

# Source of Inoculum and Development of Bean Web Blight in Costa Rica

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## ABSTRACT

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Epidemiology of bean (*Phaseolus vulgaris*) web blight (BWB) caused by *Thanatephorus cucumeris* (teleomorph of *Rhizoctonia solani*) was studied in a field with a history of severe incidence of the disease. Sclerotia and mycelium of *T. cucumeris*, either free in soil or in the form of colonized debris, were found to be the main sources of inoculum. Inoculation of bean plants occurs mainly by splashing of raindrops containing *T. cucumeris*-infested soil caused typical BWB symptoms when sprayed onto greenhouse-grown plants. Greenhouse-grown plants incubated in the experimental field on elevated platforms where rain-splashed soil could not reach the plants did not develop BWB symptoms, whereas plants in the same field showed 100% infection. Initial BWB symptoms were observed on the primary leaves 14 days after planting. Trifoliolate leaves were similarly infected by rain-splashed inoculum but more often by advancing hyphae from infected tissues that were also observed causing infection of adjacent plants. A large number of small sclerotia (0.5–1 mm diam.) were produced within 3 days of contact with plants on intact and detached infected tissues. Hymenial layers of *T. cucumeris* were first observed on the lower stem tissues of 2% of the plants about 28 days after planting. Lesions on leaves that are typical of basidiospore infection remained restricted (2–5 mm) and were observed only in plantings made during the second growing season (September to December). Progress of BWB was very rapid because of the high inoculum level and conducive weather conditions. The infection rate varied between 0.42–0.78 and 0.51–0.94 per unit per week for the cultivars Porrillo 70 (BWB-tolerant) and Mexico 27 (BWB-susceptible), respectively. Regression analysis of the data on BWB development better fitted the "compound interest disease" model sensu Vanderplank.

*Thanatephorus cucumeris* (Frank) Donk (teleomorph of *Rhizoctonia solani* Kühn) is a soil-inhabiting fungus known mainly as the incitant of damping-off and root rot diseases of many plants in the temperate regions of the world (2,19). In the humid tropics, however, this pathogen often causes severe aerial blight diseases on a variety of crops such as bean (*Phaseolus vulgaris* L.), tobacco (*Nicotiana tabacum* L.), wheat (*Triticum aestivum* L.), cotton (*Gossypium hirsutum* L.), fig (*Ficus carica* L.), rubber (*Hevea brasiliensis* Muell.-Arg.), and many other crops and weeds (8,10,16,17,20,22,24,26). Hyphae, sclerotia, and/or basidiospores have been reported as the possible primary inoculum for these diseases (3). Nevertheless, only limited data are available on the relative importance among infective propagules of *T. cucumeris* and their effect on incidence and spread of aerial blight diseases under field conditions.

Aerial blight infections caused by *T. cucumeris* are most severe under high

temperature and high relative humidity (RH) conditions (1,3,7,10,24,26). The reported optimum temperature for initial infection and further disease development is 25–30°C (1,8,26). Free moisture on the foliage of affected plants was necessary for disease incidence and development. Progress of the disease was arrested when the foliage of infected plants became dry (1).

Dry beans are an important energy component and the major protein source of the human diet in Latin America and other parts of the world (6). Bean web blight (BWB) caused by *T. cucumeris* is considered an important limiting factor in bean production in the humid tropics (24,26). The disease has been reported from every country in tropical America and is of economic importance in El Salvador, Costa Rica, Nicaragua, and Panamá (10). Seed infection with *T. cucumeris* has been reported on bean from Costa Rica at a rate of 1.5% (5). The latter suggests that seeds might be an important source of primary inoculum. Echanti (7) reported that basidiospores are the major form of inoculum causing BWB in the lowland regions of Costa Rica. He suggested that the rapid spread of BWB under the warm humid conditions might be explained by the efficient production and dissemination of basidiospores. In contrast, Weber (24) reported that sclerotia and infected debris

served as inoculum sources for BWB in Florida.

It has been proposed recently (10) that an effective control of BWB can be achieved only through development of integrated control measures. Detailed information on the epidemiology of BWB is generally lacking. Thus, the objectives of this study were to determine 1) the form and source of primary inoculum of *T. cucumeris*, 2) the time and site of initial infection of beans by *T. cucumeris*, and 3) the progress of BWB development under field conditions in Costa Rica.

