Calculating the Dimensions of the Rhizosphere

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Formulae for the calculation of rhizosphere widths, w, of cylindrical host parts and of spherical hosts (seeds) were proposed by Gilligan (9). Ferriss (7) has recently presented corrected formulae and has examined some of the factors and assumptions affecting these estimations of the true values of the rhizosphere influence on inoculum in cylindrical and spherical infection courts on hosts. In addition to the utility in determining the dimensions of such rhizospheres, these formulae have been presented as tools to determine the validity of the distinction between rhizosphere and rhizoplane phenomena proposed by Baker et al (3).

In this note, we consider the impracticality of these formulae for calculating rhizosphere widths with the information presently available in the literature on host-soilborne pathogen relationships. We also examine the validity of using calculated rhizosphere widths as a tool for distinguishing between rhizosphere and rhizoplane phenomena.

Approaches to the calculation of the dimensions of a rhizosphere. Gilligan's (9) algebraic expressions for the rhizospheres of cylindrical and spherical hosts were based not only on the volume of a cylindrical or spherical shell of propagule-containing soil around the host, but included the volume of the host as well. This inclusion of host volume and thus, host dimensions, led to the possibility of obtaining negative values for rhizosphere width as pointed out by Ferriss (7). In contrast, Ferriss (7) proposed algebraic expressions for the rhizospheres equal to cylindrical and spherical shells around these hosts, containing the inoculum involved in infection. We concur with Ferriss' expressions as those which would represent the volumes within which the propagules of the pathogen are sufficiently proximal to infect such cylindrical and spherical host infection courts in idealized cases of rhizosphere phenomena. If the size of the host were negligible with respect to the size of the rhizosphere, then the formulae of Gilligan (9) and Ferriss (7) are equivalent.

Limitations in methodology associated with calculation of the thickness of cylindrical and spherical shells in characterizing the dimensions of a rhizosphere influence on inoculum. Clearly the formulae for cylindrical and spherical shell widths (7) are dependent on representing a host with idealized dimensions and would not apply to noncylindrical and nonspherical hosts or rhizosphere volumes. For example, to conform to the actual geometry of known relationships for preemergence damping-off induced by *Rhizoctonia solani*, a spherical spermosphere surrounding the spherical host (the seed) would be inappropriate. Rather, there is an ellipsoidal spermosphere twice as wide in the equatorial plane as in the vertical plane (2). Also, as Ferriss (7) indicates, the formulae would underestimate the size of rhizospheres of cylindrical and spherical host parts where only a portion of the host is infectible. In contrast, the formulae of Baker et al (2,3) do not depend on idealizations of host parameters.

Other factors lower confidence in estimates of the extent of the rhizosphere effect on inoculum. There would be an underestimate of the volume of soil influenced by the roots if infections per unit (calculated from the multiple infection transformation, [4,11]) underestimated the number of hits (infections), as noted by Ferriss (7). An overestimate of shell width would result if the inoculum density were underestimated. At present, measurements of inoculum density in soil are conventionally made by counting colony-forming units in dilution series. Whether selective or nonselective nutrient media are used, underestimation of actual inoculum densities in soil may occur when using such a procedure. This is especially true with propagules that germinate at low and variable levels and/or go through a period of dormancy. For example, Erwin (6) observed about 10% germination of oospores of *Phytophthora megasperma* f. sp. *medicaginis* even on water agar which does not contain the toxic compounds found in selective media. However, Kuan and Erwin (15) reported 20% germination in soil. Baumer (5) also observed 5–10% germination on water agar although the high incidence of disease obtained with low levels of oospores indicated a much higher germination in soil. Again, a number of units of inoculum may be embedded in a single bit of organic matter but would only yield one colony-forming unit. Subsequent decomposition of the organic matter, even for brief periods, can increase the actual number of inoculum and infection units.

Griffin (12) found by direct microscopic observation that chlamydospore germination of *Fusarium oxysporum*, a common peanut root colonizer, was nearly 100% at the root surface and decreased gradually to zero at 1.73 mm from the root surface (Fig. 1). That all chlamydospores within the rhizosphere width (1.73 mm) did not germinate (ie, germination was dissimilar or heterogenous) contradicts the assumptions underlying the theoretical approach of Ferriss (7). Complete germination (= 100%) and complete infection (= 100% efficiency) by all germinable or viable propagules within the calculated rhizosphere width is assumed by Ferriss (7) when competence is equal to 1. The calculated shell width encompasses a volume of soil which contains a number of propagules equal to the number which actually infect the host. This would result in a gross underestimation of the distance from the root (= rhizosphere width) in which germination actually occurs (Fig. 1), and obviously limits the utility of such a calculated distance in rhizosphere biology.

