Steady-State Aerobic Microbial Activity as a Function of Soil Water Content

J. Skopp,* M. D. Jawson and J. W. Doran

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 work tends to emphasize the lowest matric potential (ie., 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_2 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 (θ_v) equal to 0.60 times the value of the total porosity (ϵ). In later studies, the maximum aerobic microbial respiration occurred between $\theta_v = 0.55$ and 0.61 times ϵ 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; Glinski 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

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(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 (θ_{max}).

THEORY

Our approach was to examine some of the physical limits on aerobic microbial activity. Physical processes outside the organism were used to define the limits on microbial activity in soil. The emphasis was 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 nonunique, 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. θ_v (Fig. 1). The dashed line segments

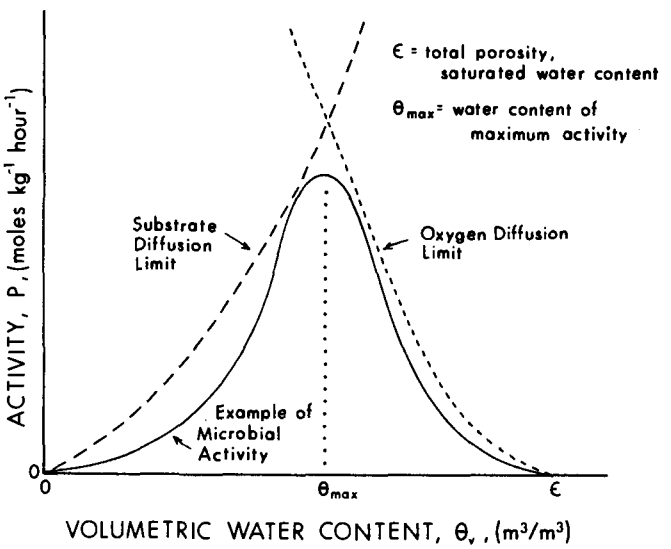

Fig. 1. Conceptual plot of microbial activity as a function of soil water content. Also, indicated by straight lines are the theoretical limits to activity posed by either the flux or total substrate.

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 θ_{max} near 0.6 ϵ. 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 θ_{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 were minimal and allowed 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

$$P = \min\begin{cases} A_n J_n \\ A_o J_o \end{cases} \quad [1]$$

where A_n and A_o 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 $A_n J_n$ and $A_o J_o$ represent the substrate and O_2 diffusion line segments, respectively, in Fig. 1. Equation [1] states that the potential 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 $J = kD\Delta C$, 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 $k\Delta C$. The difference ΔC is taken between some constant reservoir and the microbe surface. Using Assumption 2, ΔC 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

$$P = \min \begin{cases} A_n k_n D_n C_n \\ A_o k_o D_o C_o \end{cases} \quad [2]$$

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

$$D_n = a(\theta_v)^f D_e \quad [3]$$

and O_2 diffusion in the gas phase (Troeh et al., 1982):

$$D_o = b(\theta_A)^g D_g \quad [4]$$

where a, b, f, and g are empirical constants that are fixed for a given soil; D_e and D_g are molecular diffusion coefficients in pure liquid or gas phase of substrate or O_2, respectively; θ_A is the air-filled porosity, and $\theta_A = \epsilon - \theta_v$. Substituting Eq. [3] and [4] into Eq. [2], as well as expressing θ_A in terms of θ_v, yields

$$P = \min \begin{cases} aA_n K_n C_n D_e(\theta_v)^f \\ bA_o k_o C_o D_g(\epsilon - \theta_v)^g \end{cases} \quad [5]$$

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 θ_{max} is applicable:

$$aA_n k_n C_n D_e(\theta_{max})^f = bA_o k_o C_o D_g(\epsilon - \theta_{max})^g \quad [6]$$

to obtain Eq. [6] from Eq. [5], θ_v is set equal to θ_{max}, since only θ_{max} is to be evaluated.

