Oxygen Transport to Plant Roots: Modeling for Physical Understanding of Soil Aeration

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ABSTRACT

A model that couples the diffusion of O2 to plant roots at the microscale to diffusion of O2 through the soil at the macroscale is derived. The solution is complex, but if the length scales (Z, Z1, Z2; see APPENDIX for list of symbols) are equated a simple analytical expression can be obtained. This model is used to investigate relationships between a critical air-filled porosity (θa) and the other parameters; viz temperature (T), O2 concentration in the bulk soil (C*), O2 concentration at the root surface (C0), root length density (L), the ratio of root radius (a) to the water film radius (R), microbial respiration (M), and length scales (Z1, Z2) related to the depth to which microbial and plant respiration are active in the model using sensitivity analysis. The model shows that θa is not very sensitive to the O2 concentration at the root surface (C0), or the ratio of root radius (a)/water film radius (R), but is sensitive to all the other parameters in some part of their range. The results indicate that indices used to define soil aeration; O2 diffusion rate (ODR) or O2 flux, O2 concentration, or air-filled porosity, which have been previously used, are related and a single critical value for these is unlikely. If a constant critical value exists for one of these indexes it cannot exist for the other two. It is also shown that it is highly unlikely that a universal critical parameter related to soil aeration exists for any of these parameters. It is concluded that more parameters than ODR, O2 concentration, or air-filled porosity need to be measured if progress in soil aeration research is to be made.

THE CONCEPT of a nonlimiting water range (NLWR) was introduced by Letey (1985). This has been recently called the least limiting water range by da Silva and Kay (1997a, 1997b). For the NLWR to be identified the water content at which O2 supply to plants becomes limiting needs to be known or measured. The introduction and attempted uses of the NLWR concept has again highlighted the lack of a good definition for soil aeration. Here we will attempt to put such a definition on a sounder physical basis.

For most plants to grow in soil, a proportion of the pore space needs to be gas-filled. The gas-filled proportion of the pore space allows the influx of O2 into, and the efflux of CO2 from the soil. The consumption of O2 in the soil and production of CO2 is because of the oxidative demands of plant roots, microorganisms, and chemical reactions. The status of a soil in relation to the proportion of gas-filled pores and the concentration of O2 and CO2 in the soil is often referred to as the aeration status of the soil. The effect of aeration on plant growth has been reviewed recently by Gliński and Stepniewski (1985).

Although there appears to be some evidence to suggest that the concentration of CO2 in the soil may have an effect on plant growth, the major effect of poor aeration on plant growth is the lack of O2 (Gliński and Stepniewski, 1985). Like field capacity, soil aeration is a term that has an empirical basis and many different definitions. There are a number of different indices for defining the aeration status of a soil. These include: gas-filled porosity (Wesseling and van Wijk, 1957; Jayawardane and Meyer, 1985; Gliński and Stepniewski, 1985), the ODR (Lemon and Erickson, 1952; Letey and Stolzy, 1967; McIntyre, 1970; Armstrong and Wright, 1976; Blackwell, 1983), and O2 concentration or partial pressure (Grable, 1966; Armstrong and Gaynard, 1976; Blackwell and Wells, 1983; Meyer and Barrs, 1991). However, there has not been a good theoretical basis for investigating the validity of these indices for assessing the aeration status of a soil or their correlation. Traditionally, the concept of soil aeration has been based on a correlation between plant performance and these various indices of the O2 status of the soil.

At a physiological level, the minimum aeration status occurs when the flux of O2 to the root surface, especially the root tip, is just able to meet the O2 demand of the root tissues. The transport of O2 to a plant root occurs first through diffusion from the atmosphere via the gas-filled porosity of the soil to the depth of the root, and then through a boundary layer surrounding the root. Most previous studies in this area have considered this boundary layer around the root to be liquid-filled porosity, because as Bernstein et al. (1959) stated, otherwise the plant would have to have a refrigeration system if water was transported to it via a vapor gap. This liquid filled boundary layer was considered by Letey and Stolzy (1967) to be cylindrical. This assumption of a circular boundary layer was criticized by McIntyre (1970) as being highly unlikely given the heterogeneity of pore size found in soil (Fig. 1). In this study the boundary layer will be assumed cylindrical, as without such an assumption the mathematics becomes very difficult. The value of this radius is taken as that which gives the same radial gas flux through the boundary layer as would be measured.

In this study we will derive the relationships between respiration rate of roots and the transport processes at the microscale (root scale) and couple this with the transport of O2 with root and microbial respiration as distributed sinks at the macroscale (bulk soil). The resulting solutions of the differential equations will be used to define soil aeration in terms of the physical and biological parameters of the system and to determine

Abbreviations: NLWR, nonlimiting water range; ODR, O2 diffusion rate.
the interrelation of the three indices described above for defining soil aeration.