## MATERIALS AND METHODS

Plots for this study were established throughout the 1980 growing season in a field near Esparza, Puntarenas, Costa Rica, at an altitude of about 208 m. The mean annual temperature at this location is 26.5°C, with temperatures oscillating between 20 and 30°C. This region has a mean annual precipitation of 2,320 mm and the annual mean RH is 79% (12). The rainy season extends from mid-May to late November (2,221 mm precipitation). The region has been characterized as a tropical wet forest (8).

Inoculum of *T. cucumeris* in this field was increased by planting it to beans for 2 yr before establishing the experimental plots. The uniform distribution of inoculum in the field was confirmed by the high incidence and even distribution of *T. cucumeris*-infected plants in the 1979 bean plantings.

The indeterminate dry bean cultivars, Porrillo 70 and Mexico 27, were planted in four-row plots 4 m long and 0.6 m apart. Within-row spacing among seeds was 7 cm. Both Porrillo 70 and Mexico 27 are small black-seeded cultivars previously characterized as tolerant and susceptible, respectively, to *T. cucumeris* (6). Data were collected at weekly intervals from the 80 central plants of the two central rows. At each planting date, the two cultivars were planted according to a completely randomized block design replicated four times. Five plantings were established on 20 May, 3 June, 17 June, 20 September, and 6 October. Generally, farmers in this region plant beans toward the end of the rainy season during September and October. Earlier plantings were avoided because of the frequent rainfall and high RH throughout the season that make harvesting difficult and favor incidence and spread of foliar diseases including BWB (11).

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Before planting, the field was plowed once and disked twice. Planting furrows were made by tractor-mounted implements. Fertilizers (275 kg/ha, 10-30-10) and the insecticide carbofuran (Furadan, 25 kg 10% anules per hectare) for rootworm control were applied to the bottom of the furrow and covered lightly with soil. Bean seeds were then manually placed in the furrow and covered with soil. The following day, plots were treated with a mixture of the herbicides dinoseb (Herbon, 3 kg a.i./ha), and alachlor (Lazo, 1 kg a.i./ha).

The times and sites of initial infections were determined by weekly observations made on aboveground parts (stems, petioles, and primary and trifoliolate leaves) of the marked plants. Progress of BWB was determined by recording the number of infected plants and severity of infection on the marked plants at weekly intervals. Severity ratings were made on a scale of 0-5. A rating of 0 refers to healthy plants, whereas a rating of 1, 2, 3, 4, and 5 refers to 20, 40, 60, 80, and 100% of bean tissues affected, respectively. Possible secondary disease cycles were determined by taking weekly notes on the spread of the fungus to adjacent plants within the plot area and also to other plants in and outside the plot area. Damping-off caused by *T. cucumeris* was also observed and recorded.

The form and sources of primary and secondary inocula were identified from soil samples collected in the plot areas by three different methods. The first method involved sample assay following a screening procedure described by Weinhold (25). Wash materials (mostly organic debris) retained on the screen were stained with trypan blue (13) and observed directly under the microscope for the determination of fungal structures. The second method consisted of plating the washed materials onto *R. solani*-selective medium (14). The plates were incubated at 25 C for 24-48 hr and examined under the microscope for *R. solani* hyphae and other structures. The third method dealt with determining the pathogenicity of portions of the washed materials retained on the screen to 20-day-old bean seedlings (cultivar Mexico 27) under greenhouse conditions (20-24 C and 60-80% RH). Five replicates, each consisting of three plants, were used per sample.

