Relationships of Inoculum Levels of Several Soilborne Species of Phytophthora and Pythium to Infection of Several Hosts

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ABSTRACT

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The relationships of inoculum densities of several species of *Phytophthora* (*P.*) and *Pythium* (*Py.*) to percentages of infection of various hosts were determined by exposing roots to chlamydospores or oospores uniformly mixed with soil or by adding zoospores to flooded soil around plants. Between 15 and 43 oospores per gram of soil were required for 50% infection of peanut, rye, or soybean by *Py. myriotylum*; amaranthus, cotton, or tomato by *Py. aphanidermatum*; or of cabbage by *Py. polymastum*. With host-pathogen combinations of papaya-*P. palmivora* and milkweed vine-*P. citrophthora*, 0.2 to 0.9 chlamydospores per gram of soil were required for 50% infection. Two hundred and fifty, 276, or 281 zoospores of *Py. aphanidermatum*, *P. cryptogea*, *Py. ostracodes* per plant were required for 50% infection of tomato, watercress, or cotton, respectively. Slopes of regression lines of $\log_{10} \log_e [(1/1-x)]$, where x equals the percentage of infected plants, on $\log_{10}$ inoculum density were 0.62 to 0.70 with oospores of *Pythium* spp., 0.69 with zoospores of *Py. aphanidermatum* or *P. cryptogea*, and approached 1.0 with chlamydospores of *Phytophthora* spp. Inoculum density increased in soil infested with chlamydospores, but not in soil infested with zoospores, through the production of secondary propagules in the vicinity of plant roots.

Additional key words; epidemiology, *Amaranthus tricolor, Arachis hypogaea, Brassica oleracea, Carica papaya, Glycine max, Gossypium hirsutum, Lycopersicon esculentum, Morrenia odorata,* and *Nasturtium officinale.*

A great deal of information has accumulated on the roles of various spores of soilborne species of *Phytophthora* and *Pythium* in the diseases of many host plants. The important forms of inoculum in soil in the field are probably chlamydospores, oospores, sporangia, zoospores, or pieces of plant debris containing mycelia or one or more of the above spore forms (3, 7, 10, 11, 12, 13, 15, 21). *Pythium* spp., unlike *Phytophthora* spp., also may survive saprophytically in soil, but their saprophytic activities are greatly restricted because they are not vigorous competitors (7). Little is known about chlamydospores of *Pythium* spp. (6), but chlamydospores of *Phytophthora* spp. and oospores of fungi in both genera serve as the main survival units in soil and are the primary inocula that infect roots in soil (7, 10, 12, 13, 15, 21). Zoospores may be produced from zoospore cysts, microsporangia, or from sporangia formed on mycelia in soil, on roots of infected plants, on infested plant debris, or from oospores or chlamydospores in soil (8, 9, 14, 15, 21). Although zoospores probably function most often as secondary inoculum in the reinfection of infected plants or in the infection of noninfected plants in the vicinity of diseased plants, they also may serve as initial inoculum under flooded conditions when they are carried by moving water to plants in noninfested areas (8, 9, 14).

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The objectives of this study were: (i) to determine the relationships of inoculum densities of chlamydospores, oospores, or zoospores of several species of *Phytophthora* and *Pythium* to the incidences of infection of various hosts, and (ii) to present corrections for previously published incorrect log-log transformations of data as well as for subsequent erroneous conclusions based on the incorrect transformations (13, 15). Other introductory considerations about the importance of various factors or techniques in evaluating the spore forms of these fungi in the inoculum density-disease incidence relation have been commented upon in previous work (13, 14, 15).

MATERIALS AND METHODS

The hyphal tip isolates of the species of *Phytophthora* (*P.*) and *Pythium* (*Py.*) used in this study (Table 1) were maintained on V-8 juice agar and transferred monthly.

