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

I. Derivation of the models

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Summary A mathematical model is presented for diffusive transport of oxygen inside the root, for the case that oxygen can enter only through part of the root's perimeter because the remainder is blocked by soil-root contact. Without soil-root contact, concentration profiles inside the root can be shown to converge rapidly to a steady-state solution. For the case of soil-root contact a steady-state solution is presented. Steady-state solutions have also been obtained for the presence of a water film, with and without rhizosphere respiration inside the water film. Results are presented in the form of isoconcentration lines.

Introduction

Recent reviews of the literature[1,2,3,6,10] emphasize the complex nature of anaerobiosis in soils. Poor aeration may cause the accumulation of various gasses and toxic waste products, but depletion of oxygen below critical levels can, however, be considered as a major effect on plant roots[6], except for plants with special structural adaptions to overcome problems of poor oxygen supply. For practical, agricultural purpose the question then is what level of oxygen is critical. The concentration of oxygen in soil is determined by the supply of oxygen to the soil and the consumption by the soil biomass and roots plus rhizosphere. Both supply and consumption vary with soil type, water status, crop, temperature, soil tillage and organic matter inputs. The balance between supply and consumption has a high spatial heterogeneity and large temporal variation. Anaerobic spots may occur locally inside large aggregates in an otherwise well aerated soil. During periods of (partial) waterlogging after heavy rainfall, the anaerobic zones spread out and for a brief period a large part of the soil profile may become anaerobic before the larger pores have drained[7]. These highly dynamic aspects of anaerobiosis are hardly open to realistic quantification as so many parameters are involved. Somehow the problem has to be split up. A convenient way of doing this, is to distinguish 'macro-' and 'micro' models. Macromodels generally use average values of or relations between transport parameters to predict average concentrations at a certain depth, while micromodels compute gradients over short distances in and around individual roots or aggregates. Macromodels are mainly concerned with the gas phase, while for micromodels oxygen transport in both gas and water phase is relevant, the water phase (with a diffusion rate that is 10^4 times lower than in air), if present, being a major obstacle. At the water-air interface the partial pressure of oxygen will be the same on both sides, providing a link between macro- and micromodels. Macromodels can cope with temporal fluctuations; micromodels are dominated by details of the geometry of the diffusion pathway. The pathway for oxygen transport from soil air to all cells of a root requiring oxygen can be complicated, for instance by the presence of a water film at the root surface, by the presence of oxygen-consuming rhizosphere microorganisms and by partial contact of the root with the soil.

The purpose of our papers is to study the theoretical consequences of some micromodels of transport of oxygen towards and within a root. In these models, following and extending earlier work[9], we took into account effects of water film, rhizosphere respiration and of root-soil contact (Fig. 1).

In part I the models will be developed and the mathematics elaborated, part II will show biologically relevant results and discuss which model can offer a quantitative explanation for the experimentally assessed critical soil oxygen level.

The models 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.

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.

These assumptions will be discussed in the second part.

Mathematical formulation

As the derivations are given elsewhere in detail[11], it suffices here to mention the underlying principles without the complete step-by-step derivation. The object is to calculate the oxygen concentration at any point inside a root as a function of the degree of contact between root and air phase, the thickness of the water film, the root diameter, the respiration rate and the external concentration of oxygen.

Equation of continuity

Generally the equation of continuity for diffusion and consumption of oxygen in a region can be given as:

$$\frac{\delta C}{\delta T} = D\nabla^2 C - Q \tag{1}$$

where

C is the concentration of oxygen, mg/cm^3

T is time, days

D is the diffusion coefficient, cm^2/day

∇^2 is the Laplacian operator

Q is the respiration rate of the root tissue, $mg/(cm^3 \cdot day)$

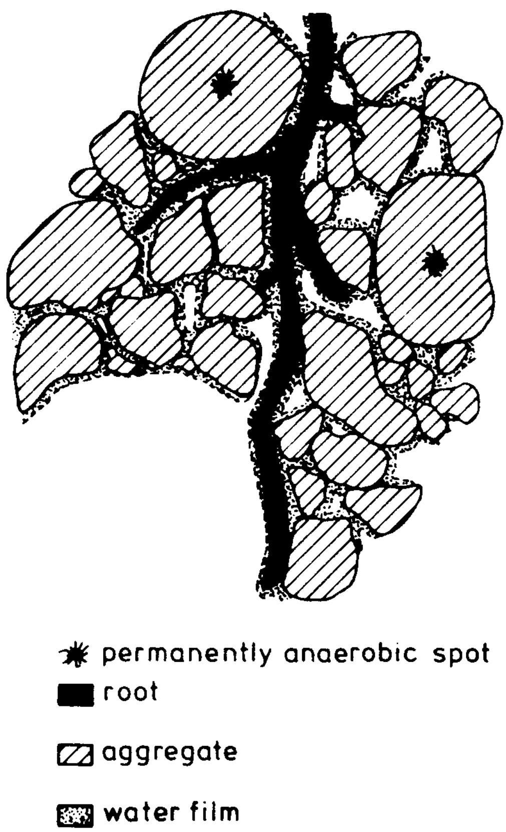


Fig. 1. Schematic representation of a root growing in an aggregated soil (with macropores and micropores) at moderate moisture content. Water films are present around soil aggregates and the root surface. The larger aggregates may contain spots almost permanently anaerobic.