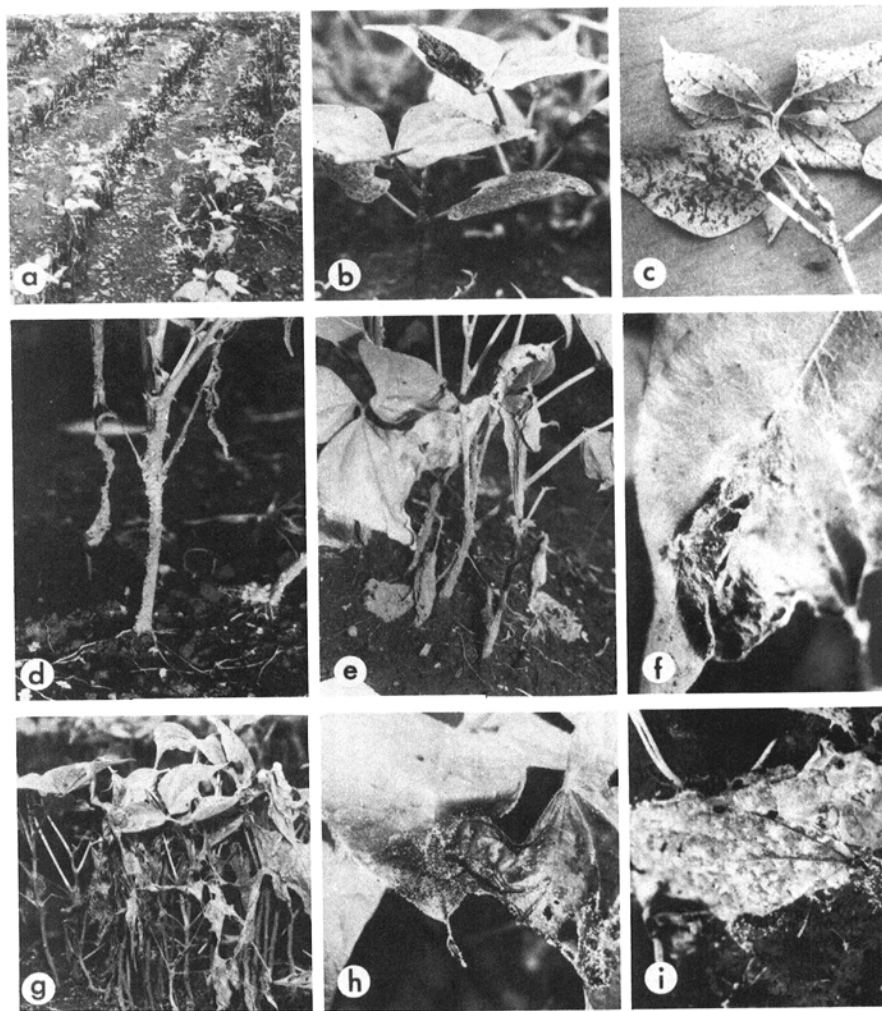
Similarly, the number of sclerotia and/or mycelial fragments of *T. cucumeris* in samples from rain-splashed soil onto bean tissues was also determined. Bean seedlings were collected randomly from the plot areas and transported in plastic bags to the laboratory. Rain-splashed soil on the hypocotyl and leaf tissues was washed off with distilled water.

Infection potential by biological trapping of *T. cucumeris* basidiospores produced under field conditions was

determined by exposing greenhouse-grown bean plants for 1 wk in a field where the teleomorph was observed. Pots were placed on an elevated bench 50 cm above the soil surface to avoid infection by rain splashing of infested soil. The plants were then returned to the greenhouse, enclosed in a plastic bag to provide high RH, and incubated for an additional 12 days. The number of BWB lesions developed that were characteristic of basidiospore infections were recorded. Also, basidiospore suspensions were obtained by cementing sections showing the hymenial layer to the underside of 9-cm petri dish covers to allow basidiospore discharge into distilled water. Plates were incubated overnight at 25 C, then examined for basidiospore discharge. Plates showing numerous basidiospores were consolidated and the concentration of the basidiospores in the resultant suspension was adjusted to about 5,000/ml. Trifoliolate leaves of 15-day-old seedlings were inoculated with the

basidiospore suspension, covered with a plastic bag for 1 wk, maintained in a greenhouse, and watered daily. Untreated check plants (24 plants) were treated similarly but sprayed only with distilled water. The number of BWB lesions was recorded 12 days after inoculations.

Soil populations of *T. cucumeris* were determined with the selective medium of Ko and Hora (14). Composite soil samples were collected monthly at depths of 0-5 and 5-10 cm, following a zigzag pattern on marked sites. Soil was transported to the laboratory in plastic bags, stored at 4 C, and assayed for *T. cucumeris* within 1 wk. Ten grams of soil was moistened with distilled water, compacted with a spatula, and distributed evenly in 15 plates with 10 clumps (about 0.7 g soil) per plate of selective medium. The perimeters of the soil clumps were examined under  $\times 100$  magnification after 24 and 48 hr of incubation at 25 C. *T. cucumeris* was identified by the distinctive morphological characteristics of its



