ABSTRACT

Soil physical properties often regulate aeration-dependent microbial activities important to nutrient cycling, soil fertility and environmental quality. Microbial activity depends on soil water content and is maximum at a water content where the limiting effects of substrate diffusion and O$_2$ supply are equal. The mechanism whereby this occurs and predictions of the soil water content where aerobic microbial activity is a maximum were the objectives of this study. In particular, this study predicted the shape of the microbial activity vs. water content function from soil physical concepts. Soil physical processes are assumed to influence microbial activity by limiting the steady flux of a required substrate or O$_2$ to sites of microbial activity. Steady-state flux relations are used to define the activity function. The dependence of diffusion coefficient on water content or air-filled porosity is assumed. With these assumptions, it is possible to show that a maximum in the activity function exists. The predicted shape of the activity curve is consistent with experimental observations. The relationship between aeration-dependent microbial activity and soil water content facilitates evaluating the indirect effects of soil management practices, such as tillage, on microbial activity.

Soil microbial activity is strongly influenced by soil water. A clear understanding of the mechanisms by which this occurs is useful to explain a variety of phenomena including the transition between aerobic and anaerobic processes, and the effect of tillage practices on microbial processes. Changes in tillage practices tend to result in rather dramatic changes in the soil physical environment (Mielke et al., 1986). This environment in turn controls microbial processes such as mineralization and denitrification that directly impact nutrient leaching or plant growth (Doran, 1980). The mechanisms through which soil water affects microbial activity have not been completely elucidated. A more detailed conceptualization would assist in the careful design of experiments as well as the interpretation of results. This research was undertaken to provide a means to conceptualize and evaluate physical mechanisms whereby soil water governs soil microbial processes. The emphasis is on aerobic microbial activity with O$_2$ and substrate availability as limiting processes. Soil respiration, specifically CO$_2$ production, is the empirical measure of microbial activity.

Several factors exist whereby physical processes influence the activity of soil microorganisms. Collis-George (1959) summarized these physical factors as (i) water availability, (ii) gas exchange, (iii) temperature, and (iv) spatial constraints. Collis-George (1959) and McLaren and Skujins (1968) emphasized that water availability is best described by the soil matric potential or equivalent quantities (e.g., water activity or relative humidity). Most recent efforts studying the influence of soil water on microbial activity have focused on microorganism response and classification based on soil matric potential (Papendick and Campbell, 1981; Harris, 1981; Griffin, 1981). This emphasis on soil matric potential or water activity developed because of the usefulness of water activity to describe microbial growth (Reid, 1980) and the availability of water to plants. However, this focus tends to emphasize the lowest matric potential (i.e., driest conditions) at which growth will occur. Furthermore, the prediction of microbial growth and activity (nonequilibrium processes) from physical principles does not appear possible using only the water activity (an equilibrium property). The high water activity of most soils (Papendick and Campbell, 1981) suggests that other processes also regulate microbial activity by limiting the diffusion of substrates and O$_2$. Substrate and O$_2$ diffusion coefficients are typically characterized using soil water content relationships. Thus, whereas soil matric potential may be viewed as an important measure of water availability, soil water content may be a more useful measurement where water availability is not limiting.

Greaves and Carter (1920) were one of the first to document a consistent relationship between soil water content and microbial activity. Microbial activity was described by measuring NH$_4$ or NO$_3$ at the end of an incubation period. For 22 soils of varying texture, maximum activity was observed at approximately 60% of water-holding capacity. Seifert (1962) observed NO$_3$ production in a variety of aggregate sizes. The samples were not amended with substrate but were incubated for 14 d prior to analysis. All aggregate sizes showed maximum activity at water contents near 40%. However, it is not stated how water content was determined, although probably it was a gravimetric procedure. Linn and Doran (1984) performed a similar study where bulk density was also determined. They found maximum aerobic microbial activity occurred at a volumetric water content ($\theta_w$) equal to 0.60 times the value of the total porosity ($\epsilon$). In later studies, the maximum aerobic microbial respiration occurred between $\theta_w = 0.55$ and 0.61 times $\epsilon$ with 16 soils of varying texture (Doran et al., 1988).