Equation [6] can be simplified by using dimensionless ratios. Introducing $\tau = aA_n k_n C_n D_e / bA_o k_o C_o D_g$ results in Eq. [6] becoming

$$\tau(\theta_{max})^f = (\epsilon - \theta_{max})^g \quad [7]$$

This equation says that θ_{max} depends on τ, f, g, and ϵ. The dimensionless ratio τ 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 θ_{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 θ_{max}/ϵ (the relative water content):

$$(\theta_{max}/\epsilon) = (1 + \tau^{1/f})^{-1} \quad [8]$$

This result states that, when water contents are expressed on a relative basis, the water content at which maximum microbial activity occurs, (θ_{max}/ϵ), 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 τ.

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 Ustipsamment, A horizon) soils. Nonlinear regression was carried out with the following equation:

$$P = \begin{cases} \alpha\theta_v^f \\ \beta(\epsilon - \theta_v)^g \end{cases} \quad [9]$$

where $\alpha = aA_n k_n C_n D_e$ and $\beta = bA_o k_o c_o D_g$, and P represents the evolved CO_2, expressed as mg CO_2/g soil. The program NREG (Madison Academic Computing Center, 1982) was used to estimate the values of α, β, f, and g. The soils were all conditioned at the same time and experimental details are described in Doran et al. (1988). Three repetitions of the experiment were carried out at three successive time periods: 11, 81, or 133 d following soil conditioning. The assay for CO_2 production extended over a 28-d period.

RESULTS

The predictions of Eq. [9] are presented in Fig. 2 and 3. Dimensionless variables are used to reduce the number of parameters to τ, f, g, and ϵ. This is done by calculating a dimensionless microbial activity (represented as P/β) and plotting vs. the ratio of soil water content to total porosity. Figure 2 shows the case where $f = g$, while Fig. 3 gives some examples where $f \neq g$. Figure 2A shows the special case where $\tau = 1$ and the maximum occurs when the ratio $\theta_v/\epsilon = 0.5$, regardless of the value of f. Figure 2B shows the case where $\tau = 0.1$, the situation where the coefficient reg-

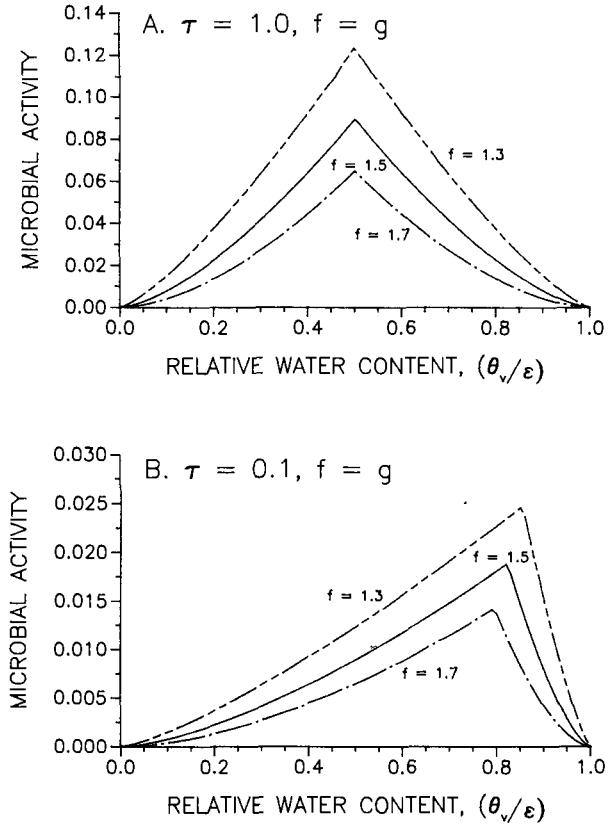

Fig. 2. Plot of Eq. [9] for the case $f = g$. Tau (τ) is the ratio of model coefficients and represents the importance of substrate diffusion (f) relative to O_2 diffusion (g). Tau controls the position and magnitude of the peak. The porosity (ϵ) = 0.4, the volumetric water content is θ_v and θ_{max} is the water content of maximum activity. A. Tau equals 1.0, θ_{max} occurs at $\theta_v = 0.5\ \epsilon$. B. Tau equals 0.1, θ_{max} occurs at $\theta_v > 0.5\ \epsilon$.