Oospores of *Py. aphanidermatum*, *Py. myriotylum*, and *Py. polymastum* were produced, quantified, and incorporated into Arrendondo fine sand with a pH of 6.5 (measurement obtained from a 1:2 suspension of soil in 0.01 M $CaCl_2$) by methods described previously (13). Techniques reported by Ramirez and Mitchell (15) were used to produce, quantify, and incorporate chlamydospores of *P. citrophthora* and *P. palmivora* into soil. The infested-soil-layer technique developed by Mitchell (13), which employs 15-g layers of noninfested plus

infested soil over 100 g of sand in 100-ml polypropylene beakers, was used to allow noninjured roots of the host to grow into soil containing various densities of oospores or chlamydospores; beakers were prepared with germinated seeds and infested soil of the following host-pathogen systems: Three seeds of milkweed vine and *P. citrophthora*; two papaya seeds and *P. palmivora*; three cabbage seeds and *Py. polymastum*; three amaranthus, cotton, or tomato seeds, each with *Py. aphanidermatum*; five rye, one peanut, or two soybean seeds each with *Py. myriotylum*. Fifty to 60 seedlings of each host were exposed to each inoculum level. The plants were watered every 48 hr and all plants were maintained in growth chambers with 12 hr of light (4,000 lx at the level of the plants) for 7 days, except for rye which was grown for 5 days. The chamber was kept at 25 C except for host-pathogen systems involving *Py. aphanidermatum* or *Py. myriotylum* which were held at 30 C.

Zoospore production by *Py. aphanidermatum* and *Py. ostracodes* was initiated by inoculating petri plates containing 15 ml of V-8 juice broth (20% Campbell's V-8 juice plus 4.5 g/liter $CaCO_3$ clarified by centrifugation at 1,275 *g*) with eight 6-mm plugs from the margin of a 1-day-old culture on V-8 juice agar. After incubation in the dark for 24 hr, the medium was drained from the plates and the mycelia were washed three times with 25-ml aliquots of an autoclaved solution of 10^{-4} M 2-(N-morpholino)-ethane-sulfonic acid in deionized water (MES); the solution had been adjusted previously to pH 6.2 with 1 N KOH. After 18-24 hr under light (4,000 lx at the level of the cultures), the cultures were washed three times with MES and suspended in 15 ml of MES. Zoospores were released from sporangia after an additional 2-5 hr of incubation. The method used for zoospore production by *P. cryptogea*, as well as the vortex mixer treatment for the induction of encystment to facilitate counting, and the hemacytometer and micro-drop methods for quantifying zoospores of all of the fungi tested were described previously (14).

Plants were inoculated with zoospores by simulating the exposure of plants to flooding with zoospore-infested water and subsequently draining the water through soil surrounding plant roots. An individual 1-day-old cotton or tomato plant was planted in 50 g of soil packed in a 50-ml beaker which had three small holes in the bottom for water movement. Fifteen beakers of each host were placed in each of two nylon pans for each inoculum level, and maintained at 25 C in growth chambers. Pans containing beakers with 7-day-old seedlings of cotton or tomato or 14-day-old rooted cuttings of watercress (14) were filled with tap water to a level that provided about 1 cm of standing water above the surface of the soil. Various zoospore concentrations of *Py. aphanidermatum*, *Py. ostracodes*, or *P. cryptogea* in MES were added to flooded beakers of tomato, cotton, or watercress, respectively. After 3 hr the water was removed from the pans and the zoospore-infested water was allowed to drain slowly through the soil in each beaker; plants were returned to the growth chambers for 2 days, except for watercress which was grown for 7 days after inoculation.

At the termination of each experiment with oospores, chlamydospores, or zoospores, the stem and roots of each host plant were washed in running tap water, dipped in 70% ethyl alcohol for 15 sec, rinsed three times in sterile deionized water, and dried on paper towels. The plants were plated on a selective medium (P_5V_{300}) (15) which was modified from that of Tsao and Ocaña (19), and the plates were observed for growth of the various species of *Phytophthora* or *Pythium* from roots or stems after 48 hr of incubation in the dark at 28 C.

