

Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil-root contact

II. Applications

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Summary In relation to explanations of anaerobiosis in the field, mathematical models presented in part I are evaluated in the light of the disparity between the low oxygen pressure required by plant roots in well-stirred nutrient solutions and the rather high values apparently required in the field. Water film and rhizosphere respiration do not fully explain this disparity. Soil-root contact as described in part I is shown to considerably affect the partial pressure of oxygen required for unrestricted aerobic respiration.

Introduction

Explanations of the occurrence of aeration problems in the field so far suffer from an apparent disparity between the measured requirements of roots in well-stirred nutrient solutions and experimental evidence in the field. In experiments in well-stirred nutrient solutions critical values of oxygen partial pressure at the root surface have been found^{3,5,8} to be around 1%. The affinity for oxygen of cytochrome oxidase is such that at the cell level the critical concentration is virtually zero. A concentration difference of 1% between the epidermis and the root centre is apparently sufficient for internal diffusion inside the root under the conditions of measurement³. Oxygen is used for various processes in the root, which have different critical oxygen pressures. Differentiation of total oxygen consumption is no simple matter¹⁹. Our assumption of a constant total oxygen use is obviously a first approximation. Critical values of oxygen pressure in soil air vary widely but values of 10–15% are not uncommon³. The explanation for the contrast between values – 1% at the root surface and around 10% in soil air – can probably be found in the diffusion pathway involved.

Lemon¹² has given a steady-state solution for oxygen diffusion towards and within a cylindrical root in the presence of a water film at the root surface. Since then, such a water film has often been

considered as being the major obstacle. The thickness of the water film might be an important parameter, but neither techniques for direct measurements nor a theory which relates it to the water status of the soil are available. A complete evaluation of the role of water films in field situations is thus impossible. As shown below, theoretically it does not give a full explanation of the 1%–10% disparity mentioned.

Other complications of the diffusion pathway have been mentioned in the literature. Oxygen consumption by rhizosphere microorganisms or by an ectomycorrhizal sheath may have an effect⁵. We have tried to evaluate these effects using the models of the preceding paper²¹.

Most measurements of root respiration reported in the literature include oxygen consumption by the rhizosphere. The relative contribution of the rhizosphere microorganisms is estimated to be up to one third of total respiration of root plus rhizosphere¹⁶. As a first approximation this oxygen sink may be assumed to be distributed evenly over the water film. Rhizosphere respiration obviously lowers the oxygen supply to the root. But as rhizosphere respiration has usually been included in measurements of root respiration, the latter has been overestimated to the same extent as the former is underestimated. A comparison should be made between situations with the same total respiration rate and varying distribution of the respiration activity over the root and water film.

The concept of a uniform water film obviously can only serve as a first approximation. Some parts of the root surface area are in direct contact with soil particles or small water-filled pores while others are in contact with larger air-filled pores, gaps and cracks (Fig. 1 of the preceding article²¹). Only for the last mentioned parts of the root is the water film of any importance. Entry of oxygen to the other part is virtually completely blocked (only a long route through water-filled pores is available). In recent theories of water uptake the possibility of a soil-root resistance plays a major role^{10,18,20}. The fact that only a part of the root circumference is in contact with the water-continuum of the soil probably restricts the possibilities for water uptake considerably. Oxygen uptake is probably restricted to the remaining part of the circumference. The consequences of this restriction are the main topic of this paper. The soil-root contact should be a compromise between the conflicting interests of a sufficient contact with the soil air and with soil water.

The soil-root interface is a recent focus of research⁹; progress so far has been limited by a lack of adequate techniques for direct observations. In some soils the immediate vicinity of the root can be

transformed into "cutans" or clay coatings⁷. Ageing of a root results in many changes of the contact zone: the mucigel-layer formed by the growing root tip may gradually disappear and the epidermis and cortex may slowly be decomposed, separating the root from the soil. Secondary thickening of the roots may subsequently reestablish contact¹. Shrinking of roots by droughts and swelling by rewatering or even in a daily cycle make the degree of soil-root contact a very dynamic parameter. For a root growing through a homogeneous sandy soil surrounded by soil particles the contact will be different from that for a root growing in an aggregated clay soil. Considering all these factors, the part of the root circumference in contact with soil air can be expected to vary from 0–100%, probably with an average between 30–70%.