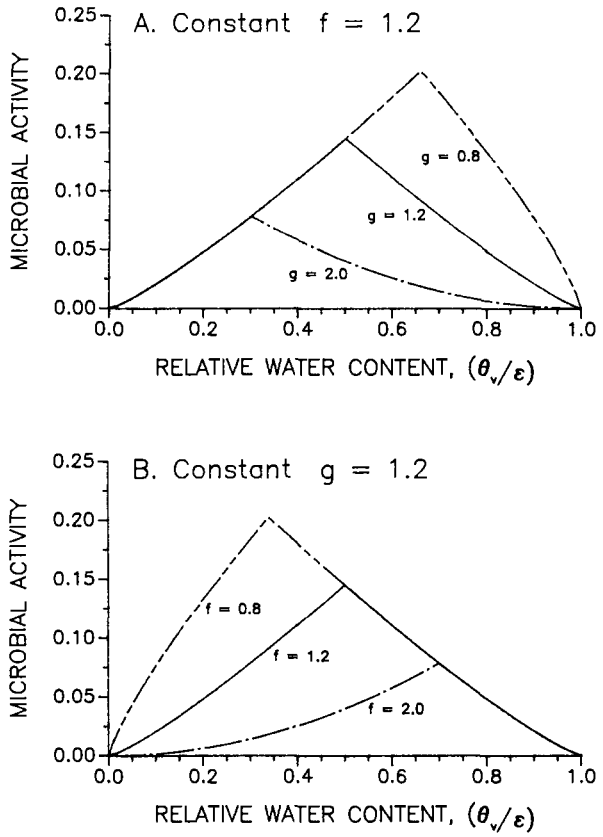

Fig. 3. Plot of Eq. [5] for the case $f \neq g$. Tau equals 1.0 for both figures and is the ratio of model coefficients. The porosity (ϵ) = 0.4 and the volumetric water content is θ_v. This figure illustrates the influence of changing the dependence on θ_v of either substrate diffusion (f) or O_2 diffusion (g). A. The case where f is fixed and g varies. B. The case where g is fixed and f varies.

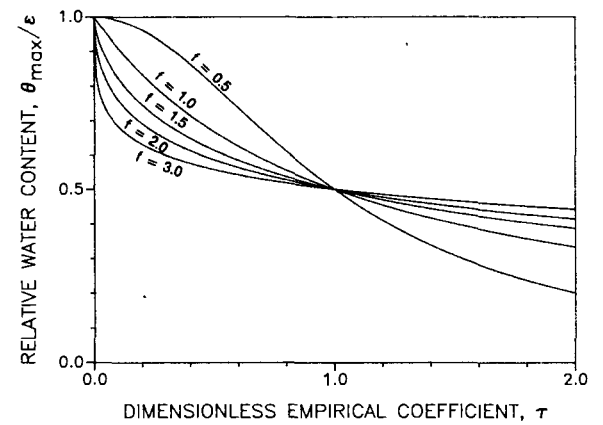

Fig. 4. Plot of Eq. [8] or the water content at maximum activity (θ_{max}) divided by porosity (ϵ) as a function of τ (the ratio of model coefficients). Note that the dependence of diffusion on water content is controlled by substrate diffusion (f) and O_2 diffusion (g). The values of f and g are equal. For $f = 1$, the dependence is linear while, for $f = 2$, the dependence is quadratic.

ulating O_2 transport is 10 times greater than the coefficient for substrate transport. Here, the maximum in microbial activity shifts to higher values of (θ_v/ϵ) as f decreases. Changes in the magnitude of the activity is more complex and depends on τ, f, g, and the denominator of the dimensionless microbial activity. Our emphasis here is on the water content of maximum