**THEORY**

The transport of O$_2$ to plant roots at the microscale can be described by radial diffusion to a cylindrical root (Letey and Stolzy, 1967):

\[
J = \frac{2\pi(\alpha C - C_o)D_i}{\ln(R/a)}
\]  

(1)

where \( J \) is the flux of O$_2$ to the root per unit length of root (kg m$^{-1}$ s$^{-1}$), \( \alpha \) is the Bunsen absorption coefficient which equals the gas solubility per unit volume of water at normal pressure (101.3 kPa) (Gliński and Stepniewski, 1985 p. 46), \( C \) is the O$_2$ concentration in the gas phase of the bulk soil (kg m$^{-3}$), \( C_o \) is the O$_2$ concentration in the liquid phase at the root surface (kg m$^{-3}$), \( D_i \) is the diffusion coefficient of O$_2$ in the liquid phase of the soil (m$^2$ s$^{-1}$), \( a \) is the root radius (m) and \( R \) is the radius of a zone of saturated soil around the root plus the root (m) (Fig. 1). Note Eq. [1] is different by \( 2\pi a \) from that of Letey and Stolzy (1967), as here we have calculated the total O$_2$ flux to the circular root surface, not the radial streamline flux. The relationship between ODR and Eq. [1] is algebraically possible but the physics is somewhat problematic as the boundary conditions are different. A good discussion of the ODR method and some of the problems with it are provided by McIntyre (1970) and Phene (1986).

The critical O$_2$ concentration at the root surface can also be calculated using a radial solution for O$_2$ transport into the root (Lemon and Wiegrand, 1962). Assuming that the concentration is zero at \( r = 0 \) (the center of the root), the concentration at the root surface is given by (Gliński and Stepniewski, 1985, p. 83):

\[
C_r = \frac{g a^2}{4D_i}
\]  

(2)

where \( g \) is the respiration rate of the root tissues (kg s$^{-1}$ m$^{-3}$) and \( D_i \) is the diffusion coefficient for O$_2$ in the root (m$^2$ s$^{-1}$).

If we assume a root length density function, \( L \) (m m$^{-3}$), with depth, \( z \) (m), of the exponential form:

\[
L = L_0 \exp(-z/Z_i)
\]  

(3)

where \( L_0 \) is the root length density (m m$^{-3}$) at \( z = 0 \) and \( Z_i \) is a length scale (m), the root respiration per unit volume of soil (Q) is then given by:

\[
Q = LJ
\]  

(4)

Assuming an exponential relationship with depth for the microbial respiration rate (Cook, 1995) the soil respiration per unit volume of soil (q) is given by adding the respiration rates:

\[
q = M_o \exp(-z/Z_m) + P_o \exp(-z/Z_i)
\]  

(5)

where \( M_o \) is the microbial respiration rate at \( z = 0 \) (kg m$^{-3}$ s$^{-1}$) and \( P_o = \frac{2\pi D_i L_0 (\alpha C_o (z) - C_i)}{\ln(R/a)} \) is the root respiration rate where \( C(z) \) is the O$_2$ concentration (kg m$^{-3}$) in the soil air at depth \( z \) and \( Z_m \) is a length scale (m). The length scales in both the root length density and microbial functions define the depth over which the respiration occurs. Ninety-five percent of the microbial respiration occurs within a depth of three length scales that is, \( z = 3Z_m \). We have not equated \( Z_i \) and \( Z_m \) as there are likely to be situations especially with a newly planted crop where they are not equal.

At the macroscale, one-dimensional O$_2$ transport into a homogeneous soil can be described by diffusion (Kirkham, 1994). Steady-state diffusion into soil with the respiration considered as a distributed sink term is described by (Gliński and Stepniewski, 1985, p. 51, Eq. [39]):

\[
D_i \frac{d^2 C}{dz^2} = q
\]  

(6)

where \( D_i \) is the diffusion of O$_2$ in the gas phase of the soil (m$^2$ s$^{-1}$). Substituting Eq. [5] into Eq. [6] results in:

\[
D_i \frac{d^2 C}{dz^2} = M_o Z_m \exp(-z/Z_m) + \frac{2\pi D_i L_0 Z_m \exp(-z/Z_m)}{D_i \ln(R/a)} (\alpha C(z) - C_i)
\]  

(7)

which is to be solved with the following boundary conditions:

\[
z = 0, C = A
\]

\[
z \to \infty, \frac{dC}{dz} \to 0,
\]

where \( A \) is the atmospheric concentration of O$_2$ (kg m$^{-3}$). The semi-infinite boundary condition used for the lower boundary condition is appropriate as the respiration tends toward zero with depth. Equation [7] is a second-order heterogeneous differential equation, which has the form:

\[
\frac{d^2 C}{dz^2} = \beta \exp(-z/Z_m) + g \exp(-z/Z_i) C
\]  

(8)

where \( \beta \) and \( g \) are parameters, with \( \beta = \frac{M_o}{D_i}, g = \frac{2\pi a D_i L_0}{D_i \ln(R/a)} \).