Notation and insight into the relative importance of the parameters are facilitated when dimensionless variables and parameter groups are used, according to the definitions:

$$c = C/C_1 \quad \text{'dimensionless concentration'} \tag{2}$$

$$t = DT/R_0^2 \quad \text{'dimensionless time'} \tag{3}$$

$$\nabla^{*2} = R_0^2\nabla^2 \tag{4}$$

$$q = QR_0^2/DC_1 \quad \text{'demand/supply ratio'} \tag{5}$$

In (2)–(5), C_1 is the constant concentration at (part of) the interface of the root and soil air or at the interface of the water film adhering to the root and solair (in that case the concentration at the root surface is denoted by C_0), and R_0 is the radius of the root.

The definition of ∇^{*2} implies that radial or rectangular coordinates with the dimension of length are made dimensionless by division by R_0.

With the definitions (2)–(5), equation (1) transforms into:

$$\frac{\delta c}{\delta t} = \nabla^{*2} c - q. \tag{6}$$

With the types of boundary conditions considered in this paper, sooner or later a steady state will be reached. Equation (6) will then reduce to:

$$\nabla^{*2} c - q = 0 \tag{7}$$

In the following only two-dimensional problems will be considered with two types of boundary conditions: a uniform boundary condition, where the value of the concentration at the complete root circumference is prescribed, and a mixed boundary condition, where the value of the concentration at part of the circumference is given, and the gradient of the concentration over the remaining part is taken to be zero.

Uniform boundary conditions

For uniform boundary conditions it is convenient to express (6) and (7) in polar coordinates, as due to the uniform boundary and initial conditions (see following paragraph) no gradients in tangential directions will occur. Equations (6) and (7) then become, respectively:

$$\frac{\delta c}{\delta t} = \frac{1}{r}\frac{\delta}{\delta r} r \frac{\delta c}{\delta r} - q \tag{8}$$

$$\frac{1}{r}\frac{d}{dr} r \frac{dc}{dr} - q = 0 \tag{9}$$

where r is the dimensionless radial distance from the root midpoint. A solution for the transient situation (eq. 8) will only be given for the simplest boundary condition: the entire circumference of the root is directly in contact with soil air. This boundary condition is thus given by:

$$r = 1 \qquad c = 1 \qquad t > 0 \tag{10}$$

When it is assumed that initially the oxygen concentration in the root has everywhere the same value, *i.e.* the value of the concentration at the root surface, the initial condition is:

$$t = 0 \qquad c = 1 \qquad 0 < r \leqslant 1 \tag{11}$$

The solution of (8) subject to (10) and (11) is given by Carslaw and Jaeger[4] (p. 330, eq (24)):

$$c = 1 - \frac{q}{4}(1 - r^2) + 2q \sum_{n=1}^{\infty} \frac{e^{-\alpha_n t} J_0(\alpha_n r)}{\alpha_n^3 J_1(\alpha_n)} \tag{12}$$

In (12), α_n is the n-th positive root of $J_0(\alpha) = 0$, and J_0 and J_1 are Bessel functions of the first kind and zeroth and first order, respectively. By taking the limit as $t \to \infty$, from (12) the steady-state solution can be derived:

$$c = 1 - \frac{q}{4}(1 - r^2) \tag{13}$$

This result could of course also be obtained directly by solving (9) together with (10). As will be illustrated under the heading Results, (12) can very soon be approximated by (13).

A steady-state solution has been derived for a somewhat more complicated boundary condition in which oxygen consumption in the water film is considered. Though in principle for this boundary condition solutions for the transient situation can be found, we will restrict ourselves to the steady state situation, because this will be approximated soon, as can be inferred from (12) and as shown in Fig. 4. When the root is surrounded by a water film in which, due to presence of microorganisms and root exudates, respiration takes place, it is convenient for the time being to denote the oxygen concentration in the two regions, *viz.*, the root and the water film, by the symbols C_i and C_e. Using (9), thus two differential equations can be formulated:

$$1 \leqslant r \leqslant r_i \qquad \frac{1}{r}\frac{d}{dr} r \frac{dc_e}{dr} - q_e = 0 \tag{14}$$

$$0 \leqslant r < 1 \qquad \frac{1}{r}\frac{d}{dr} r \frac{dc_i}{dr} - q_i = 0 \tag{15}$$

