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# Measurement of Oxygen Diffusion Rates with the Platinum Microelectrode

## I. Theory and Equipment


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## II. Factors Influencing the Measurement


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## III. Correlation of Plant Response to Soil Oxygen Diffusion Rates


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In 1952, E. R. Lemon and A. E. Erickson introduced a method for measuring the rate of oxygen diffusion to a small platinum wire electrode inserted into the soil. This was considered analogous to measuring the oxygen movement to a plant root that would be in the same position as the wire electrode.

In spite of certain limitations, the platinum microelectrode technique appears still to be the best method available at present for providing a measurement of oxygen conditions in soil which can be interpreted with respect to biological behavior.

The first two papers of this series discuss theory, equipment, and the factors that can influence measurements. The third paper reviews the literature reporting research on correlation of oxygen diffusion rates to biological response.

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# III. Correlation of Plant Response to Soil Oxygen Diffusion Rates[1]

AFTER OXYGEN diffusion rates (O.D.R.) have been measured and calculated, they must be empirically related to plant response. This paper reviews the published work on O.D.R. experiments and indicates such relationship.

## ESTABLISHED METHODS OF MEASUREMENT

Experiments for measuring O.D.R. and determining plant response are generally of two types. In the first, O.D.R. measurements are made and plant growth observed under existing soil conditions either in the field or greenhouse. In the second, soil environments are purposely modified—for example, by changing their bulk densities, the distance to water tables, or the atmospheric oxygen over the soil surface. The second method permits the easier comparison of O.D.R. and plant response because the number of soil variables has been reduced. (Measurements of O.D.R. under many other conditions have also provided valuable information on the O.D.R.-plant response relationship.)

Many of the results have been obtained by varying the oxygen concentration above the soil, thus eliminating such variables as differences in $CO_2$ concentration, water tables, etc. In the first of these studies (Letey, Stolzy, *et al.*, 1961; Letey, Lunt, *et al.*, 1961; Stolzy, *et al.*, 1961),[2] plants were grown in four soil-filled plexiglass cylinders inside metal barrels. The cylinders (10-cm diameter) passed through four circular holes in the barrel lid. After cylinders were placed in the barrel, the top was sealed by circular wooden blocks fitted into the holes in the lid. These plugs were split down the middle, and each had a hole in the center through which the plant shoot protruded. Gases of known oxygen concentration were introduced to provide a given air-bath treatment over the soil surface. This method was later modified to the more convenient system shown in figure 1. A further modification, to accommodate grass-type plants, was described by Letey *et al.* (1962*b*).

## ROOT GROWTH-O.D.R. STUDIES

Root elongation is one plant function that has a critical O.D.R. Stolzy *et al.* (1961) showed that root growth of snapdragons was reduced or stopped when O.D.R. in the soil was in the range of 18 to $23 \times 10^{-8}$ gm cm$^{-2}$ min$^{-1}$. Diffu-

[1] Submitted for publication October 2, 1963.
[2] See "Literature Cited" for citations referred to in the text by author and date.