Introduction of a new spatial variable \( X = 2Z_m g^{1/2} \exp\left(-\frac{z}{2Z_m}\right) \), with the properties that when \( z = 0 \), \( X \) is a maximum

\[X_0 = 2Z_m g^{1/2} \]

and \( z = \infty, X = 0 \). The derivative equals \( \frac{dX}{dz} = -g^{1/2} \exp\left(-\frac{z}{2Z_m}\right) = \frac{X}{2Z_m} \), which means that Eq. [8] can be rewritten as:

\[
X \frac{d}{dX} \left(X \frac{dC}{dX}\right) = 4Z_m \exp\left(-\frac{Z_m}{Z_m}\right) + X^2 C
\]  

(9a)

or

\[
\frac{1}{X} \frac{d}{dX} \left(X \frac{dC}{dX}\right) = C + \beta \left(\frac{X}{g^{(2p-1)}}\right)
\]  

(9b)

with the parameter \( p = \frac{Z_m}{Z_m} \), and the boundary conditions now:

\[X \frac{dC}{dX} \to 0, X \to 0\]
\[ C = A - \frac{C}{\alpha}, \quad X = X_0 = 2Zg^{1/2}. \]

A solution of the homogeneous equation with \( \beta = 0 \) can be found in terms of the modified Bessel function \( I_\alpha(X) \). When \( p \) is a positive integer, it is a simple explicit particular solution of the homogeneous equation. For general \( p \), the solution is given by an integral in Green’s function form (see Appendix). When \( X = X_m \) and so \( p = 1 \), the solution with the appropriate boundary conditions is

\[ C(X) = \left( A - \frac{C}{\alpha} + \frac{\beta}{g} I_\alpha(X_0) \right) - \frac{\beta}{g} \tag{10} \]

The value at \( X = 0 \) is

\[ C(X) = \left( A - \frac{C}{\alpha} + \frac{\beta}{g} I_\alpha(X_0) \right) - \frac{C}{\alpha} - \frac{\beta}{g} \tag{11} \]

since \( I_\alpha(0) = 1 \).

In terms of the original variables, in the case where \( Z_i = Z_m \), the solution is:

\[ C(z) = \left( A - \frac{C}{\alpha} + \frac{\beta}{g} I_\alpha(2Zg^{1/2}) \right) + \frac{C}{\alpha} - \frac{\beta}{g} \tag{12} \]

As \( z \to \infty \), this simplifies to:

\[ C(z) = \left( A - \frac{C}{\alpha} + \frac{\beta}{g} \frac{1}{I_\alpha(2Zg^{1/2})} \right) + \frac{C}{\alpha} - \frac{\beta}{g} \tag{13} \]

It is via \( D_s \) and \( D_t \) that the gas-filled porosity (\( \theta_f \)) is introduced into the set of relationships. Calculations of \( D_s \) and \( D_t \), and \( \theta_f \) and \( \theta_o \) are found by (Millington, 1959; Millington and Quirk, 1961):

\[ D_s = \frac{D_{o^*} \theta_i^{4/3}}{f^2} \tag{14} \]

\[ D_t = \frac{D_{o^*} f^{4/3}}{f^2} \]

where \( D_{o^*} \) is the diffusion coefficient for \( O_2 \) in air and \( D_{o^*} \) is the diffusion coefficient for \( O_2 \) in water. It can be shown that two distinct soil gas profiles are described by equations with exponentially decreasing sink terms; these are the case in which the \( O_2 \) concentration becomes zero at some finite depth and the case when the \( O_2 \) concentration tends toward a constant value as depth tends toward infinity (Cook, 1995). The soil profile will tend toward a constant \( O_2 \) concentration in the air phase (\( C^* \)) with depth as depth tends toward infinity when

\[ \left( A + \frac{\beta}{g} \right) > \frac{C}{\alpha} \]

and is given by Eq. [13]. Now if we let \( C^* \) correspond to the critical value needed to satisfy the \( O_2 \) flux to the plant roots then the rest of the soil profile will be at a value greater than this and soil aeration will be adequate throughout the soil profile. This is a similar concept to that introduced by Wesseling and van Wijk (1957) where they suggested that a \( \theta \) of 10% at the bottom of the root zone was a critical index for soil aeration.

It can also be seen that via Eq. [1], [5], [13], and [14] the three common indices for determining aeration status \( \nu \) of constant values of either \( \theta_c \), \( O_2 \) concentration (this is related to ODR) and \( C \) are unified; if the parameters needed to calculate \( C^* \) and \( \theta_c \) are known, then \( O_2 \) flux can also be calculated. The critical value for air-filled porosity (\( \theta_{i} \)) can be obtained from Eq. [13] using a binary splitting iterative procedure.

We now have a set of equations, which allows us to calculate the effects of variations in the soil physical, biological, and plant root characteristics on the aeration status of the soil. Values of either \( \theta_c \), \( O_2 \) concentration, oxygen flux, or air-filled porosity are unlikely to be universal, as in particular the temperature of the soil will vary in a growing season and diurnally and the sink terms will also vary in concert with temperature. The characteristics of the plant will also play a role in determining these critical values. The effects on \( \theta_o \) of varying the various soil and plant characteristics will be examined below. A critical \( O_2 \) concentration (\( C^* \)) will often be assumed, but this is not necessary. The critical \( O_2 \) flux can be found with Eq. [1], using the assumed values of \( C^* \) and \( C_r \).