**Fig. 1.** Symptoms and signs of bean web blight (BWB) caused by *Thanatephorus cucumeris*. (A) Severe incidence of BWB in a bean field near Esparza, Costa Rica, 5 wk after planting. (B and C) Rain-splashed soil on the upper and lower surfaces, respectively, of bean seedlings 10 days after planting. (D) Close-up of a bean plant infected by *T. cucumeris* showing rain-splashed soil on the stem and also on the shriveled and necrotic primary leaves. (E) Advanced infection of the lower parts of bean plants affected by BWB. (F) Mycelium of *T. cucumeris* growing from infected to healthy bean leaf tissues. (G) Upward progress of BWB on severely infected bean plants. (H) Small sclerotia produced abundantly on infected bean tissue. (I) Sclerotia of *T. cucumeris* growing on fallen bean leaves and adjacent soil.

mycelium (4). The number of clumps with emerging *T. cucumeris* hyphae was then determined.

## RESULTS

### Form and source of primary inoculum.

Sclerotia and hyphae of *T. cucumeris* were recovered from rain-splashed soil (Fig. 1B-D) on bean tissues. The soil was collected by washing 7-day-old seedlings with distilled water. The seedlings were collected randomly from the plot area and did not show any apparent symptom or sign of BWB. A mean of seven sclerotia and four pieces of organic debris containing mycelium of *T. cucumeris* were found per seedling. Rain-splashed soil obtained from 14-day-old bean seedlings contained a mean of 33 propagules of *T. cucumeris* per seedling. Typical BWB symptoms developed under greenhouse conditions on 66 and 100% of 20-day-old bean seedlings inoculated with a rain-splashed soil suspension or only the sclerotia recovered from such a suspension, respectively. *T. cucumeris* was reisolated from the infected plants, and the isolates obtained were identical in hyphal morphology and cultural characteristics to the isolates originally recovered from BWB lesions in the field.

During the first growing season of

1980, the hymenial layers of *T. cucumeris* were initially observed on the lower stem tissues of 2% of the bean plants 35 days after planting (Fig. 2D,E). The hymenial layers were evident on 22% of the plants 28 days after planting during the second growing season. Only 0 and 9% of the plants, however, showed symptoms typical of basidiospore infections (Fig. 2A-C) during the first and second growing season, respectively. Lesions caused by basidiospores were also observed on three weed species (*Sida rhombifolia* L., *Rottboellia exaltata* L. f., and *Cynodon dactylon* L.) growing within and adjacent to the bean plots. Isolations made from infected bean and weed leaves that showed typical lesions caused by basidiospores revealed isolates with similar cultural characteristics and hyphal morphology to those of *T. cucumeris* (4). In comparison, 100% of the bean plants growing in other plots in the same field were infected as a result of rain-splashed inoculum (Fig. 1A).

Greenhouse-grown bean plants placed on elevated benches in the field for 1-wk periods throughout the first growing season failed to develop any lesions typical of basidiospore infection. In addition, plants incubated in the experimental field during the first 4 wk

after planting in the second growing season also failed to show any basidiospore infection; however, 26, 13, and 20% of greenhouse-grown plants developed typical lesions incited by basidiospores when incubated in the field on elevated benches 5, 6, and 7 wk after planting, respectively. Basidiospore lesions that developed on greenhouse-grown plants were circular brown necrotic spots (2-4 mm diam.) and remained restricted (Fig. 2A-C).

### Time and site of initial infection of beans by *T. cucumeris*.

Initial BWB symptoms were always observed first on the primary leaves of bean seedlings about 14 days after planting. Plants of the BWB-susceptible (Mexico 27) and BWB-tolerant (Porrillo 70) cultivars showed 25 and 15% infected primary leaves, respectively, 2 wk after planting. Three weeks after planting, 100% of the plants of both cultivars had infected primary leaves, whereas only 34 and 30% of the plants of the BWB-susceptible and BWB-tolerant cultivars, respectively, had infected trifoliolate leaves. All plants of both cultivars showed infected primary and trifoliolate leaves 28 days after planting. Lesions caused by *T. cucumeris* were also observed on stem and petiole tissues after rapid destruction of leaves by the fungus. Bean seedlings infected within the first 14 days after planting were generally completely destroyed by the third week after planting. Under favorable environmental conditions, 100% of the plants of BWB-susceptible and BWB-tolerant cultivars were destroyed by 6-7 and 7-9 wk after planting, respectively (Fig. 1A).