Using the mathematical descriptions given in the first paper²⁰, we will now try to evaluate these three factors: thickness of water film, rhizosphere respiration and soil-root contact.

The models (in part I) have been derived under the following simplifying assumptions:

- a. Roots are considered to be cylindrical in shape, to have a uniform oxygen consumption rate per unit volume for all cells in a cross section and to have uniform transport characteristics with respect to oxygen diffusion.
- b. No longitudinal transport of oxygen is taken into account. A description of such transport from shoot to root has been given by Luxmoore *et al.*¹⁴; it is generally not important for young roots⁴.
- c. Oxygen consumption is taken to be independent of the oxygen concentration and considered to proceed at the same rate until oxygen pressure drops to 0%.
- d. Aeration problems are supposed to begin when at any point in the root the concentration becomes zero.

Leakage of oxygen from roots into the soil is neglected.

Estimates of the parameters in the models

The following values for the parameters were chosen:

The volumetric respiration rate Q : Brouwer and Wiersum³ gave a review of data on oxygen consumption by mostly young roots.

Assuming 7% dry matter in roots, the range of values is $2.5\text{--}50\text{ mg O}_2\text{ cm}^{-3}\cdot\text{day}^{-1}$ with an average of 13. In our calculations a value of $10\text{ mg}\cdot\text{cm}^{-3}\cdot\text{day}^{-1}$ was used, considering the fact that soil temperatures in temperate regions usually are lower than the temperatures at which oxygen consumption has been measured. Root radius R_0 varies for most herbs and grasses from 0.01 to 0.5 cm. Higher values are found in many trees and in roots with secondary thickening¹⁷. In most of the calculations we used 0.01, 0.016 and 0.023 cm. The diffusion coefficients D_i and D_e : at 20°C reasonable estimates for D_i and D_e are 0.7 and $0.85\text{ cm}^2\cdot\text{day}^{-1}$, respectively¹¹. The thickness of the water film Δ has been estimated to be

in the range $0.01\text{--}0.1\text{ cm}^3$. The oxygen concentration C_1 : At 15°C the oxygen concentration of water in equilibrium with 21% O_2 in air is $0.0096\text{ mg}\cdot\text{cm}^{-3}$, at 10°C 0.0106 , at 20°C 0.0088 , and at 25°C 0.008 . Luxmoore and Stolzy¹⁵ compared the temperature dependence on a relative scale of respiration rate and some physical parameters relevant to the transport of oxygen in soil. The solubility and the diffusivity of oxygen in water are similarly affected by temperature changes, be it in opposite directions, so that the product DC , which is important in the definition of the dimensionless respiration rate, is more or less independent of temperature. The respiration rate is, like many other biological activities, strongly (exponentially) dependent on temperature.

Results

Water film and rhizosphere respiration

Fig. 1 shows the oxygen concentration required to allow respiration by all cells of the root, in the presence of a water film with and without respiration by rhizosphere organisms. The intercept with the y-axis is comparable to the situation in well-stirred solutions during physiological measurements. From the figure the effect of a water film appears to be stronger for thicker roots, with a higher oxygen requirement per se. Ten percent oxygen pressure in soil air is only required by thick roots or in the case of a water film exceeding the root diameter in thickness.

The presence of rhizosphere respiration in the water film modifies the situation only to a small extent. Rhizosphere respiration of an additional 30% increases the oxygen requirement by 0.5–1%. If the rhizosphere respiration is subtracted from the root respiration, the oxygen requirement is lowered by 1–3%.