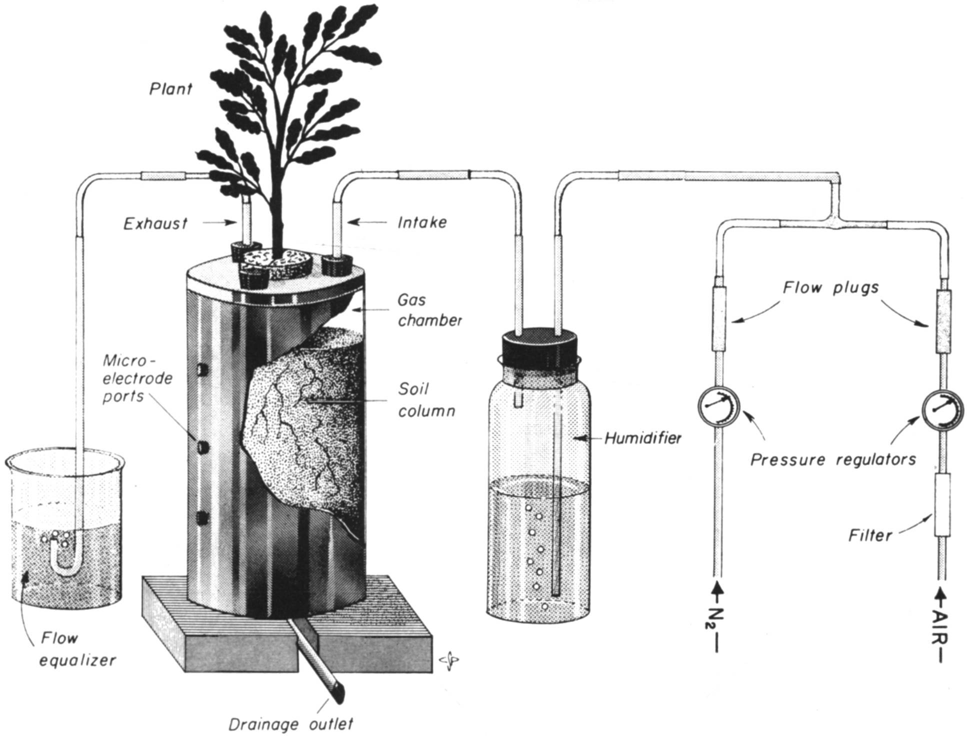


Fig. 1. Diagram shows soil column, cylinder, and plant arrangement used to change soil oxygen environment. Soil container is 12.2-cm (I.D.) plexiglass tubing. Wooden disks fit tightly into top of cylinder, allowing space for gas-exchange chamber over top of soil. Plant protrudes through hole in center of lid. Gas intake and exhaust holes flow different oxygen concentrations over soil surface. Fourth hole in lid is used for watering or for placement of silver-silver chloride cell during O.D.R. measurements. Ten small holes at various depths are used as ports for platinum microelectrodes. Air and nitrogen are taken from compressed sources through pressure regulators. Mixtures of air and nitrogen at given concentrations are obtained by controlling rates of flow by plaster of paris plugs molded in glass tubes and allowed to set. Differing flow rates through plugs are achieved by varying plug geometry, porous properties, or pressure (Letey, Lunt, *et al.*, 1961; Kohl, 1961).

sion rates above 23 permitted relatively good root growth. Letey *et al* (1961*a*) studied the effect of temperature and O.D.R. on sunflowers and cotton, and concluded that an O.D.R. value of approximately 20 prevented root growth, independent of temperature. In another study (Letey *et al.*, 1962*a*) with sunflower growth at different soil and air temperatures, roots failed to grow when the O.D.R. was less than 20. This O.D.R. value was found to be independent of the soil or air temperatures studied. These results indicate that while soil temperature has little effect on an O.D.R. that is insufficient to allow root growth, an O.D.R. that allows maximum root growth depends upon soil temperature. Studies by Berry and Norris (1949) and Jensen (1960) showed that increased temperature causes an increase in respiration rate. That increase is at least partially compensated for by an increase in O.D.R. with increased temperature.

A study on Newport bluegrass showed that an O.D.R. of $20 \times 10^{-8}$ gm cm$^{-2}$ min$^{-1}$ is required for root growth (Letey *et al.*, 1964). The optimum, however, was an O.D.R. of 40. Barley has a higher tolerance for low oxygen, and can grow roots at an O.D.R. as low as 15 (Letey *et al.*, 1962*b*).

The studies described above were conducted by means of a controlled atmosphere above the soil surface (fig. 1). Oxygen diffusion rates were made at an applied potential of –0.65 volt with 25-gauge platinum electrodes 4 mm long. Values were measured four minutes after application of the potential.