Several lesions of *T. cucumeris* were initially observed per primary leaf. Lesions first appeared as small necrotic spots (5-10 mm diam.) with brown centers and olive-green margins. The lesions advanced rapidly under conditions conducive to disease development, but lesions appeared somewhat zonate and their development was greatly decreased during dry weather periods. Often, lesions on the same leaf blade coalesced and usually the entire primary leaf was destroyed within 2-3 days of infection (Fig. 1D).

Mycelium of *T. cucumeris* was observed growing on soil splashed onto bean leaves before the first appearance of lesions. These observations were made in the field 9-11 days after planting, using a hand lens (X10), and later were confirmed in the laboratory by microscopic examination and isolation on the selective medium. The mycelium growing on the rain-splashed soil advanced to adjacent healthy bean tissues of the primary leaves and thus caused the initial infections. Small round sclerotia (1 mm or less in diameter) were produced on the soil that had been splashed onto plant parts and also on leaf, stem, and petiole tissues about 12 days after planting (Fig.

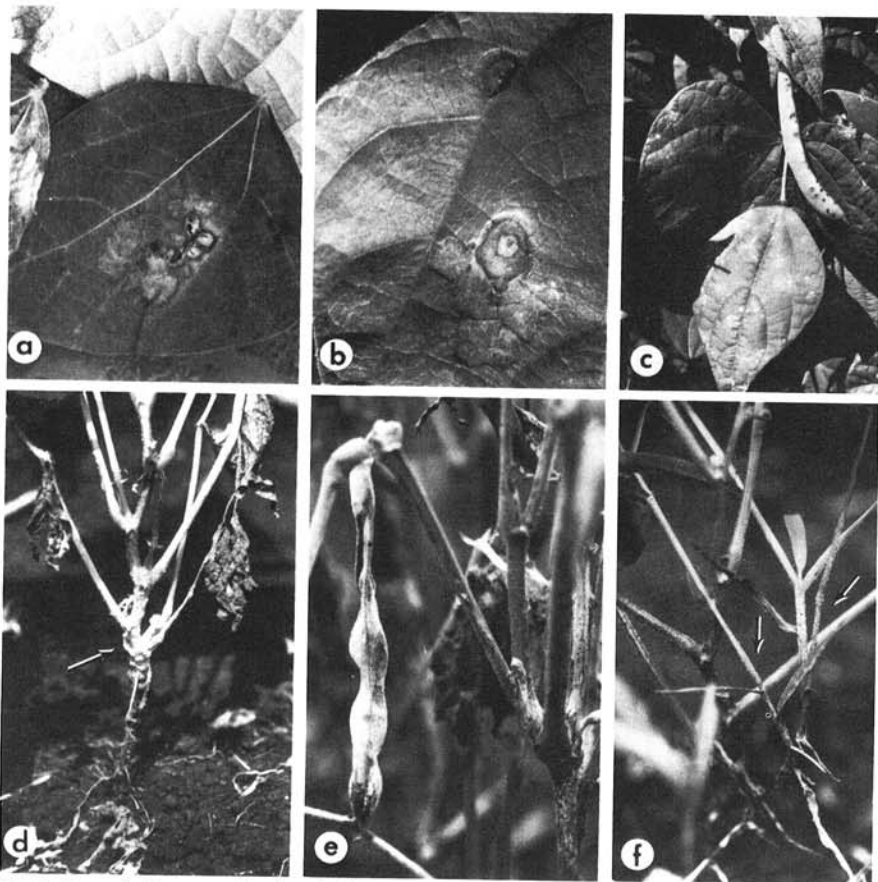


Fig. 2. Hymenial layers and lesions incited by basidiospores of *Thanatephorus cucumeris* on bean and grass tissues. (A and B) Irregular and circular lesions, respectively, caused by basidiospores infection on bean leaf tissues. (C) Lesions caused by basidiospores on bean leaf and pod tissues. (D and E) Hymenial layers of *T. cucumeris* on bean stem and petioles (arrow) and pod tissues, respectively. (F) Infection by *T. cucumeris* of leaf and stem tissues (arrows) of a common weed, *Cynodon dactylon*, in bean fields.

1D). Initially, these sclerotia were white but later turned dark brown.