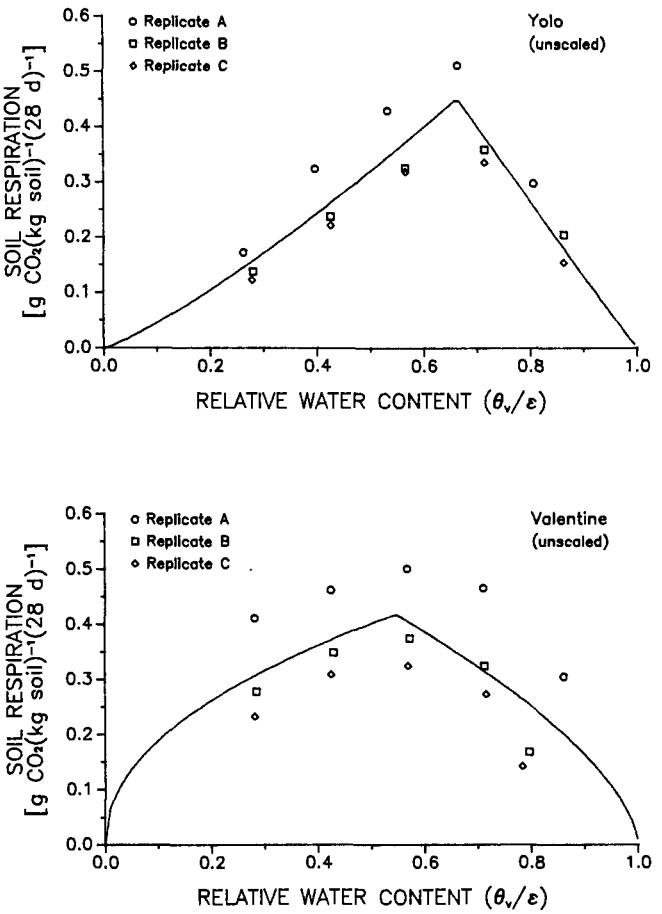

Fig. 5. Pooled regression of Eq. [9] against unscaled respiration data showing model goodness of fit and systematic variation of replicates for the Yolo and Valentine soils.

microbial respiratory activity and not on the magnitude of the activity.

Figure 3 shows the two cases when either f is fixed and g varies (Fig. 3A) or g is fixed and f varies (Fig. 3B). The two cases demonstrate the effect on microbial activity of changing the dependence on water content of either O_2 diffusion (Fig. 3A) or substrate diffusion (Fig. 3B). When f is fixed, (Fig. 3A) then the maximum (θ_{max}) shifts to larger values as g gets smaller. Increasing values of g indicate that O_2 diffusion becomes more limiting. When g is fixed (Fig. 3B), the maximum shifts to smaller values of θ_v as f gets smaller. Increasing values of f indicate that substrate diffusion becomes more limiting.

These calculated values of θ_{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 θ_{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 (θ_v/ϵ) = 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 (α, β, f, and g) are similar or important ratios such as $\tau = \alpha/\beta$ are similar.

The shift in θ_{max} as a function of one constant is best illustrated through Eq. [8]. In Fig. 4, the relative water content (θ_{max}/ϵ) is plotted vs. τ for different val-