Competence and the importance of a knowledge of efficiencies. In the equation for calculating the extent of the rhizosphere effect on inoculum, Ferriss (7) applies a correction factor (C) to the density. He designates C as "the competence of the pathogen propagule population." Competent distance, as defined by Grogan et al (13), refers to the placement of the propagule so that it "...still [has] a chance of causing infection."

We prefer the term "efficiency" because inoculum efficiency implies that a measurement can be made of inoculum performance, whereas competency does not. Therefore, dictionaries use the word "measurement" in defining efficiency, but it does not appear in the definition of competency, making the latter term of little use (by definition) for insertion of values eventually into equations. Thus, competency refers more to what inoculum should be able to do rather than what it has done. In Webster, competency is defined as "means sufficient for the necessities of life." A synonym is "able." An able propagule may infect a root in one soil but not another. Efficiency is measured after the fact—it is not an estimate of what

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should occur.

With these elements of the definitions in mind and considering the principle of independent action of propagules elaborated by Garrett (8) and the "law of the origin" (when disease is plotted against inoculum, both on arithmetic scales, the curve starts at the

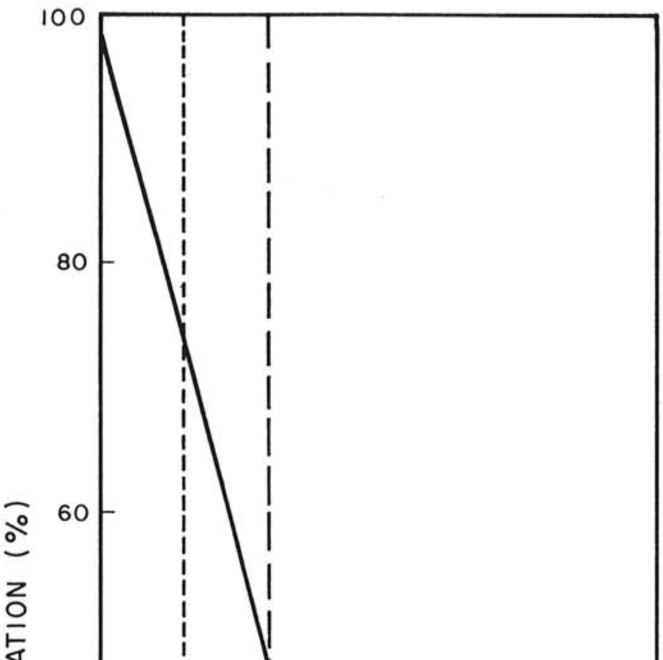

Fig. 1. Comparison of a theoretical width of the rhizosphere influence on propagules (7,9) and that obtained using direct microscopic examination of *Fusarium oxysporum* chlamydospore germination on a root slide of peanut in soil (12). Areas under the curves (= germinating chlamydospores) for the direct-microscopic-observation curve (—·—) and the theoretical rhizosphere width curve (——) were equalized using a digitizer planimeter. This was done since the theoretical approach of Ferriss (7) assumes that all propagules within the calculated rhizosphere width germinate and infect roots when competence equals 1. Thus, the theoretical rhizosphere width (*W*) for the *F. oxysporum*-peanut system is 0.64 mm or only 37% of that found for direct microscopic observation ($W = 1.73$ mm), if all germinating chlamydospores infected the peanut root (= 100% efficiency). If only one half of the germinating chlamydospores infect the root (= 50% efficiency), but this is unknown to the researcher (the typical situation [1,17]) the calculated width (------) is only 0.32 mm for the degree of chlamydospore germination shown here.

origin) expounded by Vanderplank (18), it is apparent that all viable inoculum units within the influence of a rhizoplane or rhizosphere are competent. There is abundant evidence in the literature by actual measurements (eg, 17), however, that indicates that all propagules in an infection court do not participate ultimately in the infection of the host (2). Competency does not describe this situation. Efficiency does.

