

The Oxygen Requirements for Root Growth of Three Avocado Varieties¹

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Abstract. The roots of Scott, Duke, and Topa Topa avocado varieties did not grow when the oxygen diffusion rate (O.D.R.) was less than approximately $20 \mu\text{g cm}^{-2} \text{min}^{-1}$ as measured with 0.23 mm radius platinum electrode. This value was independent of temperature. The O.D.R. required to cause maximum rate of root growth increased at higher temperatures. All 3 varieties responded similarly to oxygen conditions. Plants subjected to low soil oxygen died. Death was more rapid when the temperature was high.

INTRODUCTION

The avocado root rot formerly known as "decline" was reported by Huberty and Pillsbury (8) in 1943 to be associated with soils that had low permeability or stratified horizons which impeded drainage. Subsequent research on the problems emphasized the continued connection with soils that drain slowly (18), and recent soil surveys have correlated damage from avocado root rot with soils that have characteristics allowing the accumulation of excess water in the root zone (2, 3, 6).

Since one of the effects of high water content in the soil is the reduction of oxygen availability for the root, there has been interest in examining the effects of reduced aeration on avocados. Curtis (4), for example, found that avocado seedlings were more susceptible to low O_2 damage than citrus when plants were grown under solution culture. However, data taken under solution culture techniques cannot be used directly to determine when O_2 is insufficient for root growth in the soil. The purpose of the research reported in this paper was to study the effect of O_2 diffusion rates in soil on the growth of 3 avocado varieties and to establish critical values of the O_2 diffusion rate for root and top growth.

METHODS

Avocado seedlings and rooted cuttings were used. The plants were established in 6 cm peat pots before placing in the experimental plexiglass growth containers, illustrated in Fig. 1. The containers were 10 cm in diameter and 42 cm deep.

These containers were designed to allow the application of various soil O_2 conditions without variation in the soil packing or water content. Yolo silt loam was treated with Krilium to provide a well aggregated condition and then packed in the cylinder to a bulk density of approximately 1.25 g/cc. The upper 8 cm of soil was retained by a nylon screen, C, (Fig. 1) to leave a continuous air space, D, through which gas of a desired O_2

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concentration was passed. The peat pots were placed in the soil and the plants allowed to become established in the experimental containers. The container surface was then sealed with a waxed masonite cover, B. The area around the tree stem was sealed by placing a layer of sand and pouring latex emulsion into the sand. The emulsion solidified to form the seal, A.

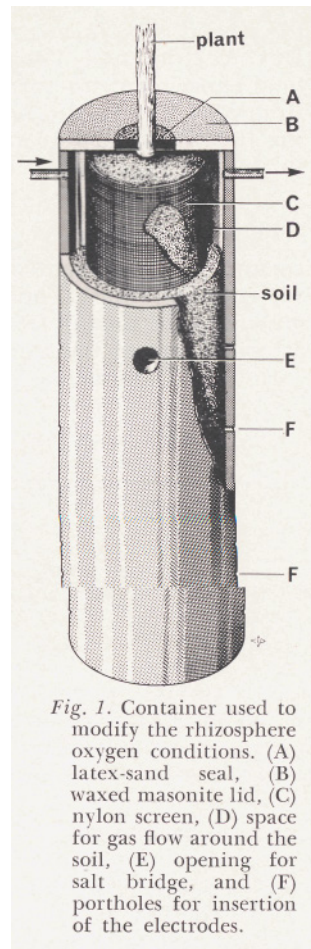


Fig. 1. Container used to modify the rhizosphere oxygen conditions. (A) latex-sand seal, (B) waxed masonite lid, (C) nylon screen, (D) space for gas flow around the soil, (E) opening for salt bridge, and (F) portholes for insertion of the electrodes.