Bertrand and Kohnke (1957) used bulk density and distances to a water table as variables, and found that an O.D.R. below 20 to $30 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ was detrimental to root growth of corn. In these studies, 22-gauge platinum electrodes, 8 mm long, were used at a potential of –0.8 volt. The 8-mm electrode would give O.D.R. values similar to or slightly lower than those with the 4-mm electrode. The applied potential of –0.8 volt would, however, give higher O.D.R. results than –0.65 volt. Using the data from Birkle *et al.* (see second paper in this series), O.D.R. of 20 and 30 measured at –0.8 volt would be 17 and 27, respectively, at –0.65 volt potential. There would be slight differences between electrode sizes (25- vs. 22-gauge) depending on the moisture content.

A study by Wiersma and Mortland (1953) on sugar beets, using constant distances to a water table with three soil types, showed that whenever the O.D.R. was higher within a treatment, the sugar beets were longer. Oxygen diffusion rates of 20 to $30 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ at 4-inch soil depth were critical in the growth of sugar beets. In this study, an applied potential of –0.8 volt with a 25-gauge (4 mm long) platinum electrode was used. The O.D.R. was measured after five minutes. Adjustment of these O.D.R. values (20 and 30) to an applied potential of –0.65 volt, using data of Birkle *et al.* (see second paper), results in values of 13 and 23, which are critical for root growth. Five minutes would give O.D.R. values slightly lower than those taken by Letey, Stolzy, *et al.* (1961), Letey *et al.* (1962*a*), and Stolzy *et al.* (1961) after four minutes. Erickson and Van Doren (1960) presented field data on sugar beets in which O.D.R. slightly above 30, due to excess rain, caused as much as 50 per cent reduction in yields.

Wiersum (1960), in studying O.D.R. in relation to soil characteristics and root penetration, constructed a rugged platinum electrode. Because of the type of construction, it was not possible to estimate areas. Therefore, none of Wiersum's results (reported in microammeter readings) is comparable with those reported in terms of O.D.R. In private correspondence, however, he indicated that an O.D.R. of $30 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ was limiting for root growth. He used 22-gauge platinum, 4 to 7 mm long, and applied a potential of 0.8 volt. The steady-state value was measured after three minutes. Referring to the data of Birkle *et al.*, this would represent an O.D.R. value of $< 27$ at –0.65 volt.

Van Diest (1962) studied the effect of soil aeration on corn. He used fertilized and unfertilized soils, three soil aeration levels, a special aerated container, compacted soil, and normal packing in a regular container. Significant differences in root dry weight were found in the unfertilized plots. The least number of roots were in the compacted soils with O.D.R. of 10 to $13 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. The controls showed root growth in the middle range, and had O.D.R. of 29 to 32; the aerated plots had the most roots, and O.D.R. of 36 to 41. The fertilized plots had more roots than the unfertilized plots, with the most roots in the fertilized, compacted soil. Oxygen diffusion rates were taken at a 3-inch soil depth following the daily water adjustment to 20 per cent by weight. A puddled appearance of the surface soil accounted for low diffusion rates. However, the finding of the greatest root weight in the compacted, fertilized plots is difficult to understand.

Root distribution down the soil column may indicate a higher concentration of roots at the soil surface in the first compacted treatment as compared with other treatments. Van Diest also measured O.D.R., after five minutes at an applied potential of –0.65 volt, with 22-gauge platinum electrodes, 4 mm long.

Data from various investigators show that an O.D.R. of about $20 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ inhibits root growth. Values between 20 and 30 retard root growth. From laboratory information on oxygen requirement of roots, Wiegand and Lemon (1958) used a theoretical approach to determine critical oxygen concentration at the root surface. In a study on Miller clay and Amarillo fine sandy loam at 4-, 8-, and 12-inch soil depths, under field conditions, comparisons were made of (1) oxygen content of the soil atmosphere (gaseous oxygen); (2) oxygen diffusion rates (moisture film); and (3) calculated oxygen concentration at root surface (dissolved oxygen). It had been previously shown that the critical value of oxygen in the soil atmosphere would be 12 per cent. At field capacity, in both soils, the gaseous compositions were considerably above the critical value for root uses. However, calculation of the oxygen concentration at the root surface in the moisture film was critical at both the 8- and 12-inch depths for Miller clay (Wiegand and Lemon, 1963). The Amarillo fine sandy loam was well above the critical value for the three soil depths. In a comparison of Wiegand and Lemon's (1958) data on O.D.R. with their findings on oxygen concentrations at the root surface, an O.D.R. value of 20 is critical for the root oxygen. The Amarillo fine sandy loam at the three soil depths had O.D.R. values of approximately 65 to 100; the Miller clay had O.D.R. values in the range of 18 to 30. These results lend considerable support to the empirically determined critical values of O.D.R. on root growth. The results are in agreement with calculations based upon respiration rates. In a soil such as Miller clay, a long period followed irrigation or rainfall in which the plant would not produce at a maximum rate. The production potential of this soil would be limited by insufficient root oxygen.