where q_e and q_i now are the dimensionless respiration rates in the water film and the root, respectively, defined from the volumetric respiration rates Q_e and Q_i and the diffusion coefficients D_e and D_i as in (5):

$$q_e = \frac{Q_e R_0^2}{D_e C_1} \qquad q_i = \frac{Q_i R_0^2}{D_i C_1}$$

while

$$r_1 = R_1/R_0$$

and

$$R_1 = R_0 + \Delta$$

Δ being the thickness of the water film. The boundary conditions applying in this situation are:

$$r = r_1 \qquad c_e = 1 \tag{16}$$

$$r = 1 \quad \begin{cases} c_e = c_i & (17a) \\ \dfrac{dc_e}{dr} = \lambda \dfrac{dc_i}{dr} & (17b) \end{cases}$$

$$r = 0 \qquad \frac{dc_i}{dr} = 0 \tag{18}$$

In (17b), λ is the ratio D_i/D_e. Condition (17a) ensures continuity of the concentration and (17b) continuity of the fluxes. Using the same symbol c for the concentration in the root and the water film, the solution of the problem can be given by the two equations:

$$1 \leqslant r < r_1 \qquad c = 1 - \frac{qe}{4}(r_1^2 - r^2) - \left\{\frac{\lambda q_i - q_e}{2}\right\} \ln\left(\frac{r_1}{r}\right) \tag{19a}$$

$$0 \leqslant r < 1 \qquad c = 1 - \frac{q_i}{4}(1 - r^2) - \frac{q_e}{4}(r_1^2 - 1) - \left\{\frac{\lambda q_i - q_e}{2}\right\} \ln r_1 \tag{19b}$$

In the absence of a water film $r_1 = 1$, and (19b) reduces to (13).

When the respiration of a root is measured, this usually includes the respiration in the water film. This respiration then is also attributed to the root proper. If the measured respiration rate per unit length of root is:

$$A = \pi R_0^2 Q_i + \pi(R_1^2 - R_0^2) Q_e$$

and this respiration is attributed to the root, the calculated volumetric respiration rate of the root will be:

$$Q = \frac{A}{\pi R_0^2} = Q_i + (r_1^2 - 1) Q_e$$

Let the ratio of the rhizosphere respiration to the total respiration be given by α $(0 < \alpha < 1)$, then

$$\frac{A_e}{A} = \alpha = \frac{(r_1^2 - 1)Q_e}{Q}$$

Likewise:

$$\frac{A_i}{A} = 1 - \alpha = \frac{Q_i}{Q}$$

So

$$q_i = \frac{Q_i}{Q} q = (1 - \alpha)q \tag{20a}$$

$$q_e = \frac{\lambda Q_e}{Q} \cdot q = \frac{\lambda \alpha q}{(r_1^2 - 1)} \tag{20b}$$

Substituting (20a) and (20b) in (19a) and (19b) gives:

$$1 \leqslant r < r_1 \qquad c = 1 + \frac{\alpha\lambda q(r^2 - r_1^2)}{4(r_1^2 - 1)} + \frac{q\lambda}{2}\left(1 - \frac{\alpha r_1^2}{r_1^2 - 1}\right) \ln\left(\frac{r}{r_1}\right) \tag{21a}$$

$$0 \leqslant r < 1 \qquad c = 1 + \frac{q}{4}(r^2 - 1) - \frac{\alpha q r^2}{4} + \frac{(1 - \lambda)\alpha q}{4} + \frac{q\lambda}{2}\left(1 - \frac{r_1^2}{r_1^2 - 1}\right) \ln \frac{1}{r_1} \tag{21b}$$

The minimum concentration is found at the centre of the root, so the supply of oxygen to the root is just sufficient if the concentration at this point is zero. The concentration at the midpoint can be found from (21b) and (using the definition of q) the concentration minimally required in the soil air to provide all cells with oxygen can be calculated as:

$$C_1 = \frac{QR_0^2}{2D_i}\left\{\frac{1}{2} + \frac{(\lambda - 1)\alpha}{2} + \lambda \ln\left(1 + \frac{\Delta}{R_0}\right) - \frac{\lambda\alpha\left(1 + \frac{\Delta}{R_0}\right)^2 \ln\left(1 + \frac{\Delta}{R_0}\right)}{\frac{\Delta}{R_0}\left(2 + \frac{\Delta}{R_0}\right)}\right\} \tag{22}$$

when $\alpha = 0$, (22) corresponds with equation 2 of Lemon and Wiegand[9].