Complementing the work on the influence of soil water on microbial activity are general studies of soil aeration. Soil physical studies of aeration focus on gas-phase diffusion coefficients without regard to interactions with microbial activity (Smith, 1977; Currie, 1984; Sallam et al., 1984). Empirical approaches commonly use a limiting gas flux or oxygen diffusion rate (ODR) to characterize soil aeration (Armstrong and Wright, 1976; Gliński and Stepniewski, 1985). Microbial studies of aeration tend to focus on threshold values controlling the shift from aerobic to anaerobic activity (Bridge and Rixon, 1976).

The role of O$_2$ and substrate diffusion in limiting microbial activity has previously been recognized...
(Stotzky and Norman, 1961; Lynch, 1982). However, the connection between these limiting processes and soil water content has not previously been emphasized. For example, increasing soil water content has two consequences: substrate diffusion becomes less limiting and O$_2$ diffusion becomes more limiting for microbial activity.

The objectives of this study were, first, to present concepts to quantify microbial activity that incorporate soil physical processes. The second objective was to compare the predictions of aerobic activity vs. water content made by such a conceptualization with laboratory data. One consequence of this work should be the ability to predict the soil water content for maximum aerobic microbial activity ($\theta_{\text{max}}$).

**THEORY**

Our approach was to examine some of the physical limits on aerobic microbial activity. Physical processes outside the soil were used to define the limits on microbial activity in soil. These assumptions are on physical processes and properties governing transport of O$_2$ and substrate. These selected soil processes control the microbial environment through the accessibility of the following: (i) an efficient electron acceptor (oxygen), (ii) a source of energy and biosynthates (substrate), and (iii) a physical volume as well as a favorable solvent activity. Each factor depends on soil water content via secondary relationships. For example, soil matric potential is related to water content by a soil water characteristic function. While hysteresis may cause the relationship to be non-unique, each soil has a distinct relationship. It is reasonable that other factors might further restrict the activity of particular organisms or the total soil microbial biomass. This analysis concentrates only on the primary soil physical factors governing O$_2$ and substrate transport. Other physical properties such as temperature will be assumed constant. This analysis will also emphasize respiratory activity as measured by CO$_2$ production, so that wherever the phrase microbial activity is used it can be taken to mean the more restrictive activity.

Substrate and O$_2$ limits to microbial activity within an undisturbed environment can be qualitatively illustrated on a plot of activity vs. $\theta$ (Fig. 1). The dashed line segments are the upper limits to either substrate or O$_2$ transport, respectively. Other mechanisms could contribute line segments that may always exceed, always be less than, or cross the two segments shown in Fig. 1 (e.g., a third segment for soil matric potential). The line segments define a fixed maximum, provided the physical processes do not change character with time. The solid line of Fig. 1 conceptualizes the activity that has been observed under a given set of environmental conditions (e.g., Greaves and Carter, 1920) with $\theta_{\text{max}}$ near 0.6 $\epsilon$. The interpretation of the hypothetical example of Fig. 1 and the explicit calculation of the limits to transport were the subject of the remainder of this study. As part of this development, a prediction of $\theta_{\text{max}}$ was obtained.

Assumptions used in this analysis were:

1. Microbial activity was limited by only a single transport process for either substrate or electron-acceptor (i.e., oxygen) diffusion under a given set of environmental conditions (Dommergues et al., 1978). The activity was directly proportional to the rate of transport.
2. Under limiting conditions, the concentration of substrate or O$_2$ at the organism was effectively zero.
3. Organisms were distributed uniformly (with no problems such as migration of organisms acting as a limit). However, there might exist regions that organisms did not exist within because the organisms did not physically fit in the space. An homogeneous soil volume was examined at a point.
4. Substrate or electron-acceptor was nonuniformly distributed so that solute or O$_2$ diffusion acted as a transport mechanism. A substrate or electron-acceptor reservoir existed that was maintained at a constant concentration.
5. Transport processes were steady-state, with the transport coefficients controlled by soil water content.

These assumptions formed a convenient focal point to provide improvements at a later time. Most importantly, they appeared sufficient to predict the qualitative behavior of Fig. 1. Thus, even though some of these assumptions might be overly simplistic, they were justified by the consequences and by the use of a theoretical development that was capable of incorporating subsequent refinements in the assumptions.

