh and dry weights of roots and shoots and root exudates were collected at various stages of growth. Results showed that aerated plants significantly outperformed flooded and BA treated plants in growth parameters due to increased root and shoot output.

The level of cytokinin in root exudate was higher during the early phase of vegetative growth. At the time of bud formation and anthesis the level of cytokinin declined. Determination of cytokinins in aerated plants showed a significant increase. However, in flooded plants, a smaller amount of cytokinins was detected. This is believed to be due to death of root apices, a major site for cytokinins production. Under these experimental conditions, the application of BA to foliage of flooded plants had an adverse effect on growth of roots and shoots of tomato plants. However, a slight increase in cytokinin level was detected.

Additional key words: Tomato (*Lycopersicon esculentum* Mill.), Benzyladenine (BA), Cytokinins, Flooding, Air.

INTRODUCTION

Roots require a supply of oxygen, water, and mineral nutrients. Oxygen is necessary to maintain aerobic root respiration so as to supply energy needed for mineral uptake, synthesis of protoplasm, and main-

tenace of cell membranes. In poorly aerated soils the anaerobic respiration of roots does not release enough energy to maintain roots functions.

The importance of the root system to plant growth and development is well recognized. Many years ago, plant physiologists postulated that roots are organs for water and salt absorption, and therefore, most root physiology research concentrated around these two functions. Presently, there is support of the concept that metabolism of aerial parts of plants is controlled by growth regulators produced in the roots.

Root tips are the major sites for synthesis of cytokinin substances in higher plants (Vaadia and Itai, 1965). Cytokinin-like substances are translocated to the shoots via the xylem sap. Cytokinin-like activity and plant growth changes occur when roots are subjected to different environments such as lack of aeration.

It is clear that when plants are subjected to flooding, the metabolic activity of the root apices declines parallel with the decline in cytokinin concentration in the sap (Burrows and Carr, 1969). Flooding also causes a reduction in plant growth due to the fact that the limit set by the roots on top growth involves internal regulation by the roots, particularly the production and the supply of growth substances (Richard and Rowe, 1977).

There are morphological and seasonal changes in cytokinin levels in xylem exudate which reflect changes in physiological status of plants. Cytokinins are found to have a high concentration during vegetative stages of plant growth, decreases as flower buds develop, and reaches a very low level at anthesis (Davey and Van Staden, 1976).

The adverse effects of stress are particularly counteracted by cytokinin-like application. It was found that exogenously applied cytokinins were involved in the regulation of various processes such as overcoming some flooding effects, flower enhancement, fruit formation, and delay of senescence (Garrison et al., 1984).

These findings provide the basis for the hypothesis "by maintaining proper aeration around the root system, cytokinin-like levels may tend to be more favourable for plant production". In order to test this hypothesis, different experiments were designed to manipulate the environ-

ment around the roots. Root environment was altered and exogenous application of benzyladenine was carried out.

The objectives were to study: (1) the influence of aeration on growth parameters and cytokinin-like substances producing; (2) the production of cytokinin-like substances at different stages of growth and (3) whether exogenous application of a cytokinin-like substance influence cytokinin production in roots and growth and yield of shoots.

MATERIALS AND METHODS

Studies were conducted at the University of Arizona Agricultural Experiment Station, Tuscon during 1986. Tomato (*L. esculentum*) cv. 'Jack Pot' was selected for these studies. Seeds were sown in polystyrene trays filled with a medium containing coarse vermiculite. Adequate moisture was applied to trays for germination. They were fertilized frequently with 20:20:20 Peter's fertilizer. After four weeks, seedlings were transplanted into 9.4 liter containers. The medium was coarse vermiculite. Watering and management practices were done as required.

Plants were arranged in a factorial design with three replications. Each replicate consisted of four treatments: (1) air applied to the root system; (2) BA applied exogenously flooded plants; and (3) control. Each treatment consisted of 27 plants. For the aeration treatment, air compressed from a compressor was applied to containers.

Plants were grown in palstic bags, tubes inserted in to the containers, filled with vermiculite and a plastic film was wrapped around the base of the plant stems to prevent air leakage and plant disturabance. Air was pumps run 24 hours a day. For flooded plants, containers were filled with water at the soil level.

For the benzyladenine (BA) treatment plants, 50 mg BA was dissolved in 1 ml of 0.1 KOH in one liter of water (Triton. 01%). pH adjusted to 8 and sprayed on flooded plants 2 days prior to flooding, and then every other day during plant growth. The first sample was taken when plants were in the vegetative stage; the second was when aerated and control plants were in the flower bud development stage; and the third sample was taken when plants (except BA and flooded plants) were in

the flowering stage. Spraying with BA was stopped after the first harvest date due to the adverse effect of BA on plant growth.