### MATERIALS AND METHODS

The critical air-filled porosity was calculated from Eq. [13] for typical values of the various parameters. A binary splitting procedure was written for Maple 7 (Waterloo Maple, 2001) and used to solve Eq. [13], so that both sides equated. Values for the various parameters were chosen from the literature, and are shown in Table 1. Each variable was then allowed to vary while the others were kept constant, to see how sensitive \( \theta_{i} \) was to variations in that parameter. These calculations were performed with the parameters calculated at a number of different temperatures. Variations in \( A, D_{o^*} \), \( D_{o^*} \), and \( \alpha \) with temperature were taken from Gliniski and Stepniewski (1985) and are shown in Table 1. Variation in \( M_t \), with temperature was calculated using the equation proposed by Lloyd and Taylor (1994):

\[ M_t = M \exp \left( -\frac{E_t}{T - T_0} \right) \tag{15} \]

where \( M \) is chosen so that the reference value of \( M_t \) is \( 3 \times 10^{-7} \) kg m^{-3} s^{-1} at a temperature of 298 K. \( E_t \) is a constant (308.6 K) and \( T_0 \) is a base temperature (227.1 K). The value of \( M \) was chosen as being representative of soil respiration values (Gliniski and Stepniewski, 1985, Table 3, p. 35; Orchard and Cook, 1983).

The values of some of the temperature dependent variables at various temperatures are given in Table 1. These values were obtained from data in Gliniski and Stepniewski (1985, p. 46). The values of some parameters that remain constant with temperature during the sensitivity analysis are given in Table 2. The source of these values will be discussed below.

### Table 1. Temperature dependence of variables (from Gliniski and Stepniewski, 1985, p. 46).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Temperature, K</th>
<th>Value ( \times 10^9 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( T )</td>
<td>273</td>
<td>283</td>
</tr>
<tr>
<td>( C_r ) m^{-3} s^{-1} *</td>
<td>1.78 *</td>
<td>1.90 *</td>
</tr>
<tr>
<td>( \alpha_{o} ) m^{-3} s^{-1} *</td>
<td>9.90 *</td>
<td>1.55 *</td>
</tr>
</tbody>
</table>

### Table 2. Constant values for nontemperature dependent variables used in sensitivity analysis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Value ( \times 10^9 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( M_t ) m^{-3} s^{-1} *</td>
<td>2.0 *</td>
</tr>
<tr>
<td>( L_o ) m^{-3} *</td>
<td>1.0 *</td>
</tr>
<tr>
<td>( a ) m</td>
<td>2.5 *</td>
</tr>
<tr>
<td>( R ) m</td>
<td>3.5 *</td>
</tr>
<tr>
<td>( C_r ) m^{-3} *</td>
<td>1.0 *</td>
</tr>
<tr>
<td>( \alpha_{o} ) m^{-3} *</td>
<td>0.5</td>
</tr>
<tr>
<td>( Z_o ) m</td>
<td>0.3</td>
</tr>
</tbody>
</table>

### Variable Value Reference

| \( M_t \) m^{-3} s^{-1} \* | 2.0 \* | Gliniski and Stepniewski (1985) |
| \( L_o \) m^{-3} \* | 1.0 \* | R.J. Stirzaker (pers. comm., 1999) |
| \( a \) m | 2.5 \* | Letey and Stolzy (1967) |
| \( R \) m | 3.5 \* | Orchard and Cook (1983) |
| \( C_r \) m^{-3} \* | 1.0 \* | Gliniski and Stepniewski (1985) |
| \( \alpha_{o} \) m^{-3} \* | 0.5 |
| \( Z_o \) m | 0.3 | Campbell (1985) |
RESULTS AND DISCUSSION

Concentration Profiles

The two different forms of an oxygen profile are seen in Fig. 2; when \( A + \frac{B}{g} \) > \( \frac{C_1}{\alpha} \), \( C \) tends toward a constant value of \( C \) with increasing depth. This is seen for the profiles when the temperature is at 273, 283, and 293 K in Fig. 2. When \( A + \frac{B}{g} \) < \( \frac{C_1}{\alpha} \), \( C \) goes to extinction at some finite depth, as is seen for the profile for a temperature of 303 K in Fig. 2. More detailed discussion of these profile shapes can be found in Cook (1995). In these calculations the temperature has been assumed to be uniform with depth. Temperature will vary with depth in soil under field conditions, although on a daily basis the amplitude is usually not large except close to the surface. However, the seasonal variation can be as much as 20 K, and these results show how this could affect the oxygen profiles for a soil on an annual basis.

The assumption that \( C \), is constant with temperature is probably correct if the respiration processes in the root are concentration dependent. It is more likely that the root respiration and root diffusion coefficient vary with temperature. Some data on root respiration as a function of temperature has been published (Boone et al., 1998; Lemon and Wiegand 1962). The way in which this flux is likely to change with temperature is that the critical O2 concentration \( (C^*) \) in the bulk soil will increase with temperature. However, no data on the variation of \( C^* \) with temperature was found. Hence we have only allowed \( P_z \) to vary with temperature because of the variation of \( D_l \) and \( \alpha \) with temperature. The temperature variations in \( M_z \), and \( P_z(z = 0) \) values are shown in Fig. 3. Figure 3 also shows that the root respiration is greater than the microbial respiration, Gliński and Stępniewski (1985) suggested that root respiration is about ten-fold that of microbial respiration. The root respiration will however decrease with depth because of both the exponential forcing function and because of decreasing concentration of O2 with depth. How realistic Eq. [1] is without applying an upper limit to the flux, is something which requires further investigation outside the scope of this study. If, as is likely, root respiration varies with temperature, then the shape of the relationship between the \( P_z \) and temperature may be more like that shown for \( M_z \) in Fig. 3. This is likely to exacerbate the differences shown in Fig. 2 between the profile shapes at different temperatures, as the sink term \( (q) \) will vary more than assumed.