The theoretical limiting aerobic respiratory activity ($P$, mol kg$^{-1}$ s$^{-1}$) resulting from transport is given as

$$P = \min\left(\frac{A_{\text{f}}}{A_{\text{r}}}, \frac{A_{\text{f}}}{A_{\text{r}}}, \frac{A_{\text{f}}}{A_{\text{r}}}, \frac{A_{\text{f}}}{A_{\text{r}}} \right)$$

where $A_r$ and $A_f$ are the areas per unit soil mass through which the flux ($J$) of either soluble substrate ($n$) or oxygen (o) occurs. The flux has units of mol m$^{-2}$ s$^{-1}$. The symbol $min$ stands for "take the minimum of the alternatives given in brackets." Equation 1 is a statement of Assumption 1 above, where the proportionality constant is assumed equal to one. This assumption about the proportionality constant would need modification if other activity was the focus. The terms $A_{\text{f}}$ and $A_{\text{r}}$ represent the substrate and O$_2$ diffusion line segments, respectively, in Fig. 1. Equation [1] states that the microbe microbial activity is the lesser of the activities calculated from either substrate diffusion or O$_2$ diffusion. This is a mathematical statement of Liebig's law of the minimum.

The fluxes are given by a steady-state, boundary-layer approximation (Danckwerts, 1970, p. 98; this is also Assumption 5) as $J = kDA C$, where $k$ is a transfer resistance, $D$ is the apparent diffusion coefficient, and $C$ is the concentration of diffusing substance in a reservoir. The $k$ is sometimes thought of as the reciprocal of a boundary-layer thickness or the reciprocal of the diffusion-path length. The concentration gradient is represented by the product $kDA C$. The difference $\Delta C$ is taken between some constant reservoir and the microbe surface. Using Assumption 2, $\Delta C$ will be re-
placed by C. The symbol C is used to represent the concentration of either O$_2$ in the atmosphere or of substrate within microbially inaccessible regions of the soil. The value of D depends on some function of either the air-filled or water-filled porosity. The liquid-phase diffusion coefficient also depends on the nature of the chemical interaction between solute and soil.

If the steady-state flux laws are combined with Eq. [1], the result is

$$ P = \min \left\{ A_n k_n D_n C_n \right\} $$

[2]

The following empirical relations are used for substrate diffusion (modified from Nye and Tinker, 1977, p. 77-78):

$$ D_n = a(\theta_c)^2 D_e $$

[3]

and O$_2$ diffusion in the gas phase (Troeh et al., 1982):

$$ D_e = b(\theta_c)^2 D_g $$

[4]

where a, b, f, and g are empirical constants that are fixed for a given soil; $D_n$ and $D_e$ are molecular diffusion coefficients in pure liquid or gas phase of substrate or O$_2$, respectively; $\theta_c$ is the air-filled porosity, and $\theta_c = \epsilon - \theta_d$. Substituting Eq. [3] and [4] into Eq. [2], as well as expressing $\theta_c$ in terms of $\theta_d$ yields

$$ P = \min \left\{ a A_n K_n C_n D_n (\theta_c)^2 \right\} $$

[5]

A maximum of the function Eq. [5] exists when the two terms are equal. This represents the point where the two line segments cross (Fig. 1) or are equal. At this point, both O$_2$ and substrate are capable of being transported at the same rate. At the maximum, the following relationship for $\theta_{max}$ is applicable:

$$ a A_n k_n C_n D_n (\theta_{max})^2 = b A_n k_n C_n D_g (\epsilon - \theta_{max})^2 $$

[6]

to obtain Eq. [6] from Eq. [5], $\theta_d$ is set equal to $\theta_{max}$ since only $\theta_{max}$ is to be evaluated.

Equation [6] can be simplified by using dimensionless ratios. Introducing $\tau = a A_n k_n C_n D_n / b A_n k_n C_n D_g$ results in Eq. [6] becoming

$$ \tau (\theta_{max})^2 = (\epsilon - \theta_{max})^2 $$

[7]

This equation shows that $\theta_{max}$ depends on $\tau, f, g,$ and $\epsilon$. The dimensionless ratio $\tau$ represents the importance of substrate diffusion, compared with O$_2$ diffusion. Values of $\tau > 1$ mean substrate diffusion is more important than O$_2$ diffusion. An analytical solution for $\theta_{max}$ in general is not possible.