Biological Assay for Cytokinin-like Quantification:

An improved bioassay using cucumber cotyledon greening was used as described by Fletcher et al. (1982). Five-day-old cucumber (*Cucumis sativus* cv. 'Sumter') plants germinated at 28°C in the dark were used. Cotyledons were treated with combinations of 1 ml of cytokinin-like substances from thawed frozen xylem sap, 40 millimolar potassium chloride (KCL) and 1 ml of distilled water. A dark incubation of 20 hours was followed by an exposure to light (300 ft.-C) for 3.5 hours. Chlorophyll from cotyledons was extracted with ethanol as described by Knudson et al. (1977). Chlorophyll a,b, and total chlorophyll was determined at 665 and 649 nm. Cotyledons were dried in 65°C and chlorophyll was expressed as Mg Chl./ g.d.w.

RESULTS AND DISCUSSION

Root Growth:

Results obtained on root growth are shown in Table 1 as fresh and dry weights of root system (RFW & RDW). It is obvious that RFW of BA-treated plants was significantly lower than RFW of flooded, air treated and control plants. Apparently BA as applied had an adverse effect on plant growth.

Reid and Railton (1974b) carried out an experiment to study the effect of BA foliar application on that flooded plants. They found that treatment with 50mg/L⁻¹ cytokinin partially overcame flood-induced dwarfing. In our experiment it is obvious that the dwarfing of BA-treated plants was dominant. It is believed flooding leads to the production of substances such as abscisic acid and ethylene; consequently, accumulation of these products of anaerobic metabolism in the roots was the major cause of this phenomenon that occurred basically in the first and the second sampling dates. However in the third sampling date, some biomass increase was noticed. This stopped when spraying with BA was

stopped; thus plant recovered and started to go through normal metabolism by increasing adventitious root production.

Flooding can cause considerable injury and reduce growth. Table 1 shows that root growth of flooded plants was significantly lower than that of control plants. It is obvious that flooding reduces plant growth.

Table 1: Tomato root growth as affected by root environment

| Sample Date ^Z | Root Treatment | Growth Parameter ^Y | |
|--------------------------|----------------|-------------------------------|---------------------|
| | | Root Fresh Weight (g) | Root Dry Weight (g) |
| First | BA | 2.20 ab | 0.139 a |
| | Flooded | 6.89 b | 0.328 b |
| | Air | 10.24 c | 0.569 c |
| | Control | 9.26 cb | 0.482 c |
| Second | BA | 3.52 a | 0.220 a |
| | Flooded | 20.59 b | 1.142 b |
| | Air | 28.07 c | 2.066 c |
| | Control | 34.37 d | 2.239 c |
| Third | BA | 10.33 a | 0.621 a |
| | Flooded | 32.17 b | 2.352 b |
| | Air | 36.17 b | 3.317 b |
| | Control | 38.73 b | 3.218 b |

Z

First = Jan. 31, 1986;

Second = Feb. 14, 1986;

Third = Feb. 28, 1986

Y

Values in columns followed by the same letter are not significantly different according to SNR multiple range test (0.05).

In comparison, flood-tolerant species often generate new roots on the original root system, on the submerged part of the stem, or on both. Roots that form in the soil originate at the points at which the original roots die when flooded (Coutts and Philipson, 1978). Often the new

roots are more succulent and permeable than the original roots. This was new adventitious roots formed and became functional, especially in the third sampling date.

Table 1 also shows that fresh and dry weights of aerated roots were significantly higher than BA-treated and flooded plants during most of the three sampling dates. This is due to the fact that control plants grown in coarse vermiculite had fairly good aeration for the root system; thus, increased growth occurred. However, for aerated plants application of air to root systems through tubings was the only contributing factor.

Shoot Growth:

Results obtained on shoot growth are shown in Table 2. The fresh weight of shoots (SFW) and dry weight of shoots (SDW) of BA treated plants were significantly lower than in flooded plants, especially during the second and third sampling dates. This is due to prolonged exposure of BA-treated plants to the treatment. BA is believed to have an adverse effect on growth of plants. Again, as mentioned in root growth, death of roots possibly occurred, resulting in decreased growth of shoots. It appeared that any environment favorable for satisfactory root growth could also benefit the shoot growth.