After the surface was sealed, O₂ treatments consisting of flowing <1, 2, 5, 10, and 21% O₂ through the air space, D, were started. The gas mixtures were achieved by mixing nitrogen gas with air as was described by Letey *et al* (11). The <1% O₂ treatments consisted of flowing nitrogen gas only, but it is unlikely that all of the O₂ was eliminated from the soil system. Each treatment was replicated 4 times.

The O₂ concentration in the air stream influenced the O₂ status in the soil. The actual O₂ condition in the root zone was characterized by O₂ diffusion rates (O.D.R.) which were measured with the platinum electrode. This technique, first described by Lemon and Erickson (10), measures the rate at which O₂ diffuses to a wire electrode. The O₂ concentration, water content, particle packing, and diffusion coefficient of O₂ in solution all influence the O.D.R. value and similarly the O₂ supply to a root. The openings, F, on the side of the container were used to insert electrodes to measure O.D.R. 3 times

during the experiment. These holes were covered with black plastic tape to prevent O₂ entry. The opening, E, was used to insert the porous cup of the salt bridge which is required to complete the circuit to measure O.D.R.

The depth of root penetration was marked on the container wall at the time treatments were started and periodically thereafter. Plastic sheeting was placed around the container to keep light from the roots except when observations were being made. The plants were watered by the weighed pot technique.

Three experiments were conducted. In the first, rooted cuttings of the Scott variety were under O₂ treatment from September 18 to November 19. Rooted cuttings of the Duke variety were used in the second experiment from December 8 to February 28. Scott and Duke cuttings and Topa Topa variety seedlings were used in the final experiment for varietal comparison. Treatments were applied from May 5 to July 9. Because of insufficient number of containers, the 10% O₂ treatment was omitted on the Scott and Duke varieties in the last experiment.