Soil-root contact

Fig. 2 shows the oxygen requirements when part of the root is blocked by soil contact. The percentage of soil-root contact appears to be a critical factor as well as root radius. A wide range of values occurs. Values of 10% oxygen are required by roots of $R_0 = 0.016$ and about 50% of soil contact. The effects of presence of a water film and of partial blocking of air contact of the root on the oxygen requirement are more than additive; in the case of a partially blocked root the same amount of oxygen has to pass through a smaller root surface area plus water film so the gradient required increases.

The effect of soil-root contact on the oxygen concentration required is twofold: 1) the total oxygen requirement of the root has to pass through a smaller root surface area and 2) the diffusion distance is increased (doubled in the extreme case, from the root radius to the root diameter). As a first approximation of the first effect the required oxygen concentration can be estimated as being proportional to $(1-B)^{-1}$

Oxygen concentration
in soil air, %

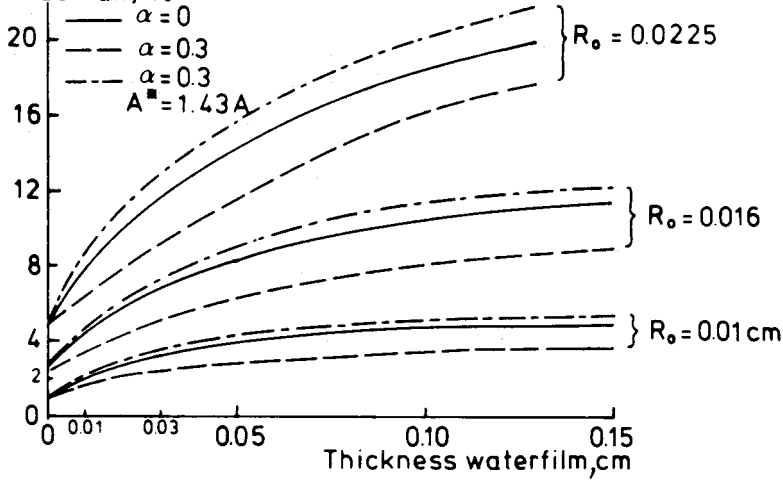


Fig. 1. Oxygen concentration required in soil air for aerobic respiration by all root cells as a function of thickness of the water film a) when respiration is restricted to the root ($\alpha = 0$), b) when the same respiration rate is distributed over root and microbial activity in the water film ($\alpha = 0.3$) and c) when rhizosphere respiration is superimposed on root respiration ($\alpha = 0.3$, $A^* = 1.43 A$). Results are given for three values of the root radius.

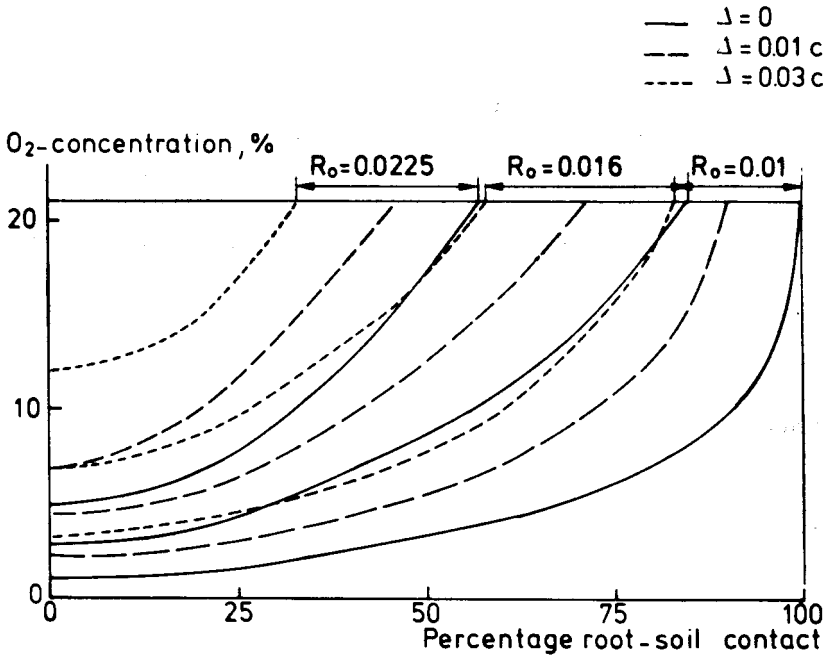


Fig. 2. Oxygen concentration required in soil air for aerobic respiration by all root cells as a function of the percentage of root-soil contact, root radius and thickness of water film (Δ).