Table 2 also shows the effect of flooding on tomato growth. Both SFW and SDW significantly decreased in flooded as compared to control plants at the second and third sampling dates. This is because of the prolonged inundation to flooding. Under constant conditions of vegetative growth, the shoot root ratio remain constant.

In this experiment, Table 2 also shows the Epinastic curvature occurred from the first sampling date on flooded plants only and increased gradually all the way. However, plants of the BA and air treatment did not show any downward movement. BA is believed to inhibit epinastic curvature.

In conclusion, aerated plant growth, as expressed by SFW and SDW, was significantly higher than in BA treatment and flooded plants. This is, again, due to the fact that aeration favours root growth; consequently, shoots are affected.

Table 2: Tomato Shoot growth and epinastic curvature as affected by soil Environment

| Sampling Date ^z | Root Environment | Growth Parameter ^y | | |
|----------------------------|------------------|-------------------------------|----------------------|------------------------|
| | | Shoot Fresh Weight (g) | Shoot Dry Weight (g) | Epinastic Curvature(°) |
| First | BA | 4.418 a | 0.504 a | 40 |
| | Flooded | 9.948 a | 0.952 a | 120 |
| | Air | 35.940 b | 3.527 b | 60 |
| | Control | 32.540 b | 2.790 b | 80 |
| Second | BA | 5.453 a | 0.642 a | 55 |
| | Flooded | 41.530 b | 5.159 b | 150 |
| | Air | 85.700 c | 11.080 c | 65 |
| | Control | 87.810 c | 11.960 c | 85 |
| Third | BA | 11.180 a | 1.676 a | 60 |
| | Flooded | 63.480 a | 10.690 b | 170 |
| | Air | 110.400 c | 17.100 c | 70 |
| | Control | 89.790 c | 15.570 c | 90 |

Z

First = Jan. 31, 1986;
 Second = Feb. 14, 1986;
 Third = Feb. 28, 1986

Y

Values in columns followed by the same letter are not significantly different by SNR multiple range test (0.05).

Cytokinin Activity:

Fig. 1 shows the effects of different treatments on cytokinin-like production. Exogenously BA application slightly increased cytokinin-like activity in the first sampling date. However, flooded plants were unable to exude due to the fact that root apices, a major site of cytokinin production had died. Burrows and Carr (1969) reported that there is a dramatic reduction in the rate of cytokinin and amino acids in the sap when the root system are flooded for 96 hours. This coincides with an increase in the blocking of root apices in flooded roots for this period of

time (Burroes and Carr, 1969). This is in agreement with our finding that prolonged flooding caused death of root tips; consequently, no exudation was collected for cytokinin bioassay purposes.

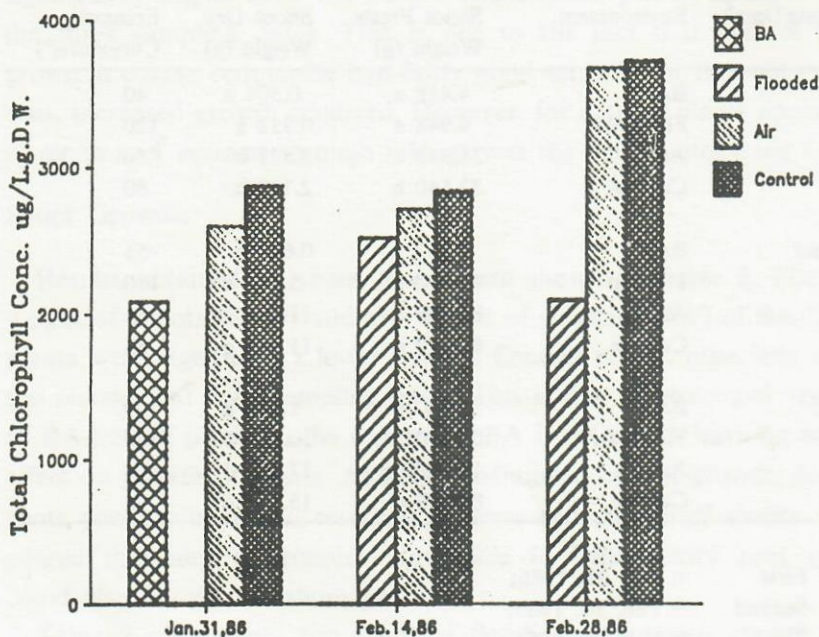


Fig. 1 Total chlorophyll concentration of cucumber cotyledons as affected by root environment and different treatments.

In the case of air and control plants, it is obvious that aeration favors root growth, thus more root tips for cytokinin production to develop. Phillips (1964) found that an adequately aerated root system supplies a growth promoter to the shoots, the effects of which were found to be similar to GA and cytokinin.