The methods and media used for evaluating the populations of the various fungi in the infested soil in beakers with or without plants have been described previously (13, 15).

The data presented in this paper are means of experiments repeated four to eight times except with host-pathogen combinations of milkweed vine-*P. citrophthora* and rye-*Py. myriotylum* which have been repeated 12 and 34 times, respectively.

RESULTS

Percentages of infection of all hosts exposed to various types of spores increased with increasing inoculum levels, but the ratio of infection to inoculum decreased as the

TABLE 1. Sources of cultures and spore forms of *Phytophthora* (*P.*) and *Pythium* (*Py.*) spp. used in inoculum density-disease incidence studies

Pathogen	Host source[a]	Spore tested
Py. myriotylum Drechs.	Peanut (*Arachis hypogaea* L.)	Oospore
Py. myriotylum	Soybean [*Glycine max* (L.) Merr.]	Oospore
Py. polymastum Drechs.	Cabbage (*Brassica oleracea* L.)	Oospore
Py. aphanidermatum (Edson) Fitzpatrick	Cotton (*Gossypium hirsutum* L.)	Oospore
Py. aphanidermatum	*Amaranthus* (*Amaranthus tricolor* L.)	Oospore
Py. aphanidermatum	Tomato (*Lycopersicon esculentum* Mill.)	Zoospore
Py. ostracodes Drechs.	Cotton (*Gossypium hirsutum* L.)	Zoospore
P. cryptogea Pethyb. and Laff.	Watercress (*Nasturtium officinale* R. Br.)	Zoospore
P. citrophthora (R.E.Sm. and E.H.Sm.) Leonian	Milkweed vine (*Morrenia odorata* Lindl.)	Chlamydospore
P. palmivora Butler	Papaya (*Carica papaya* L.)	Chlamydospore

[a]All pathogens were tested on the host from which they were isolated except *Py. myriotylum* which was tested on rye (*Secale cereale* L.) as well as on peanut.

inoculum increased (Fig. 1-A, 2-A, 3-A). Slopes determined by linear regression analyses of $\log_{10}$ [$\log_e$ (1/1-x)], where x is the % infection, on $\log_{10}$ inoculum density were 0.62 to 0.70 when various hosts were planted in soil infested with oospores of *Pythium* spp. (Table 2, Fig. 1-B). The inoculum densities required for 50% infection (ID_{50}) of several hosts were interpolated to be 15-24 oospores per gram of soil, or 225-360 oospores per plant, with *Py. aphanidermatum* and *Py. myriotylum*. Approximately twice as many oospores of *Py. polymastum* were required to infect 50% of the cabbage seedlings growing in infested soil.

Levels of infection of tomato with *Py. aphanidermatum* or watercress with *P. cryptogea* were almost identical at zoospore concentrations of 50 to 1,000 zoospores per plant (Fig. 2-A). Slopes in the log-log transformations were 0.69 for both host-pathogen combinations (Fig. 2-B), and less than 300 zoospores per plant were required for 50% infection of cotton, tomato, or watercress (Table 2). Approximately the same percentages of infection occurred at each inoculum level in plants flooded with zoospore infested water for 15 min or 3 hr; 94-100% of the points of infection were on stems when the flooded conditions were maintained for 3 hr, but varying proportions of infection points were on roots or stems after the shorter period of flooding. Although the entire range of zoospore concentrations was not tested on plants in raw soil for comparison to tests in autoclaved soil, almost identical percentages of infection of cotton occurred at several common zoospore concentrations in plants grown in raw and autoclaved soil, respectively.