Sensitivity of \( \theta_m \) to Parameters in the Model

The sensitivity of \( \theta_m \) with respect to critical O2 concentration \( (C^*) \) shows that as the critical concentration increases, so does the value of \( \theta_m \) (Fig. 4). At the same value of \( C^* \) the value of \( \theta_m \) increases with increasing temperature. The range of values chosen viz 0.025 to 0.20 kg m\(^{-3}\) is representative of values found by others (Gliński and Stępniewski, 1985, p14).

The definition of \( C^* \) used here is the constant concentration in the soil when \( z > Z \). In this we are assuming that if \( C^* \) is sufficient for root function at this depth then, since the concentration is greater than this in the upper part of the soil profile, it will be more than sufficient for root functioning. This definition is close in concept to a definition used by Wesseling and van Wijk (1957), except that their critical parameter was air-filled porosity. The values of \( \theta_m \) obtained range from 0.12 to 0.33 m\(^3\) m\(^{-3}\) for a soil with a porosity of 0.5 m\(^3\) m\(^{-3}\). This is similar to the range of values found in the literature of 0.1 to 0.25 (Gliński and Stępniewski, 1985, p. 173). Meyer and Barrs (1991) suggested a lower limit of 6%
and an upper limit of 80% of pore space ($f$) to maintain a critical O$_2$ concentration in the soil. For a porosity of 50% this would represent a $\theta_m$ range of 0.03 to 0.4. The bottom limit of the range for $\theta_m$ we found of 0.12 is higher than that found by others (Jayawardane and Meyer, 1985; Meyer and Barrs, 1991). This may have been because of the values of other variables including that of $C_i$. This value of $C_i$ also restricts the lowest value of $C^*$ that can be used in the calculations as $(\alpha C^* - C_i) > 0$ is required in Eq. [2]. If $C_i$ is allowed to vary with the value of $C^*$ constant (0.05 kg m$^{-3}$) and the other variables constant at each temperature then the value of $\theta_m$ hardly varies except when $C_i > 1 \times 10^{-4}$ Kg m$^{-3}$ (Fig. 5). The value of $\theta_m$ then decreases slightly as $C_i$ increases. This occurs because as $C_i$ increases the flux of O$_2$ to the root decreases and the total respiration decreases. These results suggests that $\theta_m$ is not very sensitive to the value of $C_i$ and hence to the values of $q_r$, $a$, and $D_r$.

The sensitivity of $\theta_m$ to the strength of the microbial and root respiration is investigated via the parameters $M$, $L_o$, and $Z_m = Z_i$ in Fig. 6. Figure 6a shows that the root respiration rate dominates the sink terms until the microbial respiration term is about $1 \times 10^{-6}$ kg s$^{-1}$ m$^{-3}$.

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**Fig. 3.** Microbial ($M_o$) and root ($P_z (z = 0)$) respiration terms as a function of temperature.

**Fig. 4.** Sensitivity of $\theta_m$ to $C^*$ for four different temperatures.
At the lower values of $M$ the root respiration is the dominant sink term, and results in convergence to a similar value of $\theta_m$ at all temperatures. This occurs because of the lack of temperature sensitivity of the root respiration term discussed above.

Similarly, the microbial respiration dominates the total respiration at low values of $L_o$, and there is little change in $\theta_m$ until high values of $L_o$ are reached (Fig. 6b). At each temperature a relatively constant value of $\theta_m$ occurs at values of $L_o \leq 1 \times 10^3$ m$^{-3}$. This is because of the microbial respiration being the dominant sink term at these low values of $L_o$. The temperature dependence of the microbial respiration (Fig. 3) is the reason why there is a different constant value for $\theta_m$ at each temperature. At high values of $L_o$ all the curves converge because of the lack of temperature dependence in the root respiration function.

When the value of $Z$ is low, respiration is concentrated near the surface and the amount of oxygen consumed by the soil profile is lower. This results in a lower value of $\theta_m$ (Fig 6c). These lower values (<0.1 m$^3$ m$^{-3}$) are similar to values found by Jayawardane and Meyer (1985). Such low values of $\theta_m$ can also be obtained if both $M$ and $P_z$ are varied in concert, so that a wide range of values of the total respiration is created (Fig. 7). Increasing the values of $Z$ leads to an increase in $\theta_m$. This is to be expected, since the total O$_2$ consumption of the soil profile will increase.