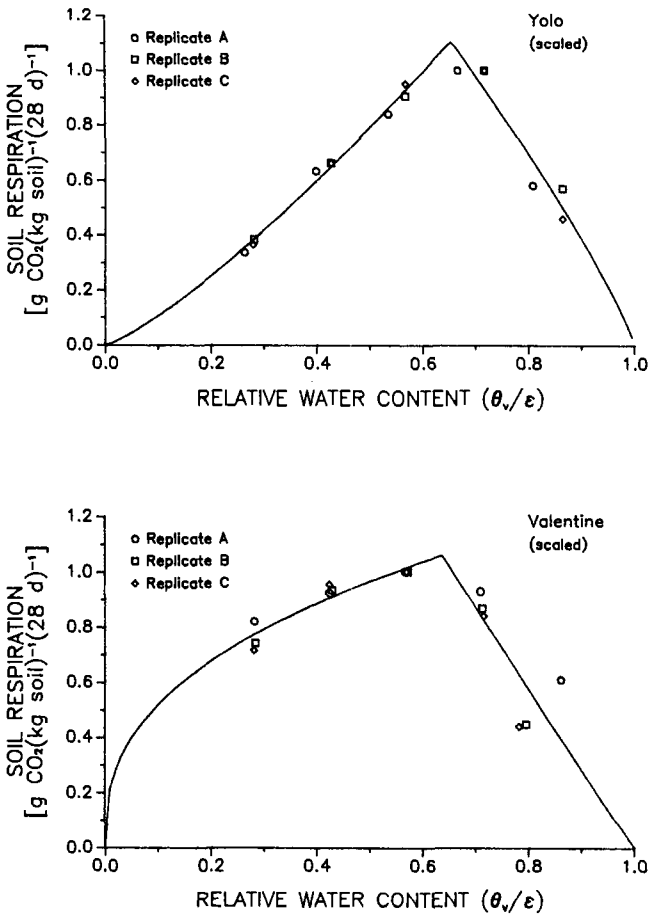

Fig. 6. Pooled regression of Eq. [9] against scaled respiration data showing how scaling reduces systematic variation for the Yolo and Valentine soils.

ues of f. The axis with τ 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, $\theta_{max} > 0.5$, while $\theta_{max} < 0.5$ in the latter. Changing the value of f changes the responsiveness of θ_{max} to τ. For large values of f, fairly large changes in τ are required to shift θ_{max}. Or θ_{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 τ may result in significant changes in θ_{max}. Similarly, if τ is near 1.0, then θ_{max} is insensitive to changes in f. Conversely, empirical observations of maximum activity occurring in a limited range of water contents suggests values of τ 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/unscaled, (ii) pooled/scaled, and (iii) individual replicates. Estimates for α, β, f, and g using Eq. [9] are given in Table 1. Values for P_{max} and θ_{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.

Table 1. Parameters determined by nonlinear regression using Eq. [9].

	f	α	g	β
		g CO_2 kg^{-1} soil (28 d)		g CO_2 kg^{-1} soil (28 d)
Yolo soil				
Pooled/unscaled	1.22	1.48	1.04	2.53
Pooled/scaled†	1.25	3.83	0.854	4.43
Individual replicates				
11 d	1.21	1.85	0.991	2.65
81 d	1.20	1.26	0.769	1.45
133 d	1.33	1.43	1.07	2.33
Valentine soil				
Pooled/unscaled	0.467	0.769	0.626	1.06
Pooled/scaled†	0.385	1.65	1.03	6.15
Individual replicates				
11 d	0.281	0.715	0.576	1.42
81 d	0.418	0.643	1.93	13.7
133 d	0.458	0.594	2.40	30.0

† There are no units for α and β for the pooled/scaled data. Scale values for Yolo soil are: 0.500, 0.373, and 0.323 g CO_2 (kg^{-1} soil (28 d)$^{-1}$; and for Valentine are: 0.510, 0.357, and 0.333 g CO_2 kg^{-1} soil (28 d)$^{-1}$.

Table 2. Characteristics of the regression analysis.†

	τ‡	P_{max}	RMS	θ_{max}/ϵ
		— g CO_2 kg^{-1} soil (28 d)$^{-1}$ —		
Yolo soil (ϵ = 0.568)				
Pooled/unscaled	0.58	0.447	0.0545	0.660
Pooled/scaled§	0.86	1.11	0.0547	0.652
Individual replicates				
11 d	0.70	0.545	0.0234	0.643
81 d	0.87	0.395	0.0066	0.669
133 d	0.61	0.389	0.0041	0.669
Valentine soil (ϵ = 0.496)				
Pooled/unscaled	0.73	0.417	0.0968	0.545
Pooled/scaled§	0.27	1.06	0.1036	0.636
Individual replicates				
11 d	0.50	0.519	0.0002	0.646
81 d	0.05	0.405	0.0146	0.666
133 d	0.02	0.360	0.0219	0.676

† P_{max} = limiting aerobic respiratory activity at maximum microbial activity; RMS = root mean square from residuals of P obtained from the nonlinear regression; θ_{max} = water content at maximum microbial activity; and ϵ = total porosity.

‡ The quantity τ, the ratio of model coefficients, was calculated as α/β from Table 1 and has no units.

§ The scale values are reported in Table 1. The scaled P_{max} and RMS have no units.

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, τ, 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 f for the Yolo soil.

If τ 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 τ 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_{max} (see Table 2). Depletion of substrate would most influence parameter α. Indeed, for the Valentine soil, α 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 α and f as well as between β 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_{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, τ 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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