Biological Control of Pythium Damping-Off of Cucumbers with *Pythium nunn*: Influence of Soil Environment and Organic Amendments

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ABSTRACT

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The effects of temperature, pH, matric potential, and organic amendments on the biological control of Pythium damping-off of cucumbers with *Pythium nunn* was investigated. Disease suppression was significant at 26 but not at 22 or 17 C, even though reduction in inoculum density of *P. ultimum* was observed at all temperatures. Reduction in disease incidence and inoculum density of *P. ultimum* occurred at pH 6.7 but not at pH 5.0 or 6.0. Differences in disease and inoculum density of *P. ultimum* between treatments with and without *P. nunn* were significant at matric potentials of -20, -40, -100, -200, -500, and $-1,000$ mb. The addition of bean leaves, cotton leaves, alfalfa, or wheat straw together with

P. nunn to raw soil infested with *P. ultimum* did not significantly influence disease incidence. In the treatment with oatmeal plus *P. nunn*, the slope of the regression line of disease incidence over time was significantly less than with other treatments. Also, saprophytic increase of *P. nunn* was greatest in the oatmeal treatment. When organic amendments were added alone to raw soil infested with *P. ultimum*, disease incidence and inoculum density of *P. ultimum* were initially greater than in treatments where *P. nunn* was added together with amendments. This evidence suggests that *P. nunn* can compete with *P. ultimum* for organic substrates and that *P. nunn* and *P. ultimum* occupy overlapping environmental niches.

Pythium nunn Lifshitz, Stanghellini and Baker, a recently described species (17,20), induced suppression to Pythium damping-off of cucumbers induced by *Pythium ultimum* Trow (19,24,25). Initial investigations with a grassland sandy loam showed that suppression at 25 C was eliminated if soil pH was lowered from 7.3 to 5.0 or if the soil was incubated at 19 C (19). This biological control system, like many others, is effective within a defined range of environmental conditions. For example, seed treatments with *Trichoderma hamatum* (Bon.) Bain did not control Pythium damping-off in soil temperatures below 17 C (10). Lowering pH values of a Salinas Valley (California) soil from 8.0 to 6.0 eliminated suppressiveness to Fusarium wilt of flax (28). Nutritional substrates available to *P. nunn* in soil also appear to influence suppression of *P. ultimum*. When only inoculum of *P. nunn* was added to raw soil, no saprophytic increase of *P. nunn* or suppression of *P. ultimum* was detected (24); however, subsequent addition of ground bean leaves (0.3% w/w) resulted in a 10-fold increase of population density of *P. nunn*.

The purpose of this research was to study the effects of soil temperature, pH, and matric potential on the saprophytic increase of *P. nunn* and *P. ultimum* and relate such environmental influences to biological control of cucumber damping-off. The influence of organic amendments on the biological control system in raw soil was also investigated.

MATERIALS AND METHODS

Soil. Nunn sandy loam (19) was used in all experiments. Soil was air-dried, sieved through a 4-mm-mesh screen, and stored for 2–3 mo before use. The population density of *P. ultimum* in this soil was 20–30 colony forming units (cfu) per gram. The soil also contained *P. nunn* at <10 cfu/g. *P. nunn* could only be detected in soils incubated for 1 wk after amendment with 0.3% bean leaves. For soil environment studies, indigenous *Pythium* spp., including *P. nunn*, were eliminated by moistening the soil to approximately

-0.3 bars, exposing to aerated steam at 55 C for 1 hr, and exposing to the air for 1 wk before use to allow microbial populations to equilibrate. Nunn sandy loam was moistened, but not steamed, for 1 wk before use in the organic substrate experiments.