Mixed boundary condition

When part of the root circumference is blocked by a soil aggregate, as is illustrated in Fig. 1, all oxygen required by the root has to enter through the remaining part. The condition for the blocked part can be given by: $\delta c/\delta r = 0$, and for the rest of the circumference by $c = 1$, when the effect of the water film is negligible (see below). For such a mixed boundary condition again only the steady-state solution shall be dealt with. In Fig. 2A the situation is depicted. The problem is now to find a solution of (7) with the conditions:

$$c = 1 \quad \text{over arc AB} \tag{23}$$

$$\frac{\delta c}{\delta r} = 0 \quad \text{over arc BCA} \tag{24}$$

It is convenient here to formulate (7) in rectangular coordinates:

$$\frac{\delta^2 c}{\delta x^2} + \frac{\delta c}{\delta y^2} - q = 0 \tag{25}$$

To find a solution, first (7) is converted into a Laplace equation by defining a new variable U as:

$$U = c - \frac{q}{4}(x^2 + y^2) \tag{26}$$

This changes (25), (23) and (24) into:

$$\frac{\delta U}{\delta x^2} + \frac{\delta U}{\delta y^2} = 0 \tag{27}$$

$$U = 1 - \frac{q}{4} = U_0 \quad \text{over arc AB} \tag{28}$$

$$\frac{\delta U}{\delta r} = \frac{-q}{2} = 2(U_0 - 1) = -F_0 \quad \text{over arc BCA} \tag{29}$$

Next the x, y-plane is considered as a complex z-plane where $z = x + iy$. The problem can now be stated as follows: find a harmonic function $U(z)$ for the disk $|z| \leqslant 1$, satisfying (28) and (29). The solution can be found by a method outlined by Lawrentjew and Schabat[8] (p. 358). First the disk $|z| \leqslant 1$ is mapped onto the upper half plane $\eta \geqslant 0$ in the ζ-plane, by the mapping function[5] :

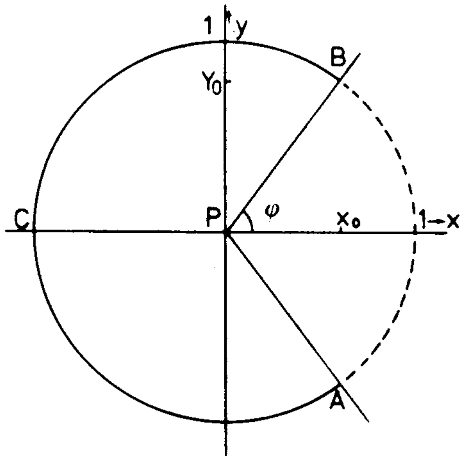
$$\zeta = h(z) = \frac{i(1-z)}{1+z} \tag{30}$$

where $\zeta = \xi + i\eta$ (see Fig. 2B). Working out (30) produces the relations between the coordinates in the z- and the ζ-plane:

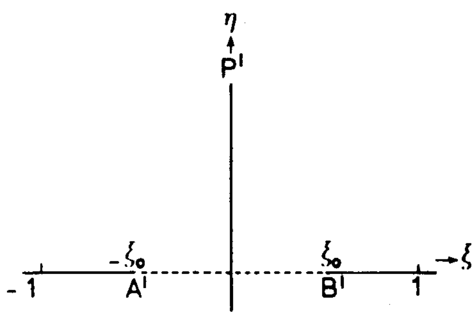
$$\xi = \frac{2y}{(1+x)^2 + y^2} \quad (31a) \qquad \eta = \frac{1-(x^2+y^2)}{(1+x)^2+y^2} \quad (31b)$$

$$x = \frac{1-(\xi^2+\eta^2)}{\xi^2+(1+\eta)^2} \quad (32a) \qquad y = \frac{2\xi(1+\eta)}{\xi^2+(1+\eta)^2} \quad (32b)$$

From (31a) and (31b) it can be seen that any point $z = x + iy$ on the circle $|z| = \sqrt{(x^2 + y^2)} = 1$ maps into a point on the ξ-axis of the



A



B

Fig. 2A. Schematic representation of a root with part of its surface (arc AB) exposed to soil air and the other part (arc BCA) blocked by an aggregate. The size of the oxygen 'window' is characterized by the angle φ.

Fig. 2B. Mapping of the circle in the z-plane of Fig. 2A to the upper half-plane $\eta \geqslant 0$ by the function $\zeta = i(1-z)/(1+z)$. Point A with coordinates $(x_0, -y_0)$ in the z-plane maps into A^1 with coordinates $(-\xi_0, 0)$ in the ξ-plane. Likewise, B maps into B^1, and C into the point of infinity.