The effect of root size and thickness of the water film surrounding the root shows that as $R/a \to 1$ the value of $\theta_m$ increases. However for the range $R/a > 10$, $\theta_m$ is relatively insensitive to $R/a$ (Fig. 8). The behavior of $\theta_m$ as $R/a \to 1$ is because of the increase in flux of O$_2$ to the root, which is assumed to happen in Eq. [1] as $R/a \to 1$. This results in an increase in the calculated root respiration and a corresponding increase in total respiration. The model then correctly suggests that $\theta_m$ will increase as $R/a \to 1$. In reality this predicted increase in respiration is unlikely to occur, as respiration of the root will only rise to a maximum rate and then plateau, whereas Eq. [1] suggests it will increase exponentially as $R/a \to 1$. Also, the limit as $R/a \to 1$ corresponds to the water content approaching zero. The plant is likely to have stopped functioning and the plant roots stopped respiring well before $R/a = 1$ because of water stress.

Equation [2] implies that $C_r$ would be sensitive to the root radius $a$, but since $\theta_m$ was shown to be insensitive to $C_r$ (Fig. 5) it would appear from this analysis that $\theta_m$ would not be sensitive to root radius. This analysis does not account for the fact that as water film thickness increases the water content increases and air-filled porosity decreases. Luxmoore et al. (1970) did attempt to relate water film thickness to soil matric potential using an analysis of water films on clays (Kemper and Rollins, 1966) to predict the water film thickness. Unfortunately their work is erroneous, as they made an order of magnitude error in converting from the units of A$^{m}$ (10$^{-10}$ m) used by Kemper and Rollins (1966) to their units of centimeters.

Increasing the total porosity $f$ is shown to increase $\theta_m$ almost linearly (Fig. 9). However, the proportion of the porosity represented by $\theta_m$ decreases as $f$ increases (not shown). This almost linear decrease is because of the term $\beta/g$ decreasing with $f$ but being compensated for by the decrease in the modified Bessel function with $f$. This result is dependent on the diffusion function of Millington and Quirk (1961) being a good representation of reality. Sallam et al. (1984) showed that Millington and Quirk’s function describes the diffusion of gases in soil well, but suggested that the power on the $\theta$ term be changed from 10/3 to 3.1. In the calculations presented here, we have not bothered with this minor variation.

The sensitivity of $\theta_m$ to temperature is shown in Fig. 4.
Fig. 6. Sensitivity of $\theta_m$ to (a) $M_0$, (b) $L_0$ and (c) $Z_m = Z$, for four different temperatures.
Values of $D_l$ will vary with both $f$ and temperature. The parameter $C_r$ may vary with temperature (Lemon and Wiegand, 1962), while $C^*$ is likely to vary with temperature and plant species. There is also likely to be an effect because of mycorrhizal microorganisms, as their respiration rate will affect the value of $C^*$. The parameter $a$ is likely to vary with plant species, while $R$ is likely to vary with soil type. Hence it is not surprising that suggested critical values vary over a wide range. It is doubtful if a universal value for a critical value of O2R exists. If such a value does exist it can be shown using Eq. [1], [13], and [14] that constant critical values for $C^*$ and $\theta_m$ cannot exist. Similarly, if a constant value for $C^*$ exists then a constant value of O2 flux or $\theta_m$ cannot exist. The respiration rate of root tissues has been found to be exponentially related to temperature (Boone et al., 1998) like microbial respiration. Yet for the existence of a constant critical flux to be correct the respiration would have to be constant with temperature. It is difficult to assess the data on O2 flux or ODR, as the temperature at which measurements were made is not given often.

Critical values for the O2 concentration in the gas or water phase have been proposed (Blackwell and Wells, 1983; Gliński and Steępniewski, 1985; Meyer and Barrs, 1991), and these values also vary over a wide range. There is evidence that a constant root O2 concentration is required for proper functioning of cytochrome oxidase (Gliński and Steępniewski, 1985, p. 141), and Gliński and Steępniewski (1985, p. 83) suggest that this constant root O2 concentration is not $<0.02$ to $0.03$ m$^{-3}$. Equation [1] then shows that, if $C_r$ is constant and $J$ is constant, then, as $D_l$ and $a$ are temperature dependent and $D_l$ is dependent on $f$, $C^*$ cannot be constant. Thus, the existence of a critical constant flux and the existence of a constant critical concentration are mutually exclusive. At a single temperature, as in the measurements of
Blackwell and Wells (1983) at 281 K, a correlation can be found, but at different temperatures this relationship is likely to be different.

