Effect of Soil Compression on Estimates of Rhizosphere Width: Comparing Ferriss's Equation with Gilligan's

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The Rhizosphere width for infection by fungi. A useful approach to studying fungal infection of roots—whether the fungi are pathogenic or mycorrhizal—is offered by the rhizosphere model of Baker et al. (1,2). They defined the rhizosphere around a root as a cylindrical volume of soil that contains as many propagules as infect the root. This is clearly a very simple model, but one that can be used to draw comparisons between different fungi or different hosts, and to estimate relative distances over which fungi can find suitable hosts. Gilligan (9) proposed a method for calculating rhizosphere volume from the probability of infection of the root and the volume density of infective propagules. His method, expressed in suitable terms for mycorrhizal work, is:

$$V = U/P \qquad (1)$$

where V is the volume of the rhizosphere, U is the number of infections on the root, and P is the number of propagules per unit volume in the soil. In mycorrhizal studies, P is usually measured by the Most Probable Numbers Method and U by staining and counting (e.g., 15).

The width of the rhizosphere, measured outward from the root surface, can be calculated from its volume. Gilligan's rhizosphere volume included the volume occupied by the root itself, and so was calculated from:

$$W_G = \sqrt{V/(\pi L)} - r \qquad (2)$$

where L is the length of the root and r is its radius. Ferriss (7) suggested that the volume occupied by the root should not be included in the rhizosphere volume, because this causes small, positive rates of infection to give a negative rhizosphere width. He applied this idea to infection of seeds, where the host volume is relatively large, and suggested that it be used for root infection as well. His rhizosphere width is given by:

$$W_F = \sqrt{V/(\pi L) + r^2} - r \qquad (3)$$

Much discussion has been devoted to the choice between the Gilligan and the Ferriss approaches (4,8,10,11), but no firm guidelines have emerged for the experimenter to use. Gilligan (11) observed that the compression of the soil by a growing root was a factor to be considered, but did not deal with the question quantitatively.

Until now, it has not been clear which approach best suits real soils. The Gilligan approach would suit models in which the growing root pushes propagules aside into nearby voids in the soil (9) or passes through voids itself without disturbing the soil (cf. 13). However, we discuss here soils that can be modeled as a continuum, with voids small on the scale of the root. For such soils, the Ferriss approach should be valid if the soil is relatively incompressible, so that the volume displaced by the growing root is pushed out a great distance. Near the root there would thus be a uniform distribution of propagules. Gilligan's approach should be valid for a soil with a compression that is so local that no propagules originally in the rhizosphere are displaced out of it during root growth. All of the propagules in the volume now occupied by the root would remain in the rhizosphere.

While applying the rhizosphere model to the study of mycorrhizal infection (15), we have been able to reach conclusions that seem more generally applicable.

Compression of soil by growing roots. The compression of soils by growing roots can be treated as a case of radial compression by a cylinder of increasing radius (4,6,12). These papers report studies of the extent of the radial movement or radial compression in two soils, a clay and a loam, on very different scales. The results seem to be scale-independent. However, they are not easy to apply to the present problem, which is to find the fraction of the material displaced by a growing root that is still contained within a given distance (rhizosphere width) of the root. Although there is a comprehensive theoretical model for calculating soil compression (6,12), with three different regimes of stress/strain relationship, it is complex to compute and needs a number of measured parameters, including angle of internal friction, Young's modulus, and slope of rebound curve. Dexter (4) offers an elegantly simplified model for soil compression due to radial expansion of a root. He models soil compression as an exponential rise in dry bulk density (d) towards the root surface:

$$d_x = d_m + (d_r - d_m) \exp(-x/q) \qquad (4)$$

where d_m is the density at the pot wall, d_r is the density at the root surface, and x is the distance from the root surface scaled by root radius. He assumes that q is independent of x, with the result that the model contains only radial distances scaled on r (see Equation 6). The solid lines in Figure 1 show examples of exponential rises in dry bulk density near a root surface, calculated from Dexter's equations (see following). He introduces a constraint that there is a maximum compressed density that cannot be exceeded at ordinary pressures; if this maximum compressed density is reached at some distance, the actual density is constant from the root surface out to this distance. This is illustrated by the dashed-line curve in Figure 1.

Dexter has estimated the dimensionless exponent q as 1.5–3 for the experimental results already quoted. He has solved the equations for his model with the condition that the volume integral of the extra density from the root surface to a finite radius (m, the pot radius) equals the mass of material displaced by the root. He finds (see his equation 6) that d_r is given by:

$$d_r = d_m[1+1/2qA)] \qquad (5)$$

where A is given by:

$$A = q[1 - (X+1)\exp(-X)] + [1 - \exp(-X)] \qquad (6)$$

and X is given by:

$$X = (m - 1)/q \quad (7)$$

For the case in which the soil reaches its maximum density, A and X are given by different but analogous expressions, for which the reader is referred to Dexter's paper. He shows (see his equation 18) that for the simple case, the additional volume compressed into the region between x = 0 and x = x is given by:

$$\Delta V = 2\pi r^2 (d_r/d_m - 1)qA'' L \quad (8)$$

where A″ is given by Equation (6) but with X″ substituted for X and given by:

$$X'' = x/q \quad (9)$$

For comparison, the Ferriss approach is equivalent to assuming that no additional volume is compressed into the region between 0 and x, and the Gilligan approach assumes that this additional volume is $\pi r^2 L$.

If we assume that the displaced volume contains a proportional number of propagules, we can calculate the expected errors in the Gilligan and the Ferriss equations if they are used for soils that behave according to Dexter's assumption. We have done this for the soils we used (15), a red sandy loam from Caliph, S.A. (14), and a mixture of this with 90% sand.