z-plane, so the points z_0 and $\bar{z}_0$ (see Fig. 2) transform into points ξ_0 and $-\xi_0$ on the ξ-axis. Referring to Fig. 2A and equation (31a) one finds:

$$\xi_0 = \frac{2y_0}{(1+x_0)^2 + y_0^2} = \frac{y_0}{1+x_0} = \frac{\sin\varphi}{1+\cos\varphi}$$

$$= \sqrt{\frac{1-\cos\varphi}{1+\cos\varphi}} \qquad (33)$$

A harmonic function U(x, y) in the z-plane transforms into a harmonic function $U(\xi, \eta)$ in the ζ-plane by a conformal mapping as given by (30). The boundary conditions transform into:

$$U = U_0 \text{ for } \zeta \text{ real and } |\zeta| < \xi_0 \qquad (34)$$

$$\frac{\delta U}{\delta \eta} = \frac{2F_0}{\xi^2+1} \text{ for } \zeta \text{ real and } |\zeta| > \xi_0 \qquad (35)$$

Now suppose that $U(\xi, \eta)$ is the real part of a function $F(\zeta) = U(\xi, \eta) + iV(\xi, \eta)$, analytic in the upper half-plane ($\eta > 0$) of the ζ-plane. Consider the derivative of F:

$$F_1(\zeta) = F'(\zeta) = u(\xi, \eta) + iv(\xi, \eta)$$

with $u = \delta U/\delta\xi$ and $v = \delta V/\delta\xi = -\delta U/\delta\eta$ according to the Cauchy-Riemann equations. So if one can find a function $F_1(\zeta) = u + iv$ analytic for $\eta > 0$, the real and imaginary part of which satisfy, respectively:

$$u = \frac{\delta U}{\delta \xi} = 0 \text{ for } \zeta \text{ real and } |\zeta| < \xi_0$$

$$v = \frac{-\delta U}{\delta \eta} = \frac{-2F_0}{\xi^2+1} \text{ for } \zeta \text{ real and } |\zeta| \geqslant \xi_0$$

then the solution of our problem is given by:

$$U = \text{Re}\left\{\int F_1(\zeta)d\zeta\right\} \qquad (36)$$

The function $F_1(\zeta)$ can be found with the formula of Keldysch-Sedov (Lawrentjew and Schabat[8] p. 353), which for our purpose can be given as:

$$F_1(\zeta) = \frac{1}{\pi i g(\zeta)}\int_{-\infty}^{+\infty} \frac{g(t)\,\psi(t)}{t-\zeta}\,dt + \frac{\gamma_0}{\sqrt{(\zeta^2-\xi_0^2)}} + \frac{F_1(\infty)}{g(\zeta)} \qquad (37)$$

with

$$g(\zeta) = \sqrt{\frac{\zeta-\xi_0}{\zeta+\xi_0}}$$

where it is to be understood that the positive root has to be taken for $\zeta > \xi_0$ and

$$\psi(t) = \begin{cases} 0 & \text{for } |t| \leqslant \xi_0 \\ \dfrac{-2F_0 i}{t^2+1} & |t| > \xi_0 \end{cases}$$

The constant γ_0 has to be chosen such that U is bounded, and $F_1(\infty)$ is the value of $F_1(\zeta)$ at the point of infinity. When the above expression for $\psi(t)$ is substituted in the integral of (37), two integrals result, (omitting the integrands):

$$\int_{-\infty}^{-\xi_0} + \int_{\xi_0}^{\infty}$$

These two integrals can be combined into one by the substitution $t = -t'$ in $\int_{-\infty}^{-\xi_0}$, yielding:

$$\frac{2F_0}{\pi g(\zeta)}\int_{\xi_0}^{\infty} \frac{2(\xi_0 - \zeta)t}{t^2 - \zeta^2} \cdot \frac{dt}{(t^2+1)\sqrt{(t^2-\xi_0^2)}}$$

When the substitution $t^2 - \xi_0^2 = s^2$ is made, one eventually obtains:

$$\frac{4(\xi_0 - \zeta)}{\pi g(\zeta)}\left\{\int_0^{\infty} \frac{ds}{s^2 + \xi_0^2 - \zeta^2} - \int_0^{\infty} \frac{ds}{s^2 + \xi_0^2 + 1}\right\}\frac{1}{1+\zeta^2}$$

Working this out and substituting the result in (37) yields:

$$F_1(\zeta) = \frac{-2F}{1+\zeta^2}\left\{i - \sqrt{\frac{\zeta^2 - \xi_0^2}{\xi_0^2 + 1}}\right\} + \frac{\gamma_0}{\sqrt{(\zeta^2 - \xi_0^2)}} + F_1(\infty)\sqrt{\frac{\zeta + \xi_0}{\zeta - \xi_0}} \tag{38}$$

From (38), by integration, choosing $\gamma_0 = -1/\sqrt{(\xi_0^2 + 1)}$ and $F_1(\infty) = 0$ as to keep U bounded, and adding the integration constant U_0, U can be given:

$$U = U_0 + \frac{F_0}{2}\ln\left\{\frac{\xi^2 + (\eta+1)^2}{\xi^2 + (\eta-1)^2}\right\} - F_0 \ln\left|\frac{\sqrt{(\zeta^2 - \xi_0^2)} + \zeta\sqrt{(\xi_0^2+1)}}{\sqrt{(\zeta^2 - \xi_0^2)} - \zeta\sqrt{(\xi_0^2+1)}}\right| \tag{39}$$