## STUDIES OF TOP-GROWTH RESPONSES

The effect of soil oxygen on top growth is most apparent in controlled studies with different degrees of soil aeration (fig. 2). Because of differences in O.D.R. in various parts of the root zone, however, it is difficult to assess a single value as critical. Studies by Letey, Lunt, *et al.* (1961), Letey, Stolzy, *et al.* (1962*a, b;* 1964) show a pronounced effect of reduced soil aeration on top growth. One study (Letey, Stolzy, *et al.,* 1962*a*), on sunflower, showed that as a very general guide, diffusion rates greater than $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ can be considered near optimum for shoot growth. It was also shown, with barley, that the optimum diffusion rate was less than 40.

Lemon and Erickson (1952), using different distances to a water table to control O.D.R., found values of 30 to $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ at an 8-inch soil depth critical for tomato plants. Although the article does not say, the observation was presumably on top growth. Lemon and Erickson used 25-gauge platinum electrodes (4 mm long) with applied potential of –0.8 volt. The steady-state value was taken after five minutes. The O.D.R. values of 30 and 40 obtained at –0.8 volt, as compared with that at –0.65 volt, would be in the range of 23 to 33.

Cline and Erickson (1959) studied the response of peas to O.D.R., in 8-inch diameter soil columns. Different soil oxygen conditions were obtained by varying the distance from the soil

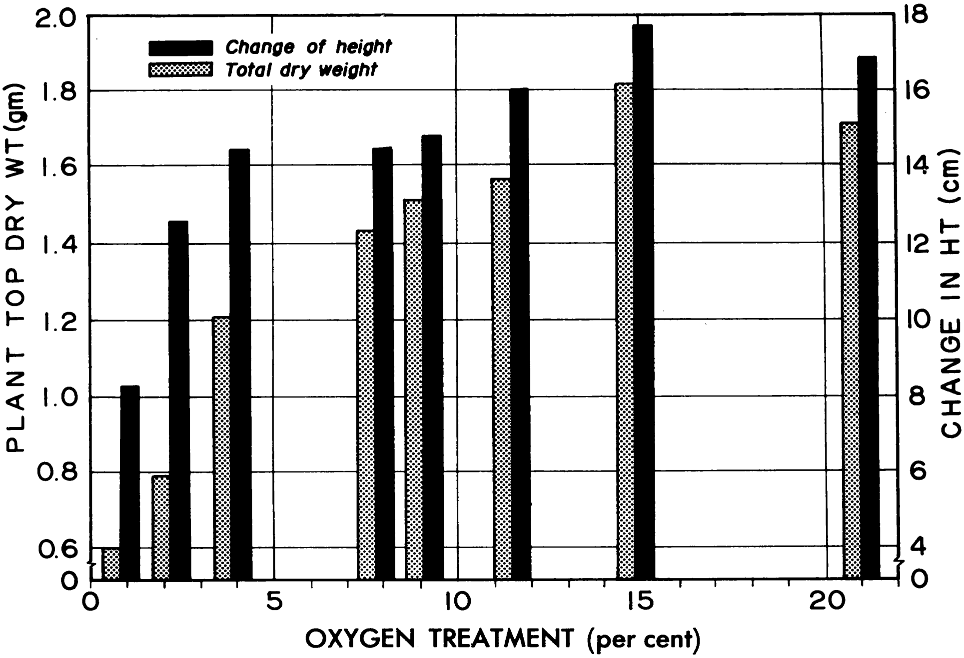


Fig. 2. Dry weight of snapdragons, and changes in height at different oxygen treatments.