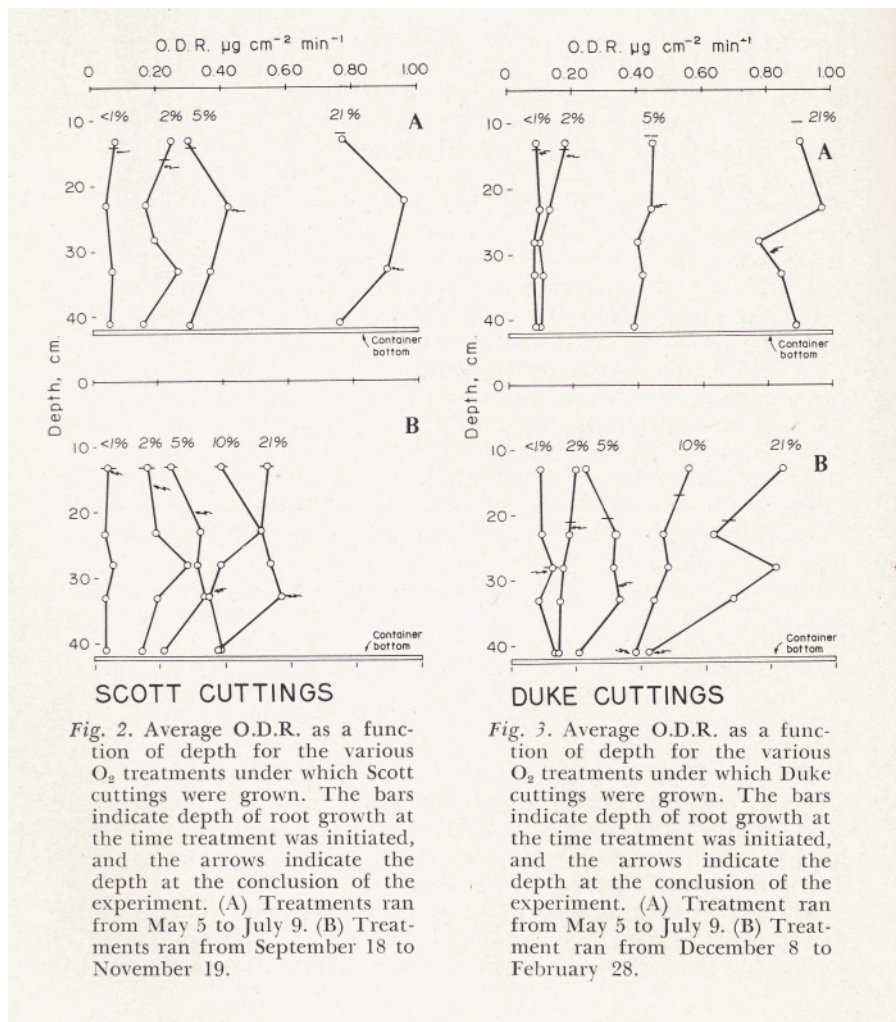


Fig. 2. Average O.D.R. as a function of depth for the various O₂ treatments under which Scott cuttings were grown. The bars indicate depth of root growth at the time treatment was initiated, and the arrows indicate the depth at the conclusion of the experiment. (A) Treatments ran from May 5 to July 9. (B) Treatments ran from September 18 to November 19.

Fig. 3. Average O.D.R. as a function of depth for the various O₂ treatments under which Duke cuttings were grown. The bars indicate depth of root growth at the time treatment was initiated, and the arrows indicate the depth at the conclusion of the experiment. (A) Treatment ran from May 5 to July 9. (B) Treatment ran from December 8 to February 28.

RESULTS

The average O.D.R. at different soil depths for the various O₂ treatments are presented in Figs. 2, 3, and 4 for Scott and Duke varieties and Topa Topa seedlings respectively. The depth of root growth at the time of treatment is marked with a bar and the depth at conclusion of the experiment is marked with an arrow for the various O₂ treatments.

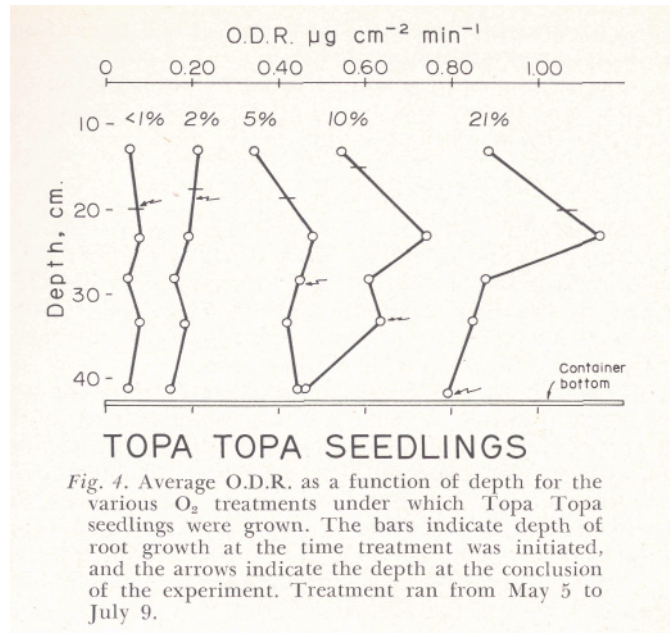


Fig. 4. Average O.D.R. as a function of depth for the various O₂ treatments under which Topa Topa seedlings were grown. The bars indicate depth of root growth at the time treatment was initiated, and the arrows indicate the depth at the conclusion of the experiment. Treatment ran from May 5 to July 9.

Almost no root growth occurred when the roots reached a zone where the O.D.R. was less than $0.20 \mu\text{g cm}^{-2} \text{min}^{-1}$ in all the experiments. This is an O.D.R. which has been found to be critical for root growth of snapdragons, sunflowers, cotton, and bluegrass (12, 13, 14, 15).

