

### A Model for Determining Spatial Distribution of Soil-borne Propagules

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Research supported in part by funds from the W-38 Federal Western Research Project.

Technical Paper No. 3551 of the Oregon State University Agricultural Experiment Station, Corvallis.

The authors wish to express appreciation to R. D. Cooke of the Chemistry Department, University of Sherbrooke, Sherbrooke, Canada, for aid in the mathematical components of this paper.

#### ABSTRACT

Propagules that are uniformly distributed in a soil system can be represented by tetrahedra with the apices representing the propagules. If the tetrahedra are arranged to form a perfect lattice, a cubic close-packed lattice will result. Using this model, the distance (D) between propagules in the soil can be estimated from the equation:

$$D = 1.1225 \sqrt[3]{\frac{V_s}{N}}$$

where ( $V_s$ ) represents the volume of the soil and (N) the number of propagules or inoculum density.

Phytopathology 64:145-147

The position and density of plant pathogens in the soil profoundly influence disease incidence. The simplest model representing propagules in soil is a tetrahedron (2, 3), and if tetrahedra are arranged to form a perfect lattice with "rotational invariant" properties, a cubic close-packed lattice is obtained (Fig. 1). An analogous example would be a sodium chloride crystal in which the sodium ions represented the propagules. In this model, the apices of the tetrahedra represent propagules in the soil with each propagule corresponding to the center of a sphere in a cubic close-packed lattice. Based on this model, the distance (D) between propagules in soil can be determined experimentally from the number (N) of propagules in a given volume ( $V_s$ ) of soil.

To relate the distance between propagules in soil to their concn, the number of propagules per tetrahedron and the number of tetrahedra in a given volume of soil must be considered. Because the volume of a tetrahedron,  $V_t = 0.11785 D^3$  (Equation I), occupies only one-third the available space in a cube, the number of tetrahedra ( $N_t$ ) in a cubic close-packed lattice in a given volume of soil can then be determined by the following equation:

$$N_t = \frac{V_s}{3V_t} \quad \text{II}$$

Because each propagule is shared by eight

tetrahedra, and each tetrahedron is drawn from four propagules, a tetrahedron represents half a propagule. Thus:

$$N = \frac{N_t}{2} \quad \text{III}$$

where (N) is the number of propagules. Solving equations I, II, and III for D as a function of  $V_s$  and N:

$$D = 1.1225 \sqrt[3]{\frac{V_s}{N}} \quad \text{IV}$$

Thus, the distance between nearest propagules can readily be determined by this equation if the number of propagules in a given volume is known, and if it is assumed that the propagules are packed in a cubic close-packed lattice. To determine the number of propagules that would have to be added to a given volume of soil to obtain a desired distance between propagules, equation IV can be solved in terms of N:

$$N = \frac{1.414 V_s}{D^3}$$

A lattice of tetrahedra was used by Baker et al. (3) in the derivation of their equation representing distance between propagules. Implicit in their equation, however, are the assumptions that a lattice of equilateral tetrahedra would occupy all available space and that one tetrahedron represents one propagule. Using their assumptions and equation I, the distance (D) between propagules in soil could be calculated:

$$D' = 2.0369 \sqrt[3]{\frac{V_s}{N}} \quad \text{V}$$

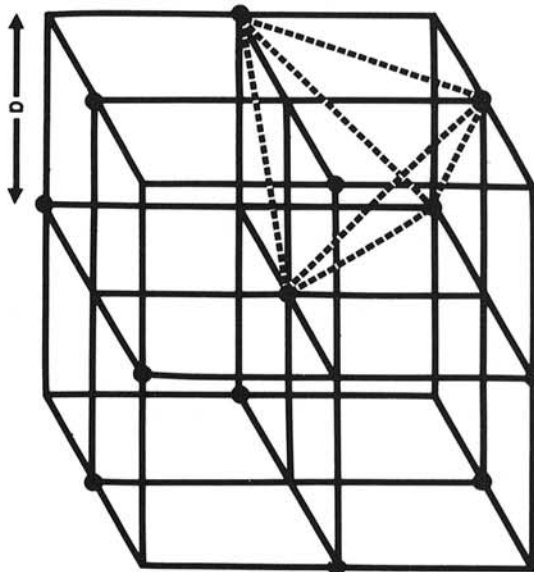


Fig. 1. A cubic close-packed lattice structure with the solid circles representing propagules. Each propagule would be shared by eight tetrahedra and each tetrahedron is inscribed in a small cube with length  $a$ .