One approach to analyzing Eq. [7] is to assume $f = g$. It is reasonable that $f$ and $g$ will be close (i.e., within a factor of 2-3) since values of $f$ are near 1.5 (Nye and Tinker, 1977) while g shows a range from 1.3 to 4.0 for a variety of soils (Troeh et al., 1982). However, the variation in the values reported suggests that the assumption of $f = g$ represents a first approximation. If $f = g$, then Eq. [7] can be solved for $\theta_{max}/\epsilon$ (the relative water content):

$$ \left( \frac{\theta_{max}}{\epsilon} \right) = \left( 1 + \tau^{0.5} \right)^{-1} $$

[8]

This result states that, when water contents are expressed on a relative basis, the water content at which maximum microbial activity occurs, $\theta_{max}/\epsilon$, does not explicitly depend in any additional way on porosity or bulk density. It may depend on these factors implicitly through their influence on the parameters included in $\tau$.

The usefulness of Eq. [5] to describe soil respiration was evaluated using the data of Doran et al. (1988) for Yolo (a fine-silty, mixed, nonacid, thermic Typic Xerorthent; Ap2 horizon) and Valentine (a mixed, mesic, Typic Ustipsam-
These calculated values of $\theta_{\text{max}}$ are within the range of those observed in the literature (Greaves and Carter, 1920; Seifert, 1962; Linn and Doran, 1984). This analysis also indicates that, while $\theta_{\text{max}}$ may be fixed for a given set of soil conditions, it is not the same for all soils or soil conditions. The observation of maximums near $(\theta_v/e) = 0.6$ for a number of soils (Linn and Doran, 1984) suggests that many soils have characteristics that are similar so that either the empirical constants important in these equations ($\alpha$, $\beta$, $f$, and $g$) are similar or important ratios such as $\tau = a/b$ are similar.

The shift in $\theta_{\text{max}}$ as a function of one constant is best illustrated through Eq. [8]. In Fig. 4, the relative water content ($\theta_{\text{max}}/e$) is plotted vs. $\tau$ for different val-
values of \( f \). The axis with \( \tau \) represents the relative importance of \( O_2 \) diffusion vs. substrate diffusion. Values of \( \tau < 1 \) indicate that substrate diffusion is more limiting. When \( \tau > 1 \), gas diffusion is more limiting. In the former case, \( \theta_{\text{max}} > 0.5 \), while \( \theta_{\text{max}} < 0.5 \) in the latter. Changing the value of \( f \) changes the responsiveness of \( \theta_{\text{max}} \) to \( \tau \). For large values of \( f \), fairly large changes in \( \tau \) are required to shift \( \theta_{\text{max}} \). Or \( \theta_{\text{max}} \) can be expected to be a fairly stable quantity across soils if \( f \) is large. If \( f \) is small, then relatively small changes in \( \tau \) may result in significant changes in \( \theta_{\text{max}} \). Similarly, if \( \tau \) is near 1.0, then \( \theta_{\text{max}} \) is insensitive to changes in \( f \). Conversely, empirical observations of maximum activity occurring in a limited range of water contents suggests values of \( \tau \) near 1.0 (most likely) or large values of \( f \) (less likely).

Figure 5 shows the data and regression line where the repetitions have been treated as simple replicates. The pattern of replicates indicates that the time from sample conditioning to assay is an important parameter. This time period is one where substrate is being depleted. Additional nonlinear regression was carried out after the data had been scaled by dividing by the maximum value for each repetition (Fig. 6). Finally, the data of each repetition was analyzed individually.

In total, three regression analyses were carried out: (i) pooled/unsealed, (ii) pooled/scaled, and (iii) individual replicates. Estimates for \( \alpha \), \( \beta \), \( f \), and \( g \) using Eq. [9] are given in Table 1. Values for \( P_{\text{max}} \) and \( \theta_{\text{max}} \) are given in Table 2. Table 2 contains additional information about the regression. Overall, Eq. [9] and, hence, Eq. [5] appear to describe the pattern of how microbial activity changes with water content. However, the consistent variation in time indicates that changes in soil substrate level with time can result in large variations in microbial activity. These changes are consistent with the model presented here.

### DISCUSSION

The desirability of expressing diffusion coefficients as functions of soil water content suggests that it is informative to study microbial activity as a function of water content in addition to soil water potential. Qualitative interpretation of microbial activity vs. water content functions and parameters in these functions is possible based on concepts of soil structure.
and transport processes. This also means that the water content where maximum aerobic microbial activity occurs is an interesting soil parameter from both physical and biological points of view.