Inoculum. Isolates of *P. nunn* (N3) and *P. ultimum* (N1) used in previous studies (19) were maintained on water agar or cornmeal agar slants. Five unwashed mycelial mats from 1-wk-old 100-ml potato-dextrose broth cultures of *P. nunn* or *P. ultimum* were added to 6 kg of Nunn sandy loam soil that had been amended with 1% (w/w) ground oatmeal and autoclaved twice. The inoculum was incubated under aseptic conditions at 26 C in $32 \times 39 \times 19$-cm plastic tubs covered with aluminum foil. After 3 wk, colony-forming units of the fungus in each substrate was determined by plate dilution on a Pythium selective medium (23).

Soil pH adjustment. Soil pH was measured by the $CaCl_2$ method (29). The pH of Nunn sandy loam was reduced from 6.7 to 2.5 by adding 10% (v/v) of 1 N H_2SO_4. This acidified soil was mixed thoroughly, air dried, ground with a mortar and pestle, and portions added to aerated steamed soil to adjust the pH from 6.7 to 6.0 and 5.0.

Soil matric potential adjustment. Drainage and wetting curves were constructed for Nunn sandy loam by use of a ceramic pressure plate extractor (Soil Moisture Equipment Co., Santa Barbara, CA) for lower (drier) water potentials and a membrane suction plate for higher (wetter) water potentials. Wetting curves were determined by use of ceramic and membrane plates modified with crossflow tubing, by using the method of Klute (14). Air-dried aerated steamed soil was adjusted to 0, -20, -40, -100, -200, -500, and $-1,000$ mb by adding distilled water to achieve the percent moisture level corresponding to the desired matric potential as determined by the wetting curve. Two-hundred grams of soil was added to 0.5-L (1 pint) glass jars, and the tops were covered with polyethylene (2 mil) to minimize water loss.

Organic amendments. The following organic amendments were added at 0.3% (w/w) to untreated soil: oatmeal (Quaker Oats Company), polished wheat straw (*Triticum aestivum* L. 'Hermosillo'), bean leaves (*Phaseolus vulgaris* L. 'Pinto'), alfalfa straw (*Medicago sativa* L. 'Titan'), or cotton leaves (*Gossypium hirsutum* L. 'Acala'). All amendments were ground in a Wiley mill and passed through a 1-mm-mesh sieve. In treatments with *P. nunn*, inoculum of *P. nunn* was added at 300 cfu/g. The organic

amendments and inoculum of *P. nunn* were mixed in the soil at the same time and planted immediately with cucumber seeds.

Cultural conditions. All experiments (except soil matric potential) were conducted in 6.5-cm^2 plastic pots, with six replicate pots per treatment. Ten cucumber seeds (*Cucumis sativus* L. 'Marketer Long') were planted in each pot after the amendments and/or inoculum was added and the soil was moistened. Plants were grown in a constant-temperature growth chamber at 26 C, with a 12-hr light/dark cycle (6,500 lux, fluorescent and incandescent lighting). In all experiments except soil matric

Fig. 1. **A,** Growth rates of *Pythium ultimum* and *P. nunn* on 2% water agar at various temperatures. Data points are averages of three trials. **B,** Rate of increase in population density of *P. ultimum* and *P. nunn* in aerated steamed soil at 17, 22, and 26 C. The rate of increase was calculated for the first 7 days. Initial inoculum density of *P. ultimum* = 100 colony-forming units (cfu) per gram, *P. nunn* = 300 cfu/g. **C,** Percent emergence (adjusted to uninoculated control) of cucumber seeds grown at 17, 22, and 26 C, in aerated steamed soil infested with *P. ultimum* alone or *P. ultimum* plus *P. nunn*. Initial inoculum density of *P. ultimum* = 100 cfu/g, *P. nunn* = 300 cfu/g. Differences between the inoculated control and treatments with *P. nunn* were significant only at 26 C, $P \le 0.05$.

potential studies, plants were watered twice daily with distilled water, and soil matric potential was maintained at >-0.1 bars at all times. Percent seedling emergence was recorded 7 days after planting. All seedlings were removed and pots were replanted weekly. Population densities of *P. ultimum* and *P. nunn* were determined at weekly intervals by dilution plating on a Pythium selective medium (23).