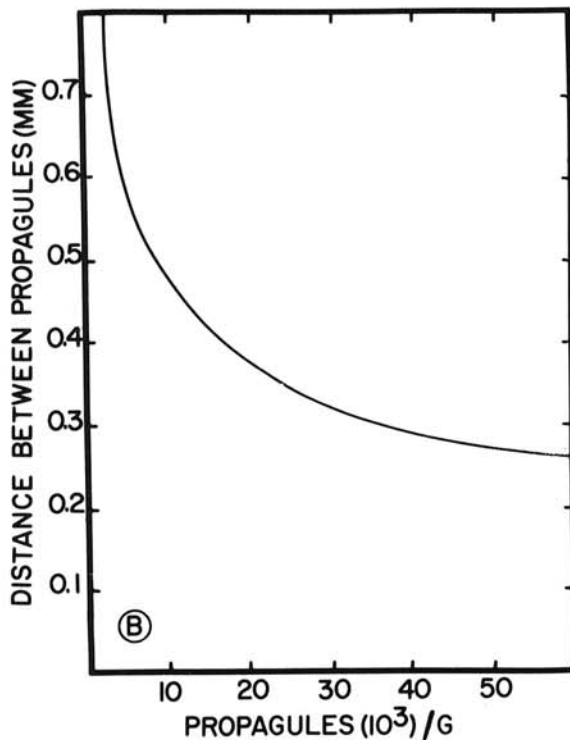
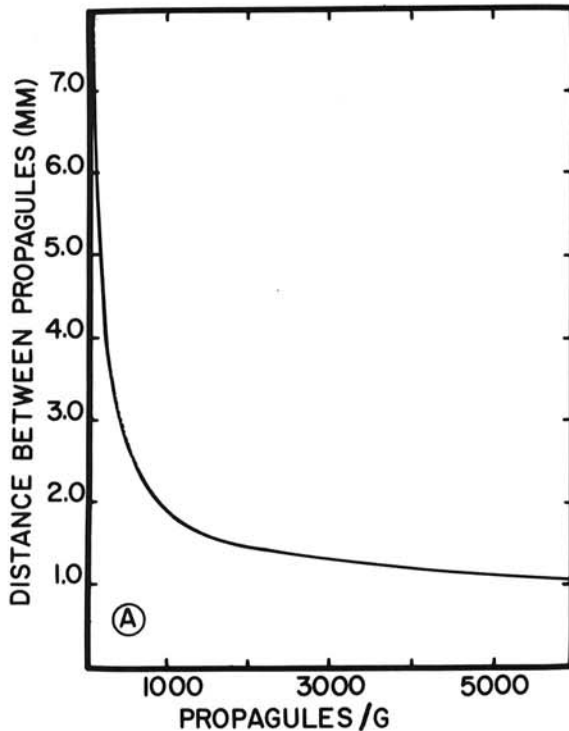


Fig. 2. Relation between inoculum density and distance between propagules in soil. A) Based on formula from Baker and McClintock (4). B) Based on equation IV.

Equation V is the same as the formula:

$$D = \frac{18.32}{I^{1/3}}$$

reported by Baker and McClintock (4), where I represents inoculum density in propagules/g. However, the distances they obtained are not in agreement with our results. In our equation IV, D differs from D' in equation V by a factor equaling the cube root of six:

$$D' = \sqrt[3]{6} D.$$

Using Baker and McClintock's formula or equation V and a soil bulk density of 1.4, the mean distance between propagules would be 1.8 and 1.4 mm for inoculum densities of 1,000 and 2,000 propagules/g of soil, respectively. Because the distances between propagules for these concns appeared to be too great, equation V was thought to be in error. Our equation (IV) which is based on the arrangement of tetrahedra in a cubic close-packed lattice would estimate distances to be almost half as great (1.1 and 0.8 mm) as those reported by Baker and McClintock (4).

Baker and McClintock (4) suggested there is no linear relationship between the concn of propagules and the distance between the propagules in soil. Using equation V and a soil bulk density of 1.4, they postulated that an increase in inoculum density would decrease the distance between propagules most rapidly up to 2,000 to 3,000 propagules/g soil (Fig. 2-A). Using our equation (IV), however, and the same soil bulk density value, the distance between the propagules decreases most rapidly with addition of propagules up to about 10,000 propagules/g of soil (Fig. 2-B). The magnitude of the decrease in distance between propagules was relatively small as the inoculum density increased above 20,000 propagules/g of soil.

Populations of soil-borne pathogens generally range from 250 to 3,000 propagules/g of soil (5, 6, 7, 8, 10) and recently Ashworth et al. (1) reported that levels of *Verticillium albo-atrum* as low as 3.5 microsclerotia/g of soil can produce 100% infection in cotton. If the inoculum density in the soil is within the limits reported (i.e., 250 to 3,000 propagules/g of soil) and if the distance between propagules decreases most rapidly as propagules are added up to about 20,000 propagules/g of soil as we have suggested, then the flattening of disease response curves as the inoculum density increases should not result from the decreasing distance between propagules as proposed by Stienstra and Lacy (9), but is probably due to all available infection sites being occupied at high inoculum densities (11).

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