Meyer and Barrs (1991) suggested that the $O_2$ in both the air and water phases needs to be taken into account in determining a critical value ($C_c$) of 0.1 kg $O_2$ m$^{-3}$:

$$C_c = C(\theta + \alpha[f - \theta])$$  \[16\]

where $\theta$ (m$^3$ m$^{-3}$) is the air-filled porosity. This concept does not take into account that the water phase is merely a conductor for $O_2$ from the gas phase to the root. Thus under steady-state flow conditions the concentration of $O_2$ in the water phase must stay constant and the flux from the atmosphere to the soil will occur predominantly in the gas phase. However, if roots have a diurnal variation in their $O_2$ uptake rate and the amount stored in the water phase is sufficient, then there may be some justification for the suggestion of Meyer and Barrs (1991). We have calculated the time it would take to deplete the $O_2$ in the water phase, at the maximum respiration rate ($z = 0$) and give no replenishment from the gas phase, for a range of values of ($f - \theta$) and at various temperatures. This shows that at low temperatures and high water contents ($f - \theta$) there is a considerable length of time that $O_2$ could be supplied from that dissolved in the liquid phase (Fig. 10). Also, at lower respiration rates than assumed here this time will increase. This would indicate that the suggestion of Meyer and Barrs (1991) might be valid when the $O_2$ demand of the soil is low, if diurnal fluctuations in the respiration rate of microbes and roots occur, allowing replenishment of $O_2$ in the liquid phase during the period of low respiration. Although there may be a universal critical value of $C_c$ (Gliński and Stepniowski, 1985 p. 141), a universal value of $C*$ is highly unlikely. The sensitivity analysis here has used a constant value of 0.05 kg m$^{-3}$ but the trends in the analysis are similar if other values are chosen.

**DISCUSSION**

For soil aeration studies to move beyond empirical statistical correlations between plant response and $O_2$ flux or $C*$ or $\theta_m$, it is necessary to make experimental measurements that allow the model presented here to be tested. The soil respiration, length scale, and $O_2$ concentration can be derived using profile methods (Cook et al., 1998) and the analysis of Cook (1995). Concurrent measurements of temperature profiles and water content are also required (Topp et al., 2000). The splitting of the total respiration into the microbial and root components is more problematic. Studies of the roots in isolation may be possible using the agar gel method of Wiengweera et al., (1997). It is possible to sieve out the roots and measure the microbial respiration rate (Orchard and Cook, 1983), but these values may not be a good measure of the in situ value.

In this study we have not included the effect of water content on microbial respiration. It has been shown that water content has a marked effect on microbial respiration (Orchard and Cook, 1983; Linn and Doran, 1984). Orchard and Cook (1983) only studied the range of water contents where $O_2$ was not limiting and found a linear decrease with water content. This relationship was confirmed in later studies (Cook et al., 1985; Orchard et al., 1992), whereas Linn and Doran (1984) showed that above a critical value the respiration rate decreases with water content because of lack of $O_2$. As we are looking for point of maximum respiration here, neglecting the effect of water content on respiration will not affect the results. However, if Eq. [12] is used to predict $O_2$ profiles the effect of water content on microbial respiration will need to be accounted for.
CONCLUSIONS

A theoretical model for aeration has been presented, showing that universal critical values for the air-filled porosity, O$_2$ concentration and ODR are unlikely to exist. The model results also imply that if a universal critical value exists for one of these parameters it cannot exist for the other critical parameters.

The results show that when a critical value for the air-filled porosity is used as an indicator the model is not very sensitive to the concentration on the root surface (C$_r$), but is sensitive to all other parameters. The model results also imply that if a universal critical value exists for one of these parameters it cannot exist for the other critical parameters.

This study shows that for progress to be made in understanding soil aeration a much larger suite of parameters needs to be measured. Some of these can be obtained by measurements of O$_2$ flux, soil O$_2$, water content, and temperature.

APPENDIX

The equation for $C(X)$ for a general value of $p$ is

$$\frac{1}{X} \frac{d}{dX} \left( X \frac{dC}{dX} \right) = C + \frac{\beta}{g^p} \left( \frac{X}{2Z_i} \right)^{2(p-1)} \quad [A1]$$

For $p = 1$, the case when the two characteristic lengths $Z_m$ and $Z_r$ are equal, this has the form

$$\frac{1}{X} \frac{d}{dX} \left( X \frac{dC}{dX} \right) = C + \frac{\beta}{g^1} \quad [A2]$$

This has a particular solution $C = \frac{\beta}{g}$ that is used in Eq. [10].

The case $p = 2$ corresponds to the relation between the two characteristic lengths $Z_i = 2Z_m$ and the equation has the form

$$\frac{1}{X} \frac{d}{dX} \left( X \frac{dC}{dX} \right) = C + \frac{\beta X^2}{g^2 Z_i^2} \quad [A3]$$

with particular solution

$$C(X) = \frac{\beta X^2}{4g^2 Z_i^2} - \frac{\beta}{g^2 Z_i^2} \quad [A4]$$

For $p = 2$ the solution satisfying the boundary conditions,$C(X_0) = A - \frac{C_i}{\alpha}$, $X \frac{dC}{dX} \to 0$ as $X \to 0$ is

$$C(X) = \frac{I_d(X)}{I_d(X_o)} \left( A - \frac{C_i}{\alpha} + \frac{\beta X_0^2}{4g^2 Z_i^2} + \frac{\beta}{g^2 Z_i^2} \right) - \frac{\beta X^2}{4g^2 Z_i^2} - \frac{\beta}{g^2 Z_i^2} \quad [A5]$$

For each integer value of $p$ a particular solution can be found as a finite series of powers of $X$.