column to a free water table. Oxygen diffusion rates were measured at a 3-inch soil depth at an applied potential of –0.8 volt, with 25-gauge platinum electrodes 4 mm long. Under the conditions of the experiment, peas did not measurably respond to low O.D.R. at early stages of growth. However, 40 to 50 days after planting, growth was increased as the O.D.R. increased from 15 to $72 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. Green weight of the shelled peas at an O.D.R. of 46 was 16.7 gm, while at an O.D.R. of 15 it was 4.6 gm.

Hanan and Langhans (1963) studied the effects of O.D.R. on snapdragons for cut-flower quality. At O.D.R. of less than $80 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$, the quality of the cut flower was lowered, and fresh weight and stem length decreased. In this study, 25-gauge, 5-mm electrodes were used. The applied potential was –0.8 volt, and measurements were taken after two minutes. Reducing the O.D.R. value of 80 at –0.8 volt to that at –0.65 volt would result in a value of 65. This value is probably still high because of the short time allowed for establishment of steady-state conditions.

Bertrand and Kohnke (1957) studied corn, using soil bulk density and the distance to free water as means of varying oxygen. They found that top growth increased as O.D.R. increased to about $25 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. The O.D.R. value of 25 measured at a potential of –0.8 volt would be approximately 19 when adjusted to –0.65 volt.

Van Diest (1962) found no yield differences in top growth of corn due to differences in soil O.D.R. His values varied from a low O.D.R. of $10 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$, on compacted soil, to a high of 50 on aerated soil.

A field study on tomatoes (Erickson and Van Doren, 1960) in which O.D.R. was varied by types of tillage, compaction, and different amounts of irrigation water, showed an increase in yield with increased O.D.R. up to $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. These data were taken with 22-gauge platinum electrodes (4 mm long) at a potential of –0.65 volt.

Information on O.D.R. in relation to plant-top response shows that soil oxygen has a wide range of influence on the plant, depending on the species and the stage of growth. For plants in a vegetative stage, O.D.R. values of 40 or less are critical; at the flower and fruit producing stages the optimum O.D.R. is somewhat higher. Plant species vary in their response to low oxygen.

## MINERAL ACCUMULATION STUDIES

The effect of soil aeration on ion accumulation in the top portion of plants varies with different ions and plants. A good example of the effect of different environmental oxygen concentrations over the soil surface on the accumulation of K, Ca, P, and Na is shown in figure 3 (Letey, Stolzy, *et al.*, 1961).

A study by Cline and Erickson (1959) on O.D.R. and applied fertilizer in relation to chemical composition of pea plants showed that N, P, and K accumulation in tops at different O.D.R. was markedly affected by fertilizer treatments. Increasing oxygen diffusion rates increased the concentration of P and K only under the two higher fertility treatments. Nitrogen concentration increased with increased O.D.R. under all fertility treatments. Calcium and Mg tended to increase in the tops when the plants were grown with low oxygen supply, the highest amount occurring at $15 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$.

A study with sunflowers (Letey, Stolzy, *et al.*, 1962*a*) found that 30 to $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ was critical for K and P. That is, O.D.R. values above 30 to 40 showed only slight increases in concentration of these two nutrients, while Na responded in the reverse direction—as the O.D.R. decreased from 30, Na increased.