The experimental data provides support for the validity of Eq. [1] by virtue of the correspondence between the shape of the theoretical function (Eq. [1]) and the data. The results also show the insensitivity of the water content at maximum aerobic activity across soils or repetitions (Table 2). This insensitivity suggests that any alteration of soil structure influences $O_2$ transport similarly to solute transport. In terms of the model, $\tau$, an index of the relative magnitude of solute diffusion vs. $O_2$ diffusion, is insensitive to small changes in soil structure for the Yolo soil (Table 2). This insensitivity could also be a consequence of high values of $j$ for the Yolo soil.

If $\tau$ is near unity (i.e., within a factor 10–100), it implies that the appropriate diffusion coefficient for transport of $O_2$ is within an order of magnitude or two of the diffusion coefficient for substrate. However, $O_2$ diffusion in the gas phase is usually $10^4$ that of gas or solute diffusion in the liquid phase. A value of $\tau$ near unity suggests that $O_2$ limitations on microbial activity may be occurring within the liquid phase or at the air-water interface. A more accurate description (e.g., Skopp, 1985) of $O_2$ transport to microorganisms may be needed to properly characterize the response of microorganisms to soil water content.

Additional information is available from the change in response due to the time lag following conditioning. Empirically, the response curves decrease in magnitude with time. This indicates the depletion of substrate and subsequent reduction in $P_{\text{max}}$ (see Table 2). Depletion of substrate would most influence parameter $\alpha$. Indeed, for the Valentine soil, $\alpha$ decreases with time. The pattern for the Yolo soil is not so clear. However, care must be taken not to overinterpret the coefficients in Table 1. The regression analysis is extremely sensitive to errors in the data and a strong correlation exists between the pairs of parameters (e.g., between $\alpha$ and $f$ as well as between $\beta$ and $g$).

Depletion of substrate suggests that scaling the replicates should improve the fit. Figure 6 shows the results of scaling. Table 2 indicates that the ratio root mean square (RMS)/$P_{\text{max}}$ decreases by about one-half with scaling. It also confirms the similarity in shape for curves determined at distinct levels of available substrate. Furthermore, regardless of the analysis, $\tau$ is always less than one, which indicates that substrate diffusion is more limiting than $O_2$ diffusion in both soils.

The prediction that a maximum in activity exists and can be calculated remains a direct consequence of Eq. [1]. Equation [1] appears adequate to describe the data presented here. Where Eq. [1] is inadequate, then the conclusions presented may need modification. It may turn out that $O_2$ or single substrate diffusion are not the limiting factors. Examples of other transport limitations include: (i) multiple substrates, e.g., energy source, C source, electron acceptor, or specific nutrients; (ii) toxic byproduct removal; (iii) population interactions, e.g., predation or parasitism. Since the coefficients of Eq. [1] cannot be measured independently, the magnitude of $P$ cannot be predicted apriori. This places an emphasis on whether Eq. [1] predicts the correct shape of the experimental data as a means to evaluate the appropriateness of the model.

In addition to the possibility of incomplete specification of the transport process, the form of Eq. [1] may be inappropriate. For example, a multiplicative law may be more suitable. Or at low water contents, nontransport characteristics such as soil matric potential probably have a direct influence on microbial activity. It is also possible that the kinetics of substrate release (i.e., depolymerization) is the limiting step. Thus, it is important not to extrapolate Eq. [1] without confirmatory empirical evidence.

Wilson and Griffin (1975) stated: “Indirectly, changes in water potential will affect the rate of solute diffusion, for this is approximately proportional to volumetric water content in a particulate matrix.” In effect, either water potential or water content can be used to examine the influence of water content. However, it is generally less desirable to express effective diffusion coefficients as a function of soil matric potential than of soil water content (Collis-George, 1959; Papendick and Campbell, 1981). This occurs since the effective nature of the diffusion process is the direct result of porosity, tortuosity, and constrictivity (van Brakel and Heertjes, 1974). This study suggests that soil water content/microbial activity relationships provide a useful means of studying soil microbial ecology. Modeling of these relationships can provide new methods of describing and quantifying both soil physical and microbial processes. Finally, the idea of a water content at which aerobic respiratory microbial activity is optimum may be a useful parameter to characterize soil.

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