For general $p$ a solution can be written down in terms of the integral of a Green’s function as

$$C(X) = \frac{\int_0^X \frac{I_d(Y)}{I_d(X)} Y^{2(p-1)} dY}{\int_0^X G(Y,X,X_o) Y^{2(p-1)} dY} \quad [A6]$$

where the Green’s function is a solution of the homogeneous equation with a “delta function” unit source term at the position $X = Y$. For this equation the Green’s function satisfying the appropriate boundary conditions is

![Graph showing the time to deplete the oxygen dissolved in the water phase.](Image)
\begin{equation}
G(Y,X,X_0) = \begin{cases} 
-YI_d(X)K_0(Y) + \frac{YI_d(Y)I_d(X)K_0(X_0)}{I_d(X_0)} & 0 \leq X \leq Y \\
-YI_d(Y)K_d(X) + \frac{YI_d(Y)I_d(X)K_0(X_0)}{I_d(X_0)} & Y \leq X \leq X_0 
\end{cases}
\tag{A7}
\end{equation}

\begin{equation}
C(X) = \left( \frac{A - C_z}{\alpha} \right) I_d(X) - \frac{\beta K_0(X)}{g''(2Z \alpha^2 \gamma^{p-1})} Y^{2p-1} I(Y) dY \\
- \frac{\beta I_d(X)}{g''(2Z \alpha^2 \gamma^{p-1})} Y^{2p-1} K_0(Y) dY \\
+ \frac{\beta K_0(X)I_d(X)}{g''(2Z \alpha^2 \gamma^{p-1})} Y^{2p-1} I(Y) dY
\tag{A8}
\end{equation}

where \( K_0 \) is a modified Bessel function of second kind and zero order. For integer values of \( p \) the integrals can be evaluated explicitly, after some manipulation of the Bessel functions.

**List of Symbols**

- \( a \) root radius (m)
- \( A \) \( O_2 \) concentration in the atmosphere (kg m\(^{-3}\))
- \( C \) \( O_2 \) concentration in gas phase of soil (kg m\(^{-3}\))
- \( C^0 \) critical \( O_2 \) concentration in gas phase of soil as \( z \to \infty \) (kg m\(^{-3}\))
- \( C_c \) critical \( O_2 \) concentration in liquid phase at root surface (kg m\(^{-3}\))
- \( D_d \) diffusion coefficient for \( O_2 \) in soil through the gas phase (m\(^2\) s\(^{-1}\))
- \( D_d^0 \) diffusion coefficient for \( O_2 \) in air (m\(^2\) s\(^{-1}\))
- \( D_d \) diffusion coefficient for \( O_2 \) in soil through the water phase (m\(^2\) s\(^{-1}\))
- \( D_d^0 \) diffusion coefficient for \( O_2 \) in water (m\(^2\) s\(^{-1}\))
- \( D_d \) diffusion coefficient for \( O_2 \) in root tissues (m\(^2\) s\(^{-1}\))
- \( E_c \) constant analogous to activation energy (K)
- \( f \) porosity of soil (m\(^{-3}\))
- \( g \) parameter defined in Eq. \([8]\) (kg m\(^{-3}\))
- \( G \) Green’s function (see Eq. \([A6]\))
- \( I_d \) modified Bessel function of first kind and zero order
- \( J \) flux of \( O_2 \) to the root per unit length of root (kg m\(^{-1}\) s\(^{-1}\))
- \( K \) Bessel function of second kind and zero order
- \( L_r \) root length density at soil surface (m m\(^{-3}\))
- \( M \) reference microbial respiration rate (kg m\(^{-3}\) s\(^{-1}\))
- \( M_i \) microbial respiration rate at soil surface (kg m\(^{-3}\) s\(^{-1}\))
- \( P_r \) root respiration rate at depth \( z \) (kg m\(^{-3}\) s\(^{-1}\))
- \( p \) dimensionless parameter defined in Eq. \([9]\)
- \( q \) total soil respiration per unit volume of soil (kg m\(^{-3}\) s\(^{-1}\))
- \( q_i \) respiration (consumption of \( O_2 \)) rate per unit length of root (kg m\(^{-3}\) s\(^{-1}\))
- \( q_o \) respiration (consumption of \( O_2 \)) rate per unit volume of root (kg m\(^{-3}\) s\(^{-1}\))
- \( R \) radius of root plus water film thickness (m)
- \( T \) temperature (K)
- \( T_b \) base temperature (K)
- \( X \) spatial variable used in Eq. \([9]\) (kg m\(^{-1}\) s\(^{-2}\))
- \( X_b \) boundary condition for \( X \) (kg m\(^{-1}\) s\(^{-2}\))
- \( Y \) is a dummy variable used in Eq. \([A6]\)
- \( z \) depth (m)
- \( Z_o \) length scale for microbial respiration function (Eq. \([5]\)) (m)
- \( Z \) length scale for root length density function (Eq. \([3]\)) (m)
- \( Z \) length scale used when \( Z = Z_r \) (m)
- \( \alpha \) Bunsen coefficient (m\(^{-3}\) s\(^{-1}\))
- \( \beta \) parameter defined in Eq. \([8]\) (kg m\(^{-3}\))
- \( \theta \) air-filled porosity (m\(^{-3}\))
- \( \theta_c \) critical air-filled porosity (m\(^{-3}\))

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