Only 600 or 900 chlamydospores per kilogram of soil (0.6 or 0.9 chlamydospores per gram of soil) were required for 50% infection of milkweed vine or papaya, respectively, in beakers under growth-chamber conditions (Table 2). When papaya plants were grown in 10-cm-diameter pots containing infested soil for 30 days in the greenhouse (15), the ID_{50} was 170 chlamydospores per kilogram.

The data in Fig. 1 for rye-*Py. myriotylum* and in Fig. 2 for papaya-*P. palmivora* have been published previously (13, 15), but the slopes of log-log transformations were erroneously calculated from linear regression analyses of $\log_e$ (1/1-x) on $\log_{10}$ inoculum density rather than $\log_{10}$[$\log_e$ (1/1-x)] on $\log_{10}$ inoculum density.

When soil from beakers containing oospores was plated routinely on P_5V_{300} at the termination of each experiment, 88-112% of the original inoculum densities of

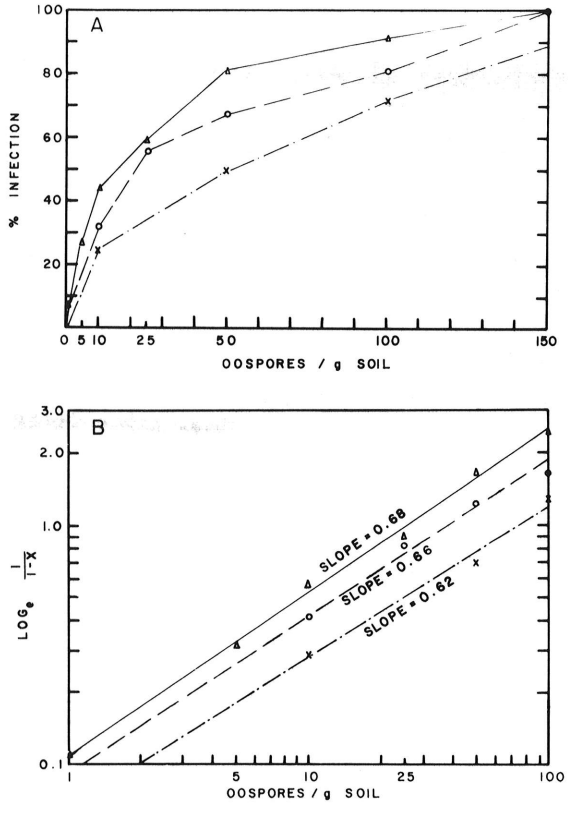

Fig. 1-(A, B). The relationship of percentages of infection of tomato, rye, and cabbage to densities of oospores of *Pythium aphanidermatum* (Δ———Δ), *P. myriotylum* (O- - - - O), and *P. polymastum* (×-·-×) respectively: **A)** percentage infection (arithmetic) and inoculum density (arithmetic), and **B)** percentage infection adjusted for multiple infections (logarithmic) and inoculum density (logarithmic).