In calculating the dry bulk densities of Figure 1, we chose values of q, d_m and maximum compressed d_m, which characterize a particular soil. Then, d_r was calculated from Equation (5), after A had been calculated from Equations (7) and (6). If d_r exceeded the maximum compressed value for that soil, the "transition radius," t, at which d_x first falls below that maximum, was calculated by an iterative procedure (3). In either case, the remainder of the curve was found by substituting d_r and r or d_t and t into Equation (1). The actual quantity of material between the root surface (x = 0) and a distance x was then calculated from Equation (8). Given this (original) volume of soil containing spores at (originally) uniform concentrations, it was possible to calculate the corresponding rhizosphere widths W_G and W_F from Equations (2) and (3).

The values are presented in Figure 2 as the relative rhizosphere width calculated with the Gilligan or Ferriss equation versus distance scaled by the root radius. The curves give values for q = 1, 2, and 4, and for two types of soil behavior, corresponding to what is expected of the loam and of the sandy mixture we used. The sandy mixture has a maximum compressed density of 1.476, rather close to its uncompressed density of 1.418. For such a soil, there should be a zone of constant maximum density near the root (Fig. 1, dashed-line curve). For a soil like this, the Ferriss value of W is never more than 4% wrong, whereas the Gilligan value is not only negative for a range of W from 0.0 to 0.4 root radii, but quite misleading even when a positive value is calculated, until W exceeds about 3 root radii (Fig. 2, dashed-line curves). For the loam, the maximum compressed density was 1.194 and the uncompressed density was 1.092; it should not reach its maximum compressed density near the root (Fig. 1). Here, the Ferriss value can be up to 13% too big at low W, but is still better than the Gilligan value over the range of 0.0 to 2.0 root radii, where they both differ most from the value we calculate (Fig. 2).

Most soils would be more like the loam than the sandy mixture in terms of the difference between density and maximum density, so the precise error in the Ferriss equation will depend on the value of q. Most soils should fall between the limits plotted, so there should be errors of less than 10% in most cases.

CONCLUSIONS

The Ferriss equation for rhizosphere width seems to be the best choice under all circumstances, because soil compression near a root is unlikely ever to be so localized as to justify the Gilligan equation. The errors produced by the Gilligan approach are not confined to the negative values previously noticed (7); the errors not only vary, but can be considerable.

The authors will supply on request a copy of the Basic program that they used to calculate the quantities shown in Figures 1 and 2.

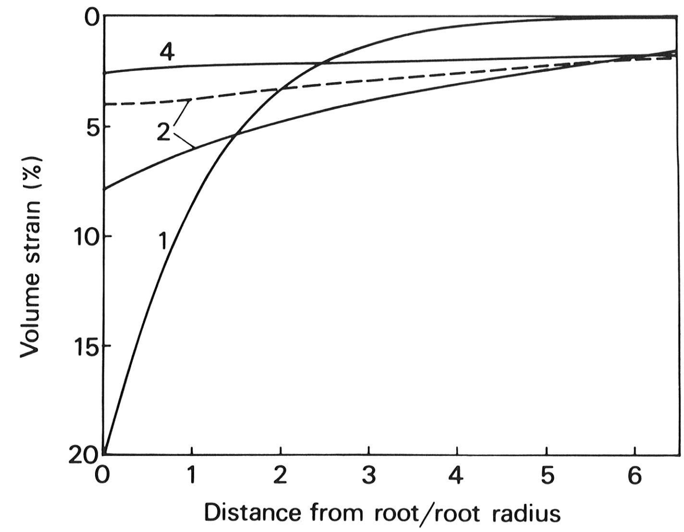

Fig. 1. Compression of soil by a growing root. Relative dry bulk density is plotted against radial distance from the root surface, scaled by root radius. The solid curves are calculated for values of q of 1, 2, and 4; see Equation (4) in text. These lines apply to any soil that does not reach its maximum compressed density at the root surface. The dashed line shows the effect, at q = 2, of a soil reaching its maximum compressed density in a narrow region near the root surface. This particular line applies only to a soil of that particular maximum compressed density.

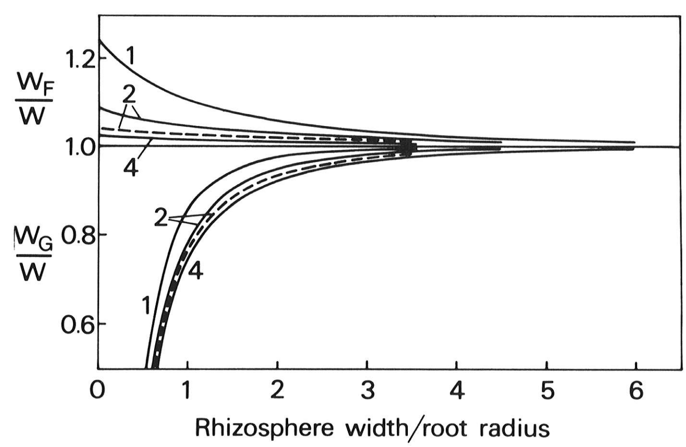

Fig. 2. Effect of soil compression on estimates of rhizosphere width by Ferris and Gilligan approaches; see Equations (3) and (2) in text, respectively. Values are plotted against the true rhizosphere width as calculated by the Dexter approach (see text). The Ferriss values occupy the upper part of the graph and the Gilligan values the lower part. As in Figure 1, the solid curves refer to any soil of the given value of q (1, 2, or 4) that does not reach its maximum compressed density. The dashed-line curves show, for q = 2, the effect of a soil reaching its maximum compressed value.

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