We use efficiency to refer to that portion of the inoculum (propagules) on or adjacent to the infection court which induce successful infection of the host. Rather than being a constant correction factor for density, efficiency is more correctly viewed as a variable, which is dependent (among other things) upon distance from the host.

It has been pointed out repeatedly (eg, 1,2) that any calculation of the dimensions of the rhizosphere must involve calculations of the efficiency of the propagules inducing infection: only a limited number of studies have reported efficiencies; these differ widely depending on the pathogen involved (0.27–0.28% for *Cylindrocladum crotalariae* [17], 50–91% for *Gaeumannomyces graminis* var. *tritici* [10]), the particular host, environmental parameters involved, and the techniques employed in measurement.

The concept of density applied to a random distribution of discrete objects. In terms of the biology of the prepenetration process associated with the infection process of soilborne pathogens, the models (3) describe those systems in which propagules must touch the infection court in order to breech the host barrier and induce successful infection. This concept is based on the mathematics of surface density relationships (14) in which a point (of contact with the host) touches a plane (the surface of the infection court). Comprehensive documentation has been published (3) to demonstrate that such systems do exist and, indeed, may be the rule rather than the exception.

Much of the criticism (9,13,16,18) of the position of Baker et al (3) is based on the implicit rejection of the concept of surface density or the supposition that the stated mathematical relationship between surface and volume densities applies only to a tetrahedral distribution. In particular, the procedure of Ferriss (7), to determine the occurrence of a surface phenomenon is circuitous unless one rejects the concept of surface density. The procedure identifies a surface phenomenon in terms of volume density and a volume having a zero third dimension or shell width, *w*. Consequently, we now consider the concept of density as it applies to a random distribution of discrete objects.

The density of a continuous, uniform material is defined as the ratio of its mass to its volume. Since mass exists only in volumes, this density applies only to volumes. In contrast, a random distribution of discrete objects can also be treated mathematically as a density. In this case, the subject of the density is not mass, but the number of objects in the distribution. Their size is not considered, only their number and location. Thus, by viewing the random distribution of objects as a locus of points, it is possible to define density as the ratio of the number of objects to the size of their locus. The locus may be a curvilinear path through the field of distribution, a surface in the field, or a volume in the field. Thus, there are three definitions of density applicable to a random distribution of discrete objects. These are linear density, surface density, and volume density. Surface density and volume density are, respectively, the square and the cube of linear density (14). This is a direct consequence of the concept of randomness and the definitions of length, area, and volume (2). Inoculum density (*ID*) eg, is the volume density of a random distribution of propagules in soil. The surface density of propagules in this same distribution is $ID^{2/3}$, and the number of propagules per curvilinear distance through the distribution is the linear density, $ID^{1/3}$.

Density and the procedure of Ferriss. Ferriss' procedure (7) for the calculation and use of a shell width, *w*, is based on some correct implications of the concept of density as treated immediately above, but it also contains some incorrect inferences and proposes some false conclusions.

Ferriss' (7) procedure correctly accepts the premise that a volume density phenomenon is evident in the direct proportion between an experimental number, N, and volume density, D_v.

$$N = kD_v \tag{1}$$

The constant of proportionality is the apparent volume of the phenomenon. However, the procedure falsely implies that volume density has an intrinsic conceptual priority over surface density and linear density. It is true that we have a predilection for volume density because of our familiarity with mass density. It is also true that it is experimentally convenient to identify or prepare a random distribution in terms of its volume density, eg, as the number of spores per volume of soil. This does not diminish the fact that the direct proportion between an experimental number, N, and surface density, D_s, is evidence of a surface density phenomenon, where the constant of proportionality is the apparent surface area of the phenomenon.

$$N = kD_s \tag{2}$$

Equation 1 has no greater conceptual or experimental validity than that of equation 2.

Density and limitation. Another correct and truly perceptive position adopted by Ferriss (7) is the premise that for a volume phenomenon, the slope of a function with respect to volume density is a constant at density equals zero. That the slope eventually decreases to zero with increasing density is evidence of limitation whether the limitation is exponential or quadratic. Furthermore, Ferriss correctly identifies the constant, at density equals zero, as the apparent volume of the phenomenon, comparable to k in equation 1, in which k is the slope of equation 1.