A study with *Citrus sinensis* var. Homassara (Stolzy *et al.*, 1963) showed that leaf concentrations of P, K, Ca, Mg, Fe, Mn, and B were reduced at diffusion rates below $33 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ as compared with leaf concentrations of plants grown in soil oxygen environments with O.D.R. above 62. Leaf concentrations of Cl were maximum at

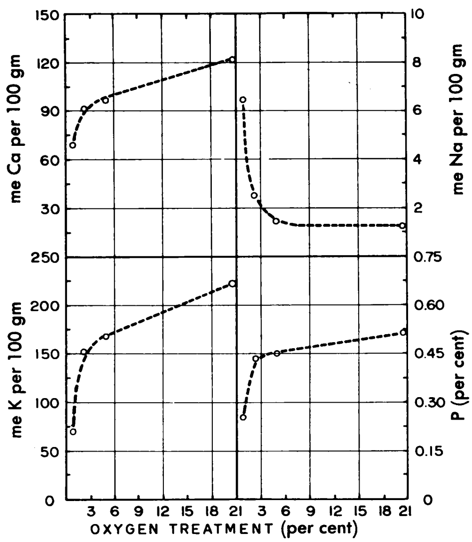


Fig. 3. Changes in mineral concentrations of sunflower tops as a result of different soil oxygen treatments.

O.D.R. of less than 22, and dropped to a minimum at about 30.

The study on corn (Van Diest, 1962) showed a significant difference in N concentration in the tops of plants on the unfertilized plots at an O.D.R. of $10 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$, as compared with the concentration in other treatments with O.D.R. values of 30 and above. Nitrogen and K were generally lower in plants in both fertilized and unfertilized treatments at O.D.R. between 10 and 13, as compared with other plants in treatments with O.D.R. of 29 to 41. Oxygen diffusion rates had no effect on P concentration in these plants.

Information on mineral accumulation in plant tops in relation to O.D.R. is relatively limited as compared with that on other plant responses. More comprehensive studies of macro- and micronutrients in relation to O.D.R. are needed before critical areas can be determined. Many of the nutrients are reduced in leaves at O.D.R. of less than 30 to 40.

## STUDIES ON GENERAL CORRELATION OF O.D.R. AND PLANT RESPONSE

The platinum microelectrode method has often been used to measure the oxygen environment in soils at a particular time with different degrees of correlation to plant response. Because of the previously considered O.D.R. and plant responses under more controlled conditions, such information is important for application of the conclusions to general field conditions.

Poel (1960*a*, *b;* 1961), in his studies of various types of plant communities in noncultivated areas of the British Isles, measured O.D.R. in transitions between different plant communities. In one area (Poel, 1960*a*), where O.D.R. was measured at a 14.5-cm depth, the plant communities were in the following order: *Pteridium* > *Juncus acutiflorus-Carex flacca-Holcus lanatus* > *Juncetum acutiflorum* > *Juncetum coglomeratum* (waterlogged). The range of O.D.R. was 25 to $5 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$.

In a study of 13 plant communities in a hill grazing area, Poel (1960*b*) found that *Molinia* and *Nardus* grew in soils with the highest O.D.R. and occurred in elevated areas but seldom in marshes. The O.D.R. associated with these plants was $17 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$.

*Juncus effusus* and *Deschampsia caespitosa* are codominant on the margin of marshes with O.D.R. of $10 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. The lowest O.D.R., of 4, was measured in stagnant areas where vegetation forms a mat over 6 feet of fluid mud.

Poel (1961) made a third study of O.D.R. in soils with transition from *Pteridium aquilinum* colonies (bracken), which require good conditions of drainage, to *Juncetum acutiflorum* colonies, which grow in less well-drained soils. Oxygen diffusion rates of $17 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ and above were found in soils with *Pteridium* colonies, while *Juncetum acutiflorum* colonies grew on O.D.R. values of less than 14.

Poel's study of plant ecology in relation to soil oxygen is one important application in areas of high rainfall and wet soils. Plant competition in noncultivated land involves various factors, soil oxygen probably being an important one.