Statistical analyses. Pots were arranged in the growth chamber in a randomized complete block design. All experiments were repeated once, with similar results. Data from the first trials are presented in this paper. Percent emergence data were adjusted to percent of uninoculated control. Adjusted percent emergence between treatments with and without *P. nunn* at each pH, temperature, and matric potential were compared with *t*-tests. Linear regression lines were constructed for disease incidence and population density data of *P. ultimum* in the organic amendment experiment. Regression analyses were performed on regression lines to determine statistical differences in regression coefficients.

RESULTS

Effects of temperature. In vitro temperature-growth curves were constructed for *P. nunn* and *P. ultimum* growing on 2% water agar and averaged in three trials (Fig. 1A). At 26 C, *P. nunn* grew only 60% as fast as *P. ultimum*. No growth of *P. ultimum* was detected above 35 C, but *P. nunn* still grew at 36 C and 37 C, although at a reduced growth rate. Saprophytic increase in aerated steamed soil (log cfu/g/day) of *P. nunn* and *P. ultimum* over the first 7 days was less at lower temperatures (Fig. 1B). Preemergence damping-off was significantly decreased at 26 C in treatments with *P. nunn* (300 cfu/g), compared to the infested control without *P. nunn* (Fig. 1C). No significant differences were observed at 17 and 22 C.

Effects of soil pH. The rate of saprophytic increase of *P. ultimum* in aerated steamed soil was slightly reduced at lower pH values, but *P. nunn* was not affected by the range of pH values used (Fig. 2A). Disease suppression was significant at pH 6.7 and 6.0 in the first planting (Fig. 2B). In the second planting, reduction in disease was significant only at pH 6.7. No disease reduction was evident at pH 5.0 in either planting. Reduction of inoculum densities of *P. ultimum* when *P. nunn* was added to the soil was significant only at pH 6.7 (Fig. 2C).

Effect of soil matric potential. When aerated steamed soil infested with *P. ultimum* (30 cfu/g) contained 300 cfu/g of added *P. nunn*, damping-off was significantly reduced at all matric potentials from -20 to $-1,000$ mb (1 bar) (Fig. 3A). No seedling emergence was observed in any water-saturated treatment (0 bars). After 7 days, inoculum densities of *P. ultimum* in the treatments without *P. nunn* were between 10^3 and 10^4 at all matric potentials except 0 bars. In the treatments with *P. nunn*, inoculum densities of *P. ultimum* were significantly reduced by up to 1 log unit at all matric potentials above saturation, compared with treatments without *P. nunn* (Fig. 3B). *P. ultimum* was not detected in saturated soils after 7 days. Population densities of *P. nunn* ranged between 1×10^3 and 5×10^3 at all matric potentials above saturation. The presence of *P. ultimum* did not have any significant effect on the population densities of *P. nunn*. Population densities of *P. nunn* were significantly reduced in saturated soil (0 bars) at 7 days, although some saprophytic increase occurred.