No attempt was made to work this equation out in terms of real functions of x and y, except in the one case treated below. When $\xi = 0$ ($\zeta = i\eta$), $y = 0$ as follows from (32b), so using (26) and (32a), the concentration on the x-axis can be given as:

$$c = 1 - \frac{q}{4}(1-x^2)$$

$$-\frac{q}{2}\ln\left\{\frac{x\sqrt{(1-x)^2+\xi_0^2(1+x)^2}+(1-x)\sqrt{(\xi_0^2+1)}}{\sqrt{(1-x)^2+\xi_0^2(1+x)^2}-(1-x)\sqrt{(\xi_0^2+1)}}\right\} \quad (40)$$

As the concentration must be symmetric with respect to the x-axis (cf. Fig. 2), it follows that the minimum concentration is to be found somewhere on this axis. By differentiating (40) with respect to x and solving for the zeros of the resulting equation, the position of the minimum concentration as a function of the angle can be found[11]. As is shown in Fig. 3, the minimum concentration occurs at $x = -1$ for $\varphi < 2.51$; at $\varphi = 2.51$ its position jumps to $x \simeq 0.5$ and then gradually moves to $x = 0$ for $\varphi = \pi$, the situation of equation (13).

Mathematically c can attain negative values, but obviously we can only give an interpretation of positive values or zero.

The root is supposed to be sufficiently supplied with oxygen when the minimum concentration is greater than or equal to zero. From (40) it can then be calculated which concentration at the root surface is minimally required to keep all parts of the root aerobic. If the position of the minimum within the root is given by x_m and the concentration at x_m is zero, the required concentration is:

$$C_0 = \frac{QR_0^2}{4D}(1-x_m^2)$$

$$-\frac{QR_0^2}{4D}\ln\left\{\frac{1}{x_m}\frac{\sqrt{(1-x_m)^2+\xi_0^2(1+x_m)^2}-(1-x_m)}{\sqrt{(1-x_m)^2+\xi_0^2(1+x_m)^2}+(1-x_m)}\cdot\frac{\sqrt{(\xi_0^2+1)}}{\sqrt{(\xi_0^2+1)}}\right\}$$

(41)

When $\varphi < 2.51$, $x_m = -1$ and the above expression simplifies to:

$$C_0 = \frac{QR_0^2}{2D}\ln\left\{\frac{\sqrt{(\xi_0^2+1)}+1}{\sqrt{(\xi_0^2+1)}-1}\right\} \quad (42)$$

The presence of a water film on the part of the root not blocked by soil aggregates increases the required oxygen pressure in the soil air. If as a first approximation it is assumed that transport in the water film occurs only in a radial direction and effects on isoconcentration lines within the root can be neglected, the concentration gradient over the

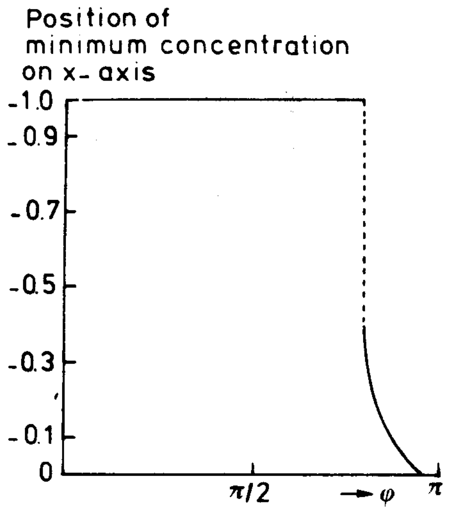


Fig. 3. The position of the minimum concentration on the x-axis as a function of the angle φ.

water film necessary to maintain the required flux can be calculated. From Lemon and Wiegand[9] (eq. 12) it follows that:

$$C_1 - C_0 = \frac{\lambda A}{2\pi D_i} \ln\left(1 + \frac{\Delta}{R_0}\right) \tag{43}$$

where C_0 can be calculated with (43) or (42). The required flux A through the 'window' in the root surface is, with a given oxygen

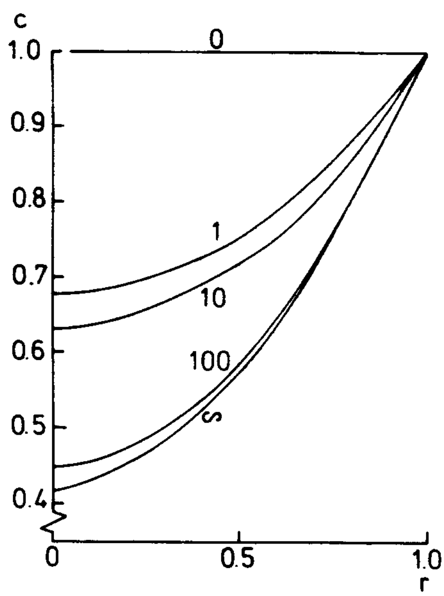


Fig. 4. Oxygen concentration as a function of radial distance from the root centre for different times (seconds).