Finn *et al.* (1961), in a study of the effect of soil moisture on grass and legumes, used O.D.R. to characterize the soil oxygen condition at different soil suction values. They used 18-gauge platinum electrodes at an applied potential of –0.8 volt. Readings were taken after two minutes. Ranges of O.D.R. at different soil suction values, reported in millibars, were: 0 mb—5; 25 mb—5 to 9; 40 mb—8 to 18; and at field capacity, 23 to 37, all $\times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. In general, bromegrass and Reed canarygrass produced more tops and roots at the 0-mb suction treatment than were produced at field capacity. Timothy, Ladino clover, and birdsfoot trefoil in the 0-mb suction treatment produced the same top and root growth, but generally less than in the field-capacity treatment, while alfalfa was very markedly reduced at all low suction values when compared with field-capacity treatments. Because the soil was kept at field capacity during the periods before and after treatment, it is difficult to determine which O.D.R. values limited growth. The exception is alfalfa, which showed that something less than $18 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ was detrimental to plant growth. An important point to remember is that the root systems were established before the moisture treatments were applied, which resulted in the low O.D.R. Data of Letey, Stolzy, and Blank (1962) show that the effect of low oxygen on plant growth depends upon how well the plant is established at the time of low oxygen.

Wheat seedling emergence was measured on soils with different textures, bulk density, and moisture. Oxygen diffusion rates were used to evaluate soil oxygen conditions (Hanks and Thorp, 1956). These investigators found that an O.D.R. of about 75 to $100 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ was necessary for the emergence of wheat. They used equipment similar to that of Lemon and Erickson (1955). The platinum electrode was 18-gauge, 5 mm long, and was applied at a potential of –0.8 volt. Readings were taken after three minutes. This procedure, under the conditions stated, would give higher O.D.R. than the procedure suggested by Birkle *et al.* (1964).

Emergence of sugar beets was shown to be influenced by the O.D.R of soil (Archibald, 1952). The two sugar beet varieties studied had different requirements for emergence. One had maximum emergence at O.D.R. of $42 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$; the other was maximum at an O.D.R. of 35. In a study on the emergence of potatoes, an O.D.R. of 24 was critical; soil with an O.D.R. above 61 showed no additional response (Erickson and Van Doren, 1960). Another study, on peas, showed a marked reduction in emergence in soils at O.D.R. of 36 to 45 and 51 to 60. Oxygen diffusion rates of 61 to 70 doubled the emergence of peas as compared with those on soils of lower O.D.R. (Erickson and Van Doren, 1960).

It is again important to point out the variability in information on plant response and O.D.R. In general, many studies report O.D.R. that are entirely too low to show the possible maximum production of plants. The studies also indicate the scope of investigations needed for an understanding of how soil oxygen is affecting the plant from germination to maturity.

## SUMMARY

Different investigators are in substantial agreement on the relationship between O.D.R. and root growth. The critical O.D.R. value of soils in which roots of many plants will not grow is $20 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. Oxygen diffusion rates between 20 and 30 retard root growth.

In studies relating to plant top response to O.D.R., a wide range of O.D.R. values influences the plant, depending on what is being considered. The production of dry materials and changes in height of plants are not affected by O.D.R. values greater than $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$. There is, however, a much lower critical area in which plants either stop growing or die. In limited studies of pea production or flowering, diffusion rates of less than 50 to 60 caused decreased yields.

The nutrition of a plant is markedly changed when O.D.R. is limiting. Oxygen diffusion rates of less than 30 to $40 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ reduced the concentration of the more important macronutrients and increased that of several other minerals.

Emergence data on various plants in relation to O.D.R. indicate that plants have a much greater need for better soil aeration during emergence than after they become established. Oxygen diffusion rates of at least 50 to $70 \times 10^{-8}$ gm $cm^{-2}$ $min^{-1}$ are needed for good emergence.

It is evident that under conditions of lower O.D.R. certain species of the grass family produce as well as or better than do some of the legumes.

Under wet soil conditions, where diffusion rates are less than $20 \times 10^{-8}$ gm

$cm^{-2}$ $min^{-1}$, very narrow ranges of O.D.R. can determine the type of plant communities which will be established under a noncultivated area.

The present need is to standardize methods so that results can be comparable. This is especially true with respect to the potential to be applied and the time to be allowed for attainment of steady-state values.

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