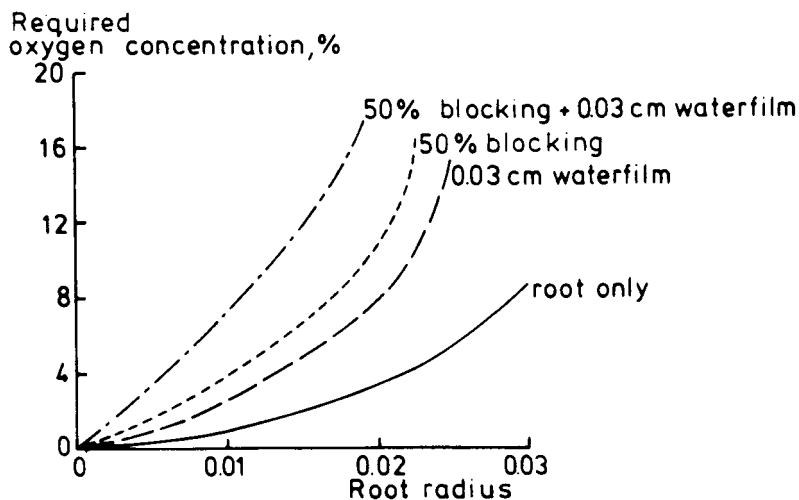


Fig. 3. The effect of root radius on the required oxygen concentration for aerobic respiration by all root cells.

where B is the fraction of the root perimeter blocked. If, for example, $2/3$ of the root perimeter is blocked, the required oxygen concentration is tripled due to the first effect, and at most doubled due to the second effect. The first effect is thus dominant.

Effect of root radius

Fig. 3 summarizes the data presented in Figs. 1 and 2 in relation to the radius of the root. The model predicts that the effect of 50% blocking is greater than the effect of a water film of 0.03 cm; the effect of a water film is doubled in the presence of 50% blocking.

Discussion

The figures presented here indicate that soil-root contact is an important factor in explaining the oxygen requirements of a root system in the soil. As shown by Fig. 2, small variations in the degree of contact can considerably change the oxygen requirements. As techniques for direct measurement of the nature of the soil-root interface *in situ* are not available, we cannot yet evaluate the way in which soil type, soil structure and plant species influence this "contact resistance" for oxygen uptake, but strong effects on the oxygen requirement may be expected in a 'normal' range of other parameters.

Root diameter is a critical parameter with respect to aeration status as shown in Fig. 3. Although Lemon and Wiegand¹³ already gave a comparable graph for situations without water film or root blocking, the importance of the root diameter has not always been realised.