The importance of this facet of the procedure of Ferriss lies in its being the key to the reconciliation of the views of Vanderplank (18) and Baker (1). Vanderplank (18) emphasized the fact that a concave downward curve is concomitant to exponential limitation of a volume phenomenon.

$$N = N_0(1 - e^{-aID}) \tag{3}$$

It appeared as if this were a mutually exclusive alternative to the surface equation of Baker et al (3) which is also concave downward as a function of ID,

$$N = kID^{2/3}. \tag{4}$$

Ferriss has indicated that the derivative with respect to volume density, at density equals zero, is the constant, k, for equation 1 and the constant, aN_0, for equation 3. Furthermore, these are the apparent volumes of the phenomena (7). It follows that for surface density phenomena, the equation showing exponential limitation is,

$$N = N_0(1 - e^{-aID^{2/3}}). \tag{5}$$

The derivatives of equations 4 and 5 with respect to surface density are, respectively, the constants, k and aN_0, at density equals zero. These are the apparent surface areas of the phenomena. Thus, concavity downward alone is not evidence of limitation on the one hand or of a surface phenomenon on the other. Also, there is no inherent conflict between the equations of Vanderplank (18) and Baker et al (3).

Distinguishing a volume from a surface. The cardinal principle upon which the procedure of Ferriss (7) is based is that a volume differs from a surface by having one more dimension than a surface (see the next section for further detail). If one were dealing with a continuous system, the minimum size of the third dimension, distinguishing a volume from a surface, would be, in concept, arbitrarily small and, in practice, the smallest one could measure. In a discrete distribution system, the minimum size of any dimension relevant to the distribution must typically include at least one object of the distribution. A dimension so small that it does not typically include at least one member of the distribution is insignificant relative to the distribution. Thus, the conceptual minimum size of any dimension relative to a random, discrete distribution is the typical distance between nearest neighbors. This is the reciprocal of the linear density, or equivalently, the reciprocal of the cube root of the volume density. In his procedure, Ferriss mistakenly chose the diameter of a member of the distribution as the minimum size of a dimension relevant to the distribution. A length equal to the diameter of a member of the distribution would typically include at least one, but exactly one, member of the distribution only if the members of the distribution were contiguous. Examples of irrelevant and relevant dimensions are: for $D_v = 1$ object $(\mathrm{km})^{-3}$, nearest neighbors are typically 1,000 m apart; a dimension of 10 m is insignificant in this distribution; for $D_v = 10^6$ objects m^{-3}, nearest neighbors are typically 1 cm apart; a dimension of 10 cm is relevant to this distribution.

The procedure fails to distinguish volume from surface phenomena. It is by the algebraic form of a function that one recognizes a volume or a surface phenomenon. As noted above, Ferriss (7) lucidly identified volume functions, not simply by the form of equation 1, but also by the following:

$$\left.\frac{\mathrm{d}f(D)}{\mathrm{d}D_v}\right|_{D=0} = \text{a constant.} \tag{6}$$

Thus, equation 3 is a volume equation.

With this in mind, an examination of Ferriss' procedure indicates that it cannot be used to distinguish volume from surface phenomena. The procedure examines each data set for linearity or concavity downward as a function of volume density. If a data set is linear, the set thereby conforms to equation 1 and no one disputes this identification as a volume phenomenon. If a data set shows concavity downward as a function of volume density, the procedure fits the data to the algebraic form of a volume phenomenon such as equation 3. By accepting this fit, one is accepting the proposition that the phenomenon is a volume phenomenon.

One could support the proposition by showing that a mathematical deduction from the proposition was in accord with known facts extraneous to the proposition and to the data set. Alternatively, one could disprove the validity of the proposition by a mathematical deduction such as the calculated value of a shell width, w, if the deduction were based on no further assumption beyond the proposition and if the deduction were known to be false when compared with extraneous facts. However, the value of w calculated by the procedure (7) is based on many assumptions (cf, the first paragraph of the section titled "Limitations of the proposed model"). Consequently, the proposition cannot be disproved by the calculated value of w, because one would not know whether the proposition or one of the assumptions was false.

What does the calculated value of the shell width, w, of a volume phenomenon signify? The calculated shell width, w, is the apparent third dimension characteristic of a volume. For the infection phenomenon to appear to be a volume phenomenon, the distance between nearest neighbors (d_w) of the experimental distributions tested, must have been less than w. If the nearest neighbor distance for a distribution were greater than w, the volume characterized by w would be too small to be relevant to the distribution. Because $d_w = ID^{-1/3}$, the nearest neighbor requirement is fulfilled by inoculum densities where,

$$ID > w^{-3} \tag{7}$$

To be consonant with one's having fitted the data to a volume equation, the inoculum densities used in the experiment must fulfill relation 7. If an experimental ID were smaller than w^{-3}, one could conclude that the proposition or at least one of the many assumptions upon which the calculation of w was based, was incorrect. Because of this uncertainty, there are no circumstances under which one could conclude that a surface phenomenon was involved.