Four to five days after lesions first appeared on the primary leaves, the lower leaves of bean seedlings in almost the entire plot were either completely necrotic or had fallen, especially the primary leaves (Fig. 1D,E,G). In contrast, the upper leaves of the plants were almost completely free of *T. cucumeris* lesions at that time. The necrotic tissues that remained attached to the plant were held together by the mycelium of the fungus (Fig. 1H). Hyphal strands growing in a fan-shaped fashion (Fig. 1F) were often observed advancing from infected to healthy tissues under conditions conducive to disease development. Newly infected trifoliolate leaves were usually destroyed within 4–5 days. Although trifoliolate leaves were generally infected by hyphal strands growing from infected primary leaves, they were also infected directly by inoculum in rain-splashed soil.

Infected leaves were rapidly covered by small sclerotia of the fungus (Fig. 1H). In addition, new small sclerotia were produced on the fallen leaves and on the soil surface under and around the leaves within 24 hr (Fig. 1I). Direct infection of stem tissues, especially near the soil line, was not observed. In addition, no hyphal strands were observed growing from the soil to the stem or advancing from the stem tissues to adjacent healthy tissues.

Lesions incited by basidiospores were 2–4 mm in diameter, circular, and appeared as brown necrotic spots with light brown centers (Fig. 2A–C). Usually, the lesions remained restricted or advanced only a few millimeters. The tissues surrounding these lesions appeared olive-green. Occasionally, the necrotic tissues in the centers of the lesions fell out, leaving a shothole appearance. In this field and throughout the study, lesions caused by basidiospores did not generally enlarge appreciably or coalesce to form larger lesions. Lesions incited by basidiospores did not cause defoliation, and infected plants reached maturity about 70 days after planting.

**Progress of infection.** After the initial infection of the primary leaves, disease development progressed rapidly through the infection of new tissues either by the growth of hyphae of *T. cucumeris* from infected tissues or by additional inoculation with rain-splashed infested soil. After the trifoliolate leaves were infected, plant-to-plant infection occurred through direct hyphal growth from previously infected leaves (Fig. 1E–H). Because this type of infection was happening at the same time as the infections originating from rain-splashed soil, complete defoliation of plants of the BWB-susceptible cultivar occurred at about blossom time, whereas plants of the BWB-tolerant cultivar were defoliated about 1–2 wk later.

Lesions of *T. cucumeris* on stem and petiole tissues generally appeared after infected plants had lost many of their leaves or after they had been completely defoliated. Lesions on stem and petiole tissues were linear to oval and reddish brown. Sclerotia were produced abundantly on infected stem and petiole tissues (Fig. 2F). Occasionally, these lesions caused complete girdling of stem and petiole tissues, which often fell prematurely to the ground.

The infection rate ( $r$ ), the rate disease increase per unit time (21), varied between 0.42 and 0.78 in Porrillo 70 and between 0.51 and 0.94 in Mexico 27 per unit per week (Fig. 3A–E). The  $r$  value was always higher for the BWB-susceptible cultivar (Mexico 27) and there were significant ( $P = 0.05$ ) differences in  $r$  values in three of the five plantings made in 1980 during the early part of the growing season (Fig. 3A,B,D). By the end of the growing season, however, BWB development became so severe that it caused complete defoliation in both cultivars. Nevertheless, plants of the cultivar Mexico 27 were defoliated 1–2 wk earlier than those of Porrillo 70.

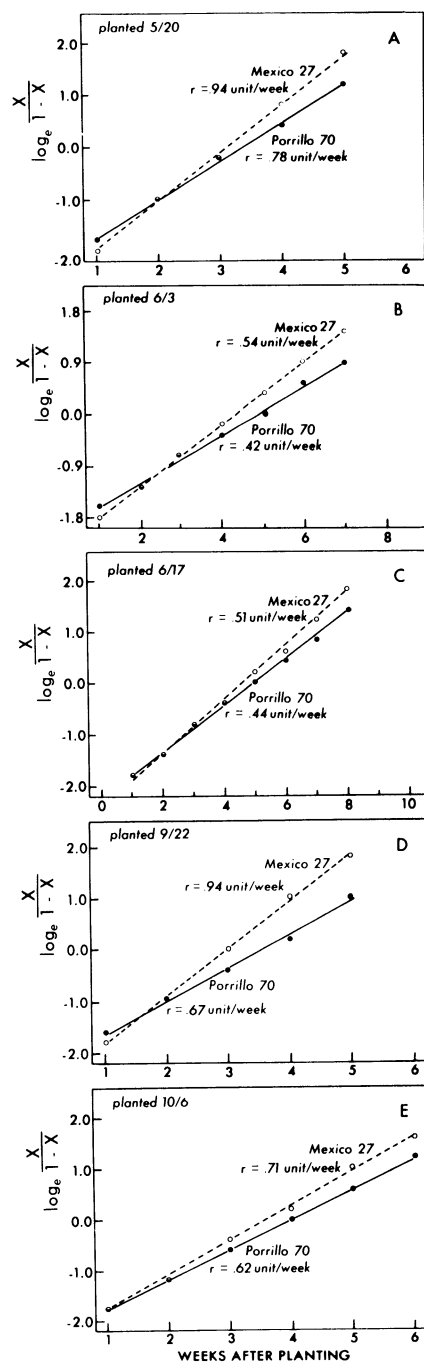
The higher  $r$  values for both cultivars were associated with periods of heavy rainfall. In the first (20 May), fourth (22 September), and fifth (6 October) bean plantings, the  $r$  values were 0.94, 0.94, and 0.71, respectively, for Mexico 27 and 0.78, 0.65, and 0.62, respectively, for Porrillo 70. These plantings corresponded with periods of high rainfall because these plots received a total of 690, 695, and 621 mm precipitation, respectively, during the first month after planting.