During the second sampling date exudate collection for bioassay purposes from BA-treated plants was difficult. However, flooded plants were able to exude due to their regeneration of new adventitious roots.

As far as air and control plant are concerned, the amount of cytokinins produced was increased slightly as plants were going into flowering processes. At the third sampling date (fruit set), again BA-treated plants failed to exude. However, flooded plants, in spite of their prolonged subjection to flooding, and that new roots were generated, had smaller amounts of cytokinin-like substances in exudates. Air and BA treated plants showed increased cytokinin activity as plants proceeded to fruit set. This finding supports the work by Davey and Van Staden (1976) who found that total zeatin and zeatin riboside concentration were increased slightly at anthesis. This level then gradually decreased as the fruits developed.

It is recognized that roots provide water, minerals, and hormones, regulators needed for plant growth. To remain healthy and provide these substances at necessary rates, roots require a constant supply of oxygen, water, and mineral nutrient. Cytokinins are synthesised in the root tips and translocated to the shoots via xylem sap. Many reports indicate the occurrence of a measurable reduction in cytokinin activity in root exudates and in growth parameters when plant roots are subjected to stressful environmental conditions (Kawase, 1972).

The purpose of this study was to determine the mechanism by which environmental factors and applied growth regulator affect plant growth and cytokinin production in roots and growth parameters of the shoots. The focal point here was in the influence of root aeration, flooding of soil, and development. The hypothesis was that by changing environmental conditions around the roots, cytokinin production and translocation would be altered forming desirable physiological response. Thus more root growth and more sites for cytokinin production were expected.

From these results, it is clear that flooding the root system decreased growth rate and cytokinin activity. Both roots and shoots increased when plants recovered from flooding.

The results of the experiment indicated clearly an important role of oxygen for root growth. A significant increase in fresh and dry weights of roots and shoots was observed. The importance of an endogenous supply of cytokinins was realized when the experiment showed that by

increasing aeration around the root system, an increase of cytokinins was translocated in the root exudate. However, a decreased amount of cytokinins was found in the root exudate when plants were flooded. The author believes that modification of the microclimate conditions to increase air circulation around the roots would tend to increase the endogenous level of cytokinins.

Results also show that cytokinins activity was elevated as air-treated and control plants approached bud formation. Activity declined when plants went into fruit development. However, flooded plants showed a decrease in cytokinins activity due to prolonged exposure to flooding. It appeared that prolonged exposure to flooding resulted in the death of some root apices which are major sites of cytokinins production.

The experiment also shows that application of BA to tomato shoots had no positive effect on growth. However, BA had a slight effect on cytokinins activity. Partial addition of exogenous cytokinin altered activity of other growth regulators such as gibberellins. The level of BA used in these experiments was injurious to the plant. The surfactant Triton may have also been a factor affecting growth patterns.

Our findings were similar to that of Kemp et al. (1957) who reported that when kinetin was used exogenously at different concentrations, the growth of tomato plant was more strongly inhibited as the dosage of kinetin was increased than 50 pm. They also found similar results with sunflower, bean, corn and wheat. Stenlid (1982) indicated that cytokinins are potent inhibitors when added exogenously to wheat roots. He attributed this phenomenon to the fact that cytokinins stimulate ethylene production synergistically. Leopold and Kawase (1964) reported that when a standard plant piece was treated with BA (30 mg/L^{-1}) to the primary leaves of beans, the leaflet of the first trifoliate growth was markedly inhibited.

The adverse effects of poorly drained soil on crop growth results from the effects of a limited supply of oxygen for respiration either for root function or for soil organisms. The effects include restricted nutrient and water uptake, interference with the formation and translocation of phytohormones and their consequent effects on shoot growth (Arkin and Taylor, 1981).

For rapid growth, the rooting medium must supply sufficient oxygen for respiration and also remove or absorb gaseous growth-inhibiting products of root metabolism such as ethylene and CO_2 . A flow of air over the roots would readily satisfy these requirements. However, roots also require water in their surroundings, and water, unfortunately, acts as an effective barrier to the diffusion of gases. Oxygen, CO_2 and ethylene all move 9,000 to 12,000 times more slowly through water than through air (Jackson, 1980).

In conclusion, aeration, supply of air to plant roots, is one of the main problems of growing vegetable crops even in hydroponic systems. Inadequate aeration may cause poor growth in the roots of many plants. While sufficient forced aeration may be very expensive. Searching for new technologies to overcome these problems ought to be reinvestigated.

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