The procedure of Baker et al. The procedure of Baker et al (3) is in marked contrast to the procedure of Ferriss (7). Baker et al (3) propose fitting data to the algebraic relation,

$$N = kID^b. \quad (8)$$

Surface and volume relationships are alternatives within equation 8. The results of this fitting have so far fallen into two categories. One category is of the form of equation 1, ie, in which the exponent of ID (without synergism [1,18]) is 1. The other category is of the form of equation 4, in which the exponent of ID is 2/3. Such values have been obtained experimentally. This has been acknowledged (16). Baker et al (3) properly conclude that data conforming to equation 4 represent surface phenomena. One cannot deny the validity of this conclusion while maintaining that data conforming to equation 1 represent volume phenomena. The identification of equation 1 as a volume equation has no greater validity than the identification of equation 4 as a surface equation.

It would be appropriate to criticize the approach of Baker et al (3) on the ground that data sets apparently conforming to equation 4, in reality conform to equation 3. However, this criticism has been met by showing that as larger values of ID are dropped from consideration, the remaining data still conform to equation 4 (Fig. 5 in 2). Indeed, if one conjectured that concave downward curvature as a function of volume density represented exponential limitation, the data should be fitted to an equation of the form,

$$N = N_0(1 - e^{-aID^b}). \quad (9)$$

Then, assuming the validity of the conjecture of exponential limitation, the value of b will be the indicator of whether the phenomenon is a surface or a volume phenomenon.

Conclusion. The calculation of a minimum rhizosphere width, w, is not useful in describing the actual dimensions of a biological rhizosphere influence on inoculum or as a tool in distinguishing rhizosphere from rhizoplane infection phenomena. Further, present methodology used to measure actual inoculum density and other parameters required for obtaining values for use in equations is not yet sufficiently developed. However, as one in a series (2,3,7,9,13,16,18) of conflicting viewpoints, it was useful (indeed essential) to the dialectical development of the subject.

The suggestion to calculate a shell width, w, necessitated an examination of the principles of density which we have touched upon in this note. Volume phenomena and surface phenomena are distinguished by algebraic relationships. Ferriss (7) has incisively pointed out that an equation as a function of volume density, whose slope equals a constant at density equals zero, represents a volume phenomenon. This leads to a generalization of the algebraic forms representing both volume and surface phenomena, namely equation 9, and provides the key to reconciling the equations of Vanderplank (18) and Baker et al (3).

The close fit of a data set to a volume equation is sufficient evidence of a volume phenomenon in the absence of evidence to the contrary. However, if the question is whether a surface or a volume phenomenon is involved, data should be fitted to algebraic forms which include both possibilities.

The procedure of Ferriss (7), by fitting data to equations 1 and 3, assumes the existence of a volume phenomenon. It then deduces the value of w to check the assumption. A mathematical deduction, such as a calculation w, based on the form of the equation fitted to the data, may be consonant with the choice of the equation for the fitting. Alternatively, it could be used to disprove the validity of the choice, if the result is based on no assumptions beyond the original choice of the equation. However, the proposed calculated shell width, w, is based on many assumptions (7). Under no circumstances could one conclude, on the basis of Ferriss' (7) procedure, that a surface phenomenon was involved. Consequently, the procedure cannot be used to distinguish volume infection phenomena from surface infection phenomena.

In contrast, the procedure of Baker et al (3) fits data to an equation (equation 8) which accommodates both volume and surface infection phenomena. The value of the parameter, b, in equation 8, as determined by the data, then indicates whether a volume or surface infection phenomenon was present.

The proper conceptual approach, in disagreeing with the identification of equations 2 and 4 as surface phenomena equations, is to offer a different equation in their stead and to demonstrate the validity of that equation. We maintain that this is impossible without denying the definitions of length, area, and volume or without making an incidental error along the way. Leonard (16), eg, took this proper conceptual approach, but made an incidental error in calculus by identifying the expression for the derivative as the differential (2).

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