**Inoculum density.** The soil population of *T. cucumeris* was determined throughout 1980 in the experimental field. Inoculum densities in the fractions 0–5 and 5–10 cm deep varied between four to 82 and two to six propagules per 10 g of soil, respectively. Soil population density was lowest during March and April, reached a maximum population in October, and then steadily declined. Highest populations were detected during the months with the highest rainfall, when the incidence and severity of BWB was also high. Isolates of *T. cucumeris* recovered from the soil samples were similar in cultural characteristics and hyphal morphology to the isolates recovered from BWB lesions and were pathogenic to bean seedlings inoculated under greenhouse conditions.

## DISCUSSION

In this study, sclerotia and mycelium of *T. cucumeris* in rain-splashed soil were found to be the most important structures of the fungus serving as the primary source of inoculum for BWB in Costa Rica. These results are in agreement with those of Weber (24), who also reported that sclerotia were produced abundantly

in bean fields in Florida and served as an inoculum source for infection of bean. He also suggested that the lightweight sclerotia were airborne and disseminated mainly by wind and rain. Soilborne sclerotia and mycelium of *T. cucumeris* have also been reported as an important



**Fig. 3.** Progress of disease by weeks and infection rate ( $r$ ) sensu Vanderplank (21) of bean web blight (BWB) caused by *Thanatephorus cucumeris* on the bean cultivars Mexico 27 (BWB-susceptible) and Porrillo 70 (BWB-tolerant) in five plantings (A–E) made in 1980. Each data point represents the mean of four replicates and the infection rate  $r$  values were calculated by the following formula:  $r = [1/t_2 - t_1] \times [\log_e(x_2/1-x_2) - \log_e(x_1/1-x_1)]$ , where  $t_1$  and  $t_2$  = dates in which proportions of disease were estimated,  $x_1$  = proportion of disease in date  $t_1$ , and  $x_2$  = proportion of disease in date  $t_2$ .



**Table 1.** Regression analysis of progress of bean web blight (BWB) epidemics on the cultivars Porrillo 70 (BWB-tolerant) and Mexico 27 (BWB-susceptible) using both simple- and compound-interest disease equations

Planting dates	Porrillo 70		Mexico 27	
	SID <sup>a</sup>	CID <sup>a</sup>	SID	CID
20 May	0.693 <sup>b</sup>	0.945	0.750	0.969
3 June	0.516	0.833	0.617	0.883
17 June	0.663	0.918	0.715	0.940
22 September	0.842	0.895	0.778	0.960
6 October	0.589	0.907	0.707	0.943

<sup>a</sup>SID and CID refer to the simple- and compound-interest disease, respectively, sensu Vanderplank (21). Infection rates of SID and CID were calculated by using  $\log_e \frac{x}{1-x}$  and  $\log_e \frac{x}{1-x}$  respectively, where  $x$  = amount of disease expressed as a proportion.

<sup>b</sup>Refers to the correlation coefficients, which were all significant at  $P = 0.05$  (19–35 degrees of freedom).

source of inoculum on cowpeas (*Vigna sinensis* (Torner) Savi) (17,18), soybeans (*Glycine max* L.) (16), tobacco, yam (*Dioscorea alata* L.), and sweet alyssum (*Labularia maritima* (L.) Desv.) (3).