Effects of organic amendments. The addition of bean leaves, cotton leaves, alfalfa, or wheat straw to soil infested with *P. ultimum* did not significantly increase disease incidence over the unamended control when *P. nunn* was added at 300 cfu/g with the amendments (Fig. 4A). In treatments with oatmeal and *P. nunn*, the disease incidence was initially higher than in the unamended control. However, the slope value of the regression line relating the rate of increase of disease incidence in soil amended with oatmeal was significantly less than in other treatments. The correlation coefficient of the regression line for inoculum density of *P. ultimum* over time was significant ($P = 0.05$) in all treatments (Fig. 4B) except oatmeal plus *P. nunn*, which was not significantly different from zero. At 7 and 14 days, population densities of *P. nunn* in the oatmeal treatment were significantly higher than all
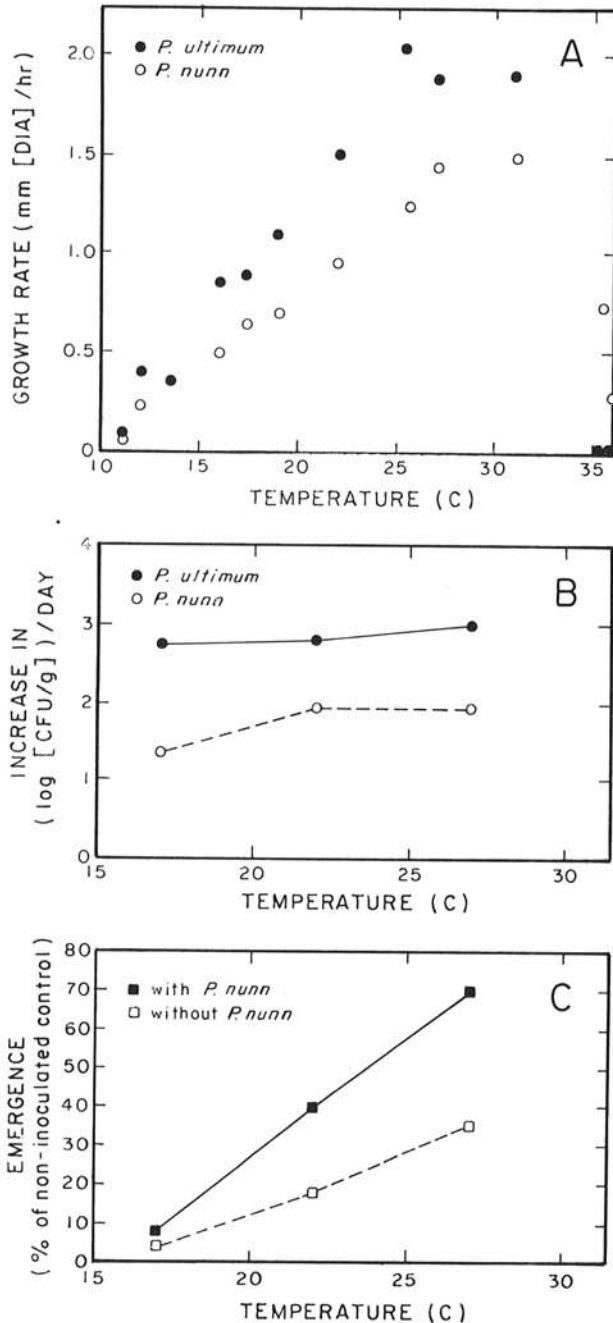
other treatments (Fig. 4C). Population densities of *P. nunn* in the wheat straw treatment were not significantly different from the unamended control, where *P. nunn* did not increase saprophytically. By 28 days, population densities of *P. nunn* in all treatments were not significantly different.

In treatments where bean leaves, cotton leaves, alfalfa straw, or oatmeal were added to the soil with no artificial addition of *P.*

nunn, disease incidence was significantly greater than the unamended control in the first four plantings (Fig. 5A). Disease incidence in the first four plantings of these treatments were also significantly greater than in the corresponding treatments where *P. nunn* was added with the amendments (Fig. 4A). However, in the fifth, sixth, and seventh plantings, the disease incidences in these treatments were not significantly different from the unamended control.

The inoculum density of *P. ultimum* during the first 4 wk in treatments where only oatmeal, bean leaves, cotton leaves, or alfalfa were added (Fig. 5B) was significantly greater than in the corresponding treatments where *P. nunn* was added with the amendments (Fig. 4B). At the same time, population densities of *P. nunn* were lower in the treatments where only amendments were added. At 1 wk in the amendment-only treatments, the indigenous population densities of *P. nunn* ranged from 200 to 700 cfu/g. In treatments where *P. nunn* was added along with the amendment, population densities ranged from 450 to 1,500 cfu/g.

DISCUSSION

Environmental conditions adversely affecting seedling growth are most conducive for preemergence damping-off induced by *P.*