demand, proportional to the size of the window

$$A = QR_0^2\varphi$$

Results

Here only some relevant mathematical features of the solutions will be shown, a discussion of the biological significance being given in part II. Fig. 4 shows the development of the concentration profile in the root with time (eq. 12). The values for t (0.0046, 0.046 and 0.46) correspond, for normal values of diffusion constant D_i, root radius R_0, external concentration C_1 and respiration rate Q (See part II for a discussion and justification of the choice of the parameter values) to 1, 10, and 100 seconds, respectively. It appears that within a few minutes the steady-state situation is attained. Fig. 5 shows the steady-state concentration in the root and adhering water film, when the latter acts as a diffusion barrier only and both as barrier and oxygen sink (eq. 19a and 19b). In the case of uniform boundary conditions (eq. 13),

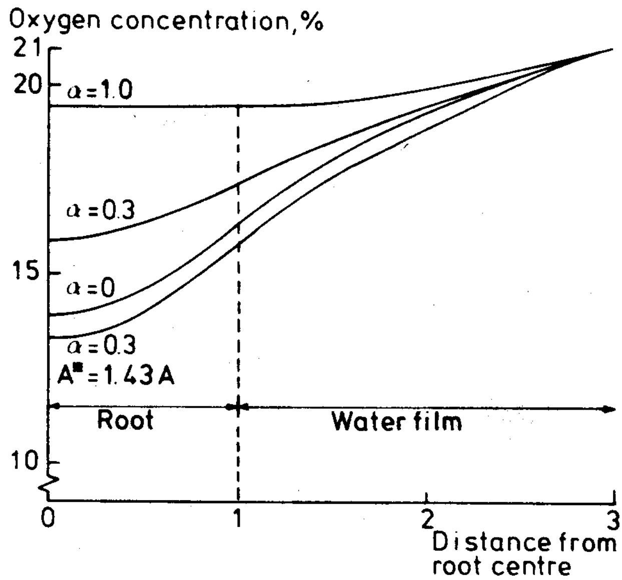


Fig. 5. Oxygen concentration in water film and root. The upper three lines apply to situations with the same total respiration for root plus rhizosphere (α indicates the fraction of respiration taking place in the rhizosphere). The lower line has the same root respiration as the α = 0 line, plus an additional rhizosphere respiration (30% of the root respiration).

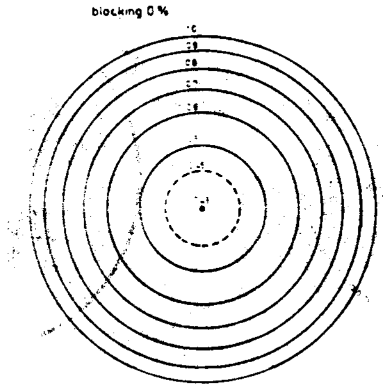


Fig. 6. Isoconcentration lines of oxygen in a root when the entire circumference of the root is exposed to soil air.

isoconcentration lines are obviously circles (see also eq. 12, 19a and b) as depicted in Fig. 6. This figure serves as reference for Fig. 7A–F where isoconcentration lines are given for the case of mixed boundary conditions. The parameter values in Fig. 7A–F were chosen so as to