It was found recently (9) that mulching was very effective in controlling BWB of beans in Costa Rica. Mulching with rice (*Oryza sativa* L.) husks or through the local production practice “frijol tapado” (seeds were broadcast in vegetation that was later cut and left as a mulch) were equally effective. Mulching greatly reduced rain splashing of infested soil onto bean tissues. The latter is further evidence substantiating the major role of sclerotia and infected debris in soil in the epidemic development of BWB. Furthermore, BWB symptoms on pole beans are generally observed on the lower parts of the plant and rarely on the upper parts (26). Similar observations were reported concerning infection of China aster (*Callistephus chinensis* L.) (3) by *T. cucumeris*. These observations also add to the evidence pertaining to the soilborne nature of *T. cucumeris* inoculum.

Echandi (7) reported on the production of basidiospores of *T. cucumeris* in Costa Rica and described the BWB symptoms produced by basidiospore infections. He reported that the lesions were small and numerous and eventually coalesced to cover the entire leaf blade. Lesions caused by basidiospores of *T. cucumeris* were also observed on beans during this investigation, but these lesions were not numerous and remained restricted, thus causing minor damage. In addition, the hymenial layers and, subsequently, the lesions resulting from basidiospore infections appeared rather late (4–5 wk after planting) in order to contribute significantly to the epidemic development of BWB.

Basidiospores of *T. cucumeris* have been considered important sources of inoculum for inciting aerial blight diseases on other crop species such as tobacco (22), cotton (15), jute (*Corchorus olitorius* L.) (20), rubber trees (2,3), and sugar beets (*Beta vulgaris* L.) (3). The relative importance of basidiospores as sources of inoculum for foliar blights

caused by *T. cucumeris* may be influenced by the host crop, the prevailing environmental conditions, or both. Production of basidiospores is also important in the long-distance dissemination of the fungus and in increasing the probability for exchange of genetical information such as through recombination among wild-type isolates. The latter may result in production of new types with considerable variation in their virulence (3).

BWB development on the BWB-susceptible cultivar Mexico 27 during the first few weeks after planting was somewhat faster than on the BWB-tolerant cultivar Porrillo 70. As the season advanced, however, the differences in disease severity on the two cultivars appeared less pronounced, and finally, plants of both cultivars became severely and completely affected. These same bean cultivars were previously shown (6) to differ considerably in their tolerance to BWB under field conditions. Symptom expression and severity of diseases caused by *T. cucumeris* has been reported to be influenced by inoculum concentration (3). Thus, the effect of inoculum density on incidence and severity of BWB on tolerant and susceptible bean cultivars needs to be undertaken and is specially warranted before the initiation of breeding programs. Warren (23) concluded that it was not possible to differentiate grades of resistance to *T. cucumeris* in lima bean (*Phaseolus lunatus* L.) cultivars at high soil population of the pathogen.

Root rot diseases caused by *T. cucumeris* are generally considered as a “simple interest disease” (SID) sensu Vanderplank (21). The latter is based on the assumption that the “inoculum present in the soil at the beginning of the season remains the main source of inoculum during a single season.” BWB observed in Costa Rica on several plantings during the 1980 growing season appeared to have the characteristics of a “compound interest disease” (CID) (21). The pathogen multiplied through successive generations of sclerotia in the course of BWB epidemics. These new sclerotia along with old sclerotia were

again splashed onto bean tissues by rain, providing inoculum for further disease development. Also, the mycelium of the fungus was observed spreading from infected to healthy tissues within the plant and to adjacent plants. Furthermore, the basidial state was produced on infected tissues later in the season and provided further inoculum for new infection under favorable conditions. Regression analysis comparing the disease development under the two models of CID and SID showed that the data better fit the CID model (Table 1). These data on the development of BWB epidemics have implications in planning measures to control the disease (21).

Several foliar applications of selected fungicides during the growing season have been generally recommended for control of BWB (10,11). Results of this study demonstrated that the main source of primary inoculum is sclerotia and mycelium in the organic debris in the soil. Consequently, control measures involving chemicals or other means may have to be directed to the soil to reduce the number of infective propagules of *T. cucumeris* and also to avoid the splashing of such inoculum onto bean tissues. Investigations aimed at reducing soilborne inoculum by cultural practices (cropping sequence, time of planting, mulching, etc.), chemical treatments, and development of BWB-tolerant cultivars are urgently needed. These studies are essential for development of an effective and practical integrated control program for BWB in the tropics.

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