It is noted in Figs. 2 and 3 that the O.D.R. for a given O₂ treatment in the experiment running from May to July is higher than the previous experiments. This increase in O.D.R. is interpreted as being the results of higher temperatures during the last experiment. Both theory and previous results (12, 14) indicate that the G.D.R. increases with increased soil temperature for a given gas phase O₂ concentration. The O.D.R. which limits root growth is not influenced by temperature as can be noted from the data presented in Figs. 2 and 3. This result was also found for sunflowers (14). Although temperature does not influence the O.D.R. which will inhibit root growth, the O.D.R. which will allow maximum rate of root growth is affected by temperature both for avocados (Figs. 2, 3, 4) and sunflowers (14).

All plants growing under the <1% oxygen treatment wilted and died. All of the plants grown under the 2% O₂ treatment had some wilt and several plants died. Plants died more rapidly when temperatures increased. None of the plants growing under 5% O₂ treatment died, but a considerable amount of tip burn occurred on the leaves. Growth was not as rapid as under the 10 and 21% treatments.

All 3 varieties responded similarly to soil O₂ conditions with respect both to root and top

growth.

The roots were examined and cultured by plant pathologists. No *Phytophthora cinnamomi* was found to be present. All injury was attributed to the insufficient supply of O₂.

DISCUSSION

The results found are in general agreement with those of Curtis (4). Avocado roots and plants die if O₂ is too low. Our results, however, give a basis for evaluating field conditions. If the O.D.R. in a soil zone is less than approximately 0.20 μg cm⁻² min⁻¹, no roots will grow in that zone and existing roots will eventually deteriorate if the low O.D.R. is maintained.

In soil surveys in connection with avocado root rot (2, 3, 6), both soil conditions conducive to the establishment of low O₂ supply and *P. cinnamomi* were associated with root rot. Since both low soil oxygen and *Phytophthora* have been demonstrated to be harmful to avocados, it is not immediately apparent which is the dominating factor contributing to root rot. Avocado root rot was not found to be prevalent in Ventura County in California (1) where the soils are relatively free from infestation by *P. cinnamomi*. This information supports the contention that low soil O₂ is not the primary factor in avocado root rot. Very likely low soil O₂ can decrease tree growth and production, but *P. cinnamomi* is necessary for severe tree damage.

Curtis and Zentmyer (5) conducted experiments in solution cultures which were inoculated with *P. cinnamomi* and had various O₂ treatment applied. The root injury due to the fungus was more rapid and severe under the highest O₂ treatment. From an O₂ point of view, these results would indicate that *Phytophthora* damage should be greater on a well drained than a poorly drained soil because the rate of O₂ supply would be greater in the drained soil. This is not what has been observed in the field. Other factors must therefore be involved. Some of these factors have been discussed by Zentmyer (18).

The attraction of *P. cinnamomi* zoospores to avocado roots has been established (17). It is believed that some chemical is diffusing from the root that attracts the zoospores. The diffusion rate of a chemical is very dependent upon the soil moisture content. Data of Klute and Letey (9) show that the chemical diffusivity decreases very sharply as the water content is decreased from saturation. The diffusion of the chemical attractant may be so low under moisture conditions less than saturation that the zoospores are less attracted to the root. Furthermore, the rate of movement of the zoospores to the root would also be reduced in a proportional amount. The decrease in diffusion of a chemical attractant and rate of movement of zoospores could account for the reduced damage by *Phytophthora* under well drained conditions. The effect of soil water, therefore, would be different than its influence on O₂ supply.

There is, however, another explanation on the effect of soil water on *Phytophthora* damage which is associated with the O₂ supply. Data of Stolzy *et al.* (16) and Grineva (7) indicate that roots subjected to low O₂ excrete compounds such as sugars, amino acids, and organic acids. Release of the zoospore attractant may thus be increased under low O₂ supply conditions of saturated soil.

The data presented in this paper show the effect of O.D.R. on avocado root growth independently of water and in the absence of *P. cinnamomi*. This information will be helpful in separating out the causative factors in avocado root rot.

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