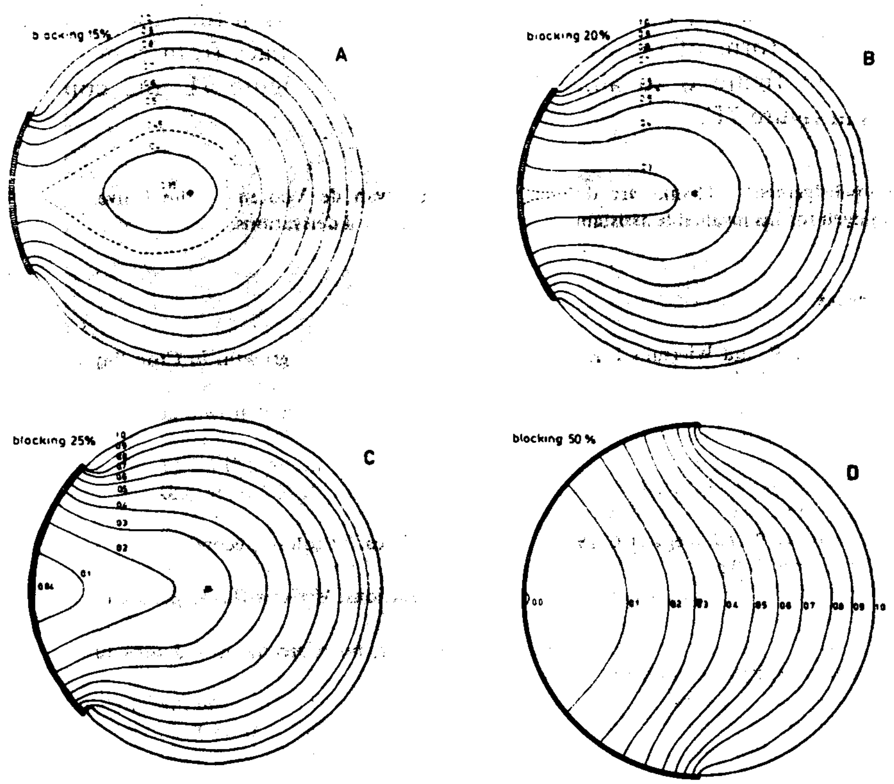


Fig. 7A–D.

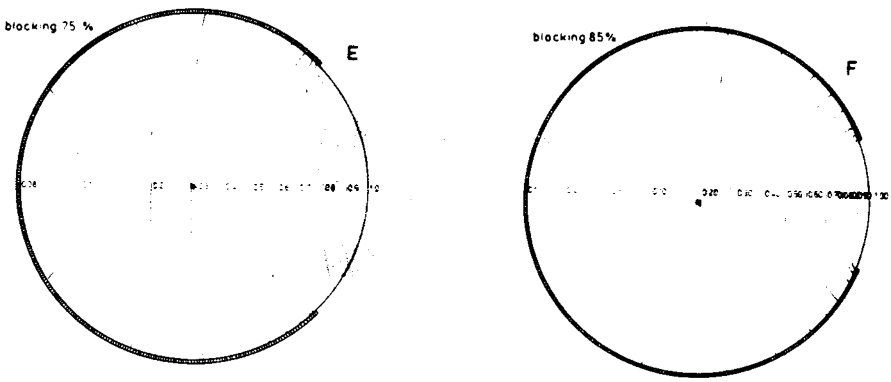


Fig. 7A–F. Isoconcentration lines of oxygen in a root when an increasing part of the root circumference is blocked. A: 15%; B: 20%; C: 25%; D: 50%; E: 75%; F: 85%.

assure that the concentration does not attain negative values in the root. The percentage of the root perimeter which is blocked (given by $100(1 - \varphi/\pi)$) increases gradually from Fig. 7A–F. It can be seen that the position of the minimum concentration shifts from somewhere near the midpoint of the root in A to the epidermis in the blocked part at B. The form of the isoconcentration lines changes from concentric circles in figure 6 to almost straight lines in figure 7E and convex lines in figure 7F.

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References

1 Brouwer R and Wiersum L K 1977 Root aeration and crop growth. *In* Crop Physiology Vol II. Ed. U S Gupta. Oxford Univ. Press and IBN Publ. Co., New Delhi. pp 157–201.
2 Cannel R Q 1977 Soil aeration and compaction in relation to root growth and soil management. Appl. Biol. 2, 1–86.
3 Cannel R Q and Jackson M B 1981 Alleviating aeration stresses. *In* Modifying the Root Environment to reduce Crop Stresses. Eds. G F Arkin and H M Taylor. ASAE monograph no 4, 141–194.
4 Carslaw H S and Jaeger J C 1959 Conduction of heat in solids. Second edition. Oxford, Clarendon, 510 p.
5 Churchill R V 1971 Complex variables and applications. McGraw-Hill-Kogakusha, Tokyo, 332 p.
6 Drew M C and Lynch J M 1980 Soil anaerobiosis, microorganisms and root function. Annu. Rev. Phytopathol. 18, 37–66.
7 Fluehler M, Ardakani M S, Szukiewicz T E and Stolzy H 1976 Field measurements of nitrous oxide concentration, redox potentials, oxygen diffusion rates and oxygen partial pressures in relation to denitrification. Soil Sci. 122, 107–114.
8 Lawrentjew M A and Schabat B W 1967 Methoden der komplexen Funktionentheorie. VEB Deutscher Verlag der Wissenschaften, Berlin, 846 p.

9 Lemon E R and Wiegand C L 1962 Soil aeration and plant root relations. II. Root respiration. Agron. J. 54, 171–175.
10 Stolzy L H and Fluehler H 1978 Measurement and prediction of anaerobiosis in soils. *In* Nitrogen in the Environment. Eds. D R Nielsen and J G MacDonald. Academic Press, New York, Vol. 1. pp 363–426.
11 Willigen P de 1984 Mathematical analysis of the significance of partial blocking of the root perimeter for oxygen and nutrient supply (*In preparation*).