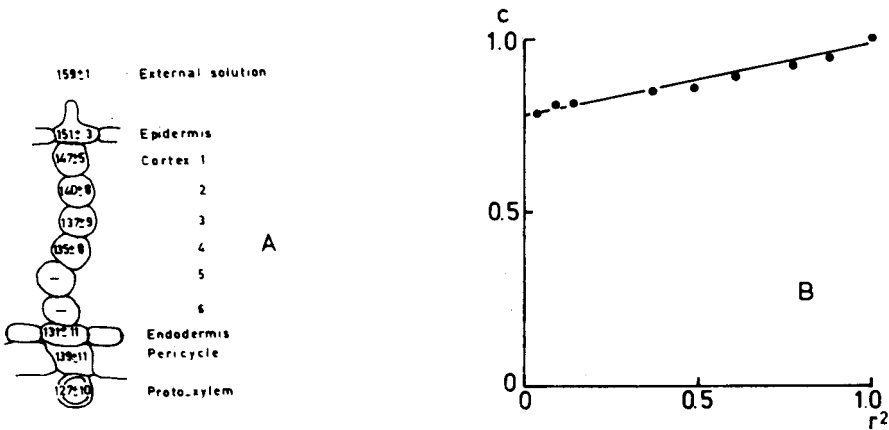


Fig. 4. Oxygen profiles inside the root according to Bowling². A) shows the data as presented originally, B) shows a plot of concentration versus r^2 , which gives an approximately straight line.

Testing the Crafts-Boyer hypothesis that oxygen deficiency of the stele plays a role in root pressure exudation, Fiscus and Kramer⁶ used roots of 1 mm diameter and found evidence of a low supply of oxygen to the stele under conditions of the measurement. Bowling² made direct measurements of the oxygen partial pressure gradient in an intact root and came to the conclusion that the stele was well supplied with oxygen. The smaller root diameter in his experiment (about 0.4 mm) may explain the difference. According to eq. (21) in part I²¹ a plot of c versus r^2 should yield a straight line when steady state has been attained. When Bowling's data are plotted in this way (Fig. 4A and B) a straight line is indeed obtained. From the intercept of this line, $(1-q/4)$ can be estimated to have been approximately 0.8, and assuming the usual values for D and C the respiration rate Q can be calculated as:

$$Q = 13 \text{ mg O}_2 \text{ cm}^{-3} \text{ day}^{-1}$$

which is in agreement with the range of Q given above, and with the respiration rate in Fiscus and Kramer's experiment. It follows that q in their experiment can be estimated at $(0.1/0.04)^2 \times 0.8 = 5$. Substituting this value in (21) it is found that the concentration in the root would become zero when r^2 is about 0.2, so that possibly 20% of the volume of the root was not aerated adequately.

The internal structure of the root has been highly simplified in the models. No differentiation between transport in apoplast and symplast is possible at the moment due to lack of knowledge about the transport processes involved other than diffusion in a water-like medium. Air

voids between the cells, however, may not be neglected nor can aerenchyma, if present. As air voids do not normally form a continuous pathway in a root cross section their role will be small in the present problem. As a first approximation one might reduce the root radius to an equivalent root radius without voids with the same surface area of apoplast and symplast in a cross section. In longitudinal sections, however, air voids can be continuous along cell strands. If aerenchyma is present, the continuity of air channels is obvious. This provides a completely different situation for oxygen transport. Luxmoore *et al.*¹⁴ have presented a mathematical treatment of longitudinal transport from shoot to root through such channels. Calculations show that a considerable fraction of the oxygen requirement of the root can be provided by the above-ground parts in species adapted to permanently wet soils, *e.g.* rice. In this case those properties which limit gaseous exchange between the root and its environment, *i.e.* large root radius and a thick water film, improve the supply to the the root tip. But such air channels are not found in most crop species. Greenwood⁸ stated that oxygen diffusion through air voids that are continuous along the length of the root can be sufficient for several centimeters of root to be in a completely anaerobic environment. In roots growing through soil aggregates some sections will be completely enclosed by the soil while others may be fully exposed to soil air. This requires a three-dimensional description rather than the two-dimensional given here. Especially the supply to the root tip with its high demand and poor supply situation (no aerenchyma) requires attention. Another extension of the model presented here would be to consider roots with several alternating parts of soil and air contact along their circumference. Without elaborating the mathematics of this situation, it is intuitively clear that the same total fraction of soil-root contact distributed over two or more parts of the root perimeter is more favourable than an uninterrupted blocking of one part. Further refinements of the theory in this direction are necessary. The theory presented here can, at least so we hope, stimulate direct measurements of the degree of soil-root contact and of the pathway for oxygen transport in various situations.

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