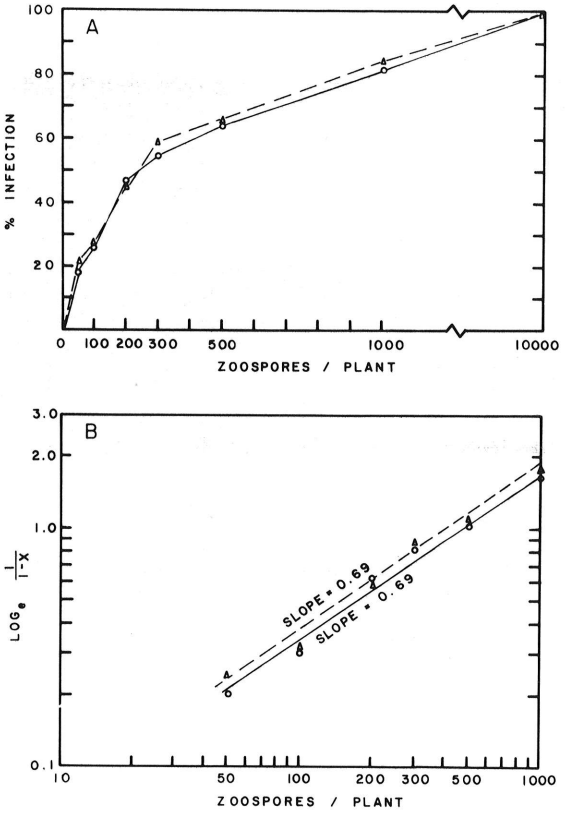

Fig. 2-(A, B). The relationships of percentages of infection of tomato and watercress plants to concentrations of zoospores of *Pythium aphanidermatum* (Δ———Δ) and *Phytophthora cryptogea* (O———O), respectively: **A)** percentage infection (arithmetic) and zoospore concentration (arithmetic), and **B)** percentage infection adjusted for multiple infections (logarithmic) and zoospore concentration (logarithmic).

Py. aphanidermatum and *Py. myriotylum* in beakers with plants and 63-102% of the original inoculum density of soil in beakers without plants were detected. Populations of *P. citrophthora* and *P. palmivora*, however, were two to five times greater than the original inoculum density after 7 days of incubation in beakers with plants. In beakers containing chlamydospore-infested soil without plants, the populations were 65-97% of the original chlamydospore density after 7 days of incubation.

DISCUSSION

The determination of the quantitative relationship of inoculum density of *Phytophthora* or *Pythium* spp. to the incidences of infection and subsequent disease is complicated by many factors that may be important for various periods of time during different stages of pathogen and host development. These factors may include: host tolerance or resistance at different growth stages to infection and/or disease (15); soil moisture, temperature, hydrogen-ion concentration, cation composition, aeration, and biotic components (6, 18, 21); and the inoculum density and form, as well as the virulence, of the pathogen (6, 10, 11, 12, 13, 14, 15, 21). Because of the complexity of factors influencing infection and then disease development, an understanding of the influence of inoculum density on plant infection is important before attempting to elucidate quantitatively the overall interactions of the host, pathogen, and environment. With this consideration in mind and because of the lack of information on inoculum density-disease incidence relationships obtained under controlled conditions which consider both (i) forms and densities of inoculum during the time of exposure of the host to the pathogen, and (ii) specific, quantifiable infection or disease data (eg, percentages of plants infected) rather than indices or subjective disease estimates, this study was limited to generating information specifically on the percentages of infection of several hosts attained at carefully defined levels of the various spore forms.

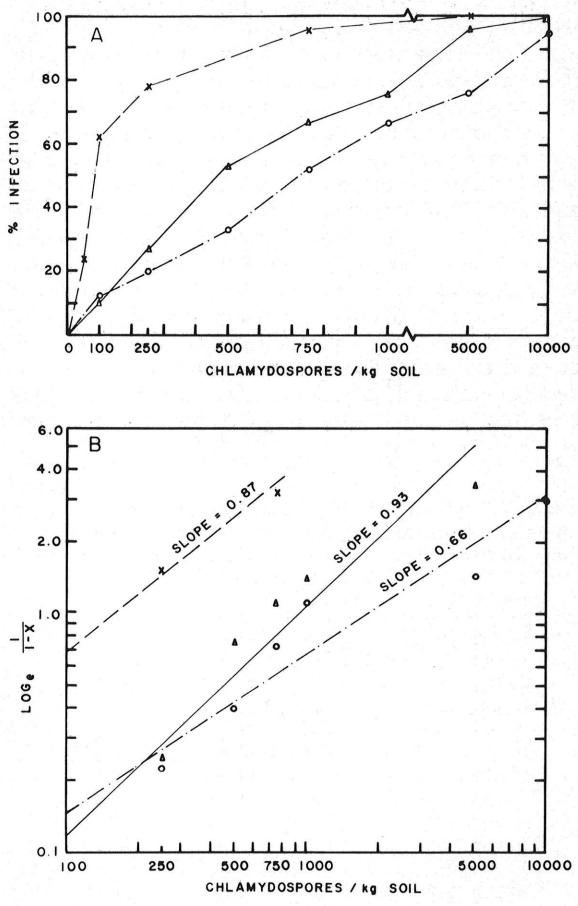

Fig. 3–(A, B). The relationships of percentages of infection to densities of chlamydospores with milkweed vine exposed to *Phytophthora citrophthora* for 7 days (Δ——Δ) and papaya exposed to *P. palmivora* for 7 days (O-·-O) or 30 days (×---×): **A)** percentage infection (arithmetic) and inoculum density (arithmetic); and **B)** percentage infection adjusted for multiple infections (logarithmic) and inoculum density (logarithmic).

After quantification of infection has been ascertained, the influence of inoculum density on the incidence of disease occurring over time can be studied (10, 13, 15). In some host-pathogen combinations tested with suitable inoculum sources under favorable conditions, percentages of infection and subsequent percentages of disease or mortality may be similar. For example, approximately the same levels of rye and tobacco plants that were infected by *Py. myriotylum* or *P. parasitica* var. *nicotianae*, respectively, subsequently died under favorable conditions (10, 13). Conversely, although 50% infection of watercress or cotton plants occurred with 250 to 300 zoospores of *P. cryptogea* or *Py. ostracodes* per plant, respectively, few or none of the plants died even after prolonged periods of exposure under favorable conditions [(14) and D. J. Mitchell, *unpublished*]. Fifty percent of the plants of either host died when the inoculum was increased to 10^4 zoospores per plant. Approximately 10^4 to 10^5 zoospores of *P. parasitica* var. *nicotianae*, *P. palmivora*, or *P citrophthora* per container of tobacco, papaya, or milkweed vine plants, respectively, also were required to approach 50% mortality (5, 11, 12, 14, 15).

Under the conditions employed with the host-pathogen combinations used in this and related studies, ID_{50}'s for several hosts were in the range of 15 to 50 oospores per gram of soil with *Py. aphanidermatum*, *Py. debaryanum*, *Py. myriotylum*, and *Py. polymastum* (13, 16), 250-300 zoospores per plant with *P. cryptogea*, *Py. aphanidermatum*, and *Py. ostracodes*, and 100 to 1,000 chlamydospores per kilogram of soil with *P. citrophthora*, *P. palmivora*, and *P. parasitica* var. *nicotianae* (10, 15). By taking into consideration the amount of soil in the beaker and assuming that plant density did not influence the percentage of infection in short term studies (13), ID_{50}'s can be related to total numbers of spores to which hosts are exposed. Although 645 oospores of *Py. polymastum* per plant were required for 50% infection of cabbage seedlings, similar total numbers of zoospores of *Py. aphanidermatum* (250-300 per plant) or oospores of various host-*Pythium* spp. combinations (225-360 per plant) were required for 50% infection of several hosts. Since (i) initial populations of less than 15 chlamydospores per plant were required for ID_{50}'s with seedlings of several hosts, (ii) the inoculum

density increased sharply in soil with plants, and (iii) an average of approximately 16 zoospores could be expected by the production and germination of one sporangium per chlamydospore, it appears that similar levels of secondary propagules from chlamydospores (ie, approaching ID_{50} values of 250 propagules per plant) as compared to primary levels of oospores of *Pythium* spp. or zoospores of both fungi may be required for infection of individual hosts. Ko and Chan (12) observed that mortality of papaya seedlings inoculated with the same concentrations of three spore forms was greater with sporangia than with chlamydospores which were in turn more effective than zoospores.

While similar levels of infection occurred at selected inoculum densities near the ID_{50} for each of several host-pathogen combinations in raw as compared to autoclaved soil infested with chlamydospores, oospores, or zoospores in this and related studies (10, 13, 15), additional work with low levels of different types of spores in raw soil is needed to ascertain the percentages of infection that occur at very low inoculum densities. Significant percentages of infection occurred in this study at the lowest levels of inoculum tested; ie, 15 oospores of *Pythium* spp., 50 zoospores of *Pythium* or *Phytophthora* spp., or 1.5 chlamydospores of *Phytophthora* spp. per plant.

Nearly 100% infection of various hosts occurred in this study at about 150 oospores/g of soil with *Pythium* spp., 10^4 zoospores/plant with *P. cryptogea* or two *Pythium* spp., or at 5 to 10 chlamydospores/g of soil with *Phytophthora* spp. Similar levels of chlamydospores of *P. cinnamomi* (18) and *P. parasitica* var. *nicotianae* (4) are required for 100% infection of *Persea indica* seedlings or 100% mortality of tobacco plants, respectively, but little is known about the quantitative role of oospores of *Phytophthora* spp. in the inoculum density-disease incidence relationship. Banihashemi and Mitchell (2) reported that 50,000 oospores of *P. cactorum* per g of soil were required for 100% infection of safflower seedlings within 15 days; only 45% of the safflower seedlings were infected at 100 oospores per gram of soil after 3 wk. Baumer and Erwin (University of California, Riverside, *personal communication*), on the other hand, found that enzyme-treated oospores of *P. megasperma* behaved similarly to chlamydospores of other *Phytophthora* spp. with an ID_{50} of about 1 oospore/g of soil when alfalfa seedlings were exposed to oospores in infested soil in the greenhouse.

The results of the experiments with oospores and zoospores basically conform to the predictions of Baker (1) of slopes of 0.67 for the log-log transformations of both: (i) model systems involving nonmotile inoculum (oospores) invaded by a motile infection court if the inoculum density-disease incidence relationships are limited by a rhizoplane effect, and (ii) for model systems involving motile inoculum (zoospores) and motile infection courts. The slopes of linear regression equations (Table 2) were between 0.66 and 0.70 for seven of the nine host-pathogen combinations used for evaluating the role of oospores or zoospores in infection. Stasz and Harman (17) obtained a similar slope of 0.70 in the log-log transformation of the disease rating of susceptible peas on the density of oospores of *Pythium ultimum* in soil. Baker (1) also predicted a slope of 1.0 for nonmotile propagules (chlamydospores) that produce motile propagules under a rhizosphere influence based on the consideration that for mathematical purposes the moving propagule acts as a germination hypha. Slopes of log-log transformations with *P. palmivora* on papaya after 30 days in infested soil and with *P. citrophthora* on milkweed vine approached 1.0 in this study, and Kannwischer and Mitchell (*unpublished*) observed a slope of 0.98 with *P. parasitica* var. *nicotianae* on 50-day-old tobacco plants. The lesser slope of 0.66 attained with *P. palmivora* and 7-day-old papaya seedlings as compared to *P. citrophthora* and 8-day-old milkweed vine seedlings reflects lower percentages of infection at higher inoculum levels which probably resulted from the availability of fewer

TABLE 2. Numbers of oospores, zoospores, or chlamydospores of several *Pythium* (*Py.*) and *Phytophthora* (*P.*) species required for 50% infection (ID_{50}) of various hosts, and linear regression equations of the incidence of infection on inoculum density[a]

Pathogen	Inoculum density range[b]	Host	ID_{50}	Linear regression equation	r[c]
Py. myriotylum	1–100 opg	Rye	22 opg	$Y = -1.06 + .66x$	.998***
Py. myriotylum	10–100 opg	Peanut	17 opg	$Y = -1.01 + .69x$	.964*
Py. myriotylum	10–100 opg	Soybean	16 opg	$Y = -.92 + .63x$	.988*
Py. polymastum	1–100 opg	Cabbage	43 opg	$Y = -1.17 + .62x$	.991**
Py. aphanidermatum	1–100 opg	Cotton	24 opg	$Y = -1.13 + .70x$	.982*
Py. aphanidermatum	1–100 opg	Amaranthus	16 opg	$Y = -1.00 + .69x$	.979***
Py. aphanidermatum	1–100 opg	Tomato	15 opg	$Y = -.95 + .68x$	.996***
Py. aphanidermatum	50–1,000 zpp	Tomato	250 zpp	$Y = -1.81 + .69x$	.998***
Py. ostracodes	200–1,000 zpp	Cotton	281 zpp	N.C.[d]	N.C.
P. cryptogea	50–1,000 zpp	Watercress	276 zpp	$Y = -1.84 + .69x$	.989***
P. citrophthora	100–5,000 cpk	Milkweed vine	600 cpk	$Y = -4.325 + .93x$	.971**
P. palmivora	100–5,000 cpk	Papaya	900 cpk	$Y = -2.15 + .66x$	.989***
P. palmivora (pots)[e]	50–750 cpk	Papaya	170 cpk	$Y = -1.92 + .87x$	.966*

[a]Linear regression equations were calculated from $\log_{10}$ [$\log_e$ (1/1-x)] (where x = % plant infection) on $\log_{10}$ inoculum density.
[b]Abbreviations: opg = oospores per gram of soil; zpp = zoospores per plant; and cpk = chlamydospores per kilogram of soil.
[c]The linear correlation coefficient (r) was significant at $P = 0.05$ (*), $P = 0.01$ (**), or $P = 0.001$ (***).
[d]Abbreviation: N.C. = not calculated because an insufficient range of zoospore levels was evaluated.
[e]Inoculated papaya plants were maintained in soil in 10-cm-diameter pots in a greenhouse for 75 days compared to short incubation periods of 5-7 days in growth chambers for the other host-pathogen combinations.

susceptible sites on the slower growing papaya roots than on milkweed vine roots during the short incubation period.

Van der Plank (20) interprets the type of relationship observed in this study, ie, infection increases as inoculum increases but the ratio of infection to inoculum decreases as the amount of inoculum increases, to represent infection without interaction between spores but with competition for susceptible sites on the host. On this basis, slopes of less than 1.0 in all of the host-pathogen combinations resulted from competition for susceptible sites at higher inoculum levels or from other factors that reduced the survival or effectiveness of the various spore forms in infection.

Although van der Plank (20) views the plotting of log-log transformations of arithmetic data with disdain, the presentation of log-log plots in combination with the curvilinear arithmetic plots provides an undistorted presentation of the inoculum density-disease incidence relationship as well as a basis, within limits, for characterizing various host-pathogen combinations with respect to interpolated ID_{50} and slope. Eventually it should be possible to characterize quantitatively diseases caused by soilborne pathogens under various conditions at defined inoculum levels with apparent infection rates and yield losses as well as with percentages of infection and disease. Kannwischer and Mitchell (10), for example, determined that black shank of tobacco progressed at an apparent infection rate of 0.08 to 0.11 per unit per day under greenhouse or field conditions; that the rate was altered similarly in the greenhouse and in the field by host resistance or chemical control; that yield was directly related to the influence of resistance and chemical control on disease development; that the inoculum density-incidence of infection relationship was characterized by a curvilinear arithmetic plot and a linear log-log transformation with a slope of 0.98 and an interpolated ID_{50} of about 0.2 chlamydospores per gram of soil; and that populations of 0.25 to 0.75 propagules of *P. parasitica* var. *nicotianae* per gram of soil at planting time in three different fields resulted in about 60 and 100% mortality of moderately resistant and susceptible tobacco plants, respectively. After this type of information has been obtained, it will be possible to evaluate more accurately under controlled conditions that closely simulate field conditions the influence of various factors such as biological control agents, fungicides, host resistance or tolerance, and environmental conditions on the epidemiology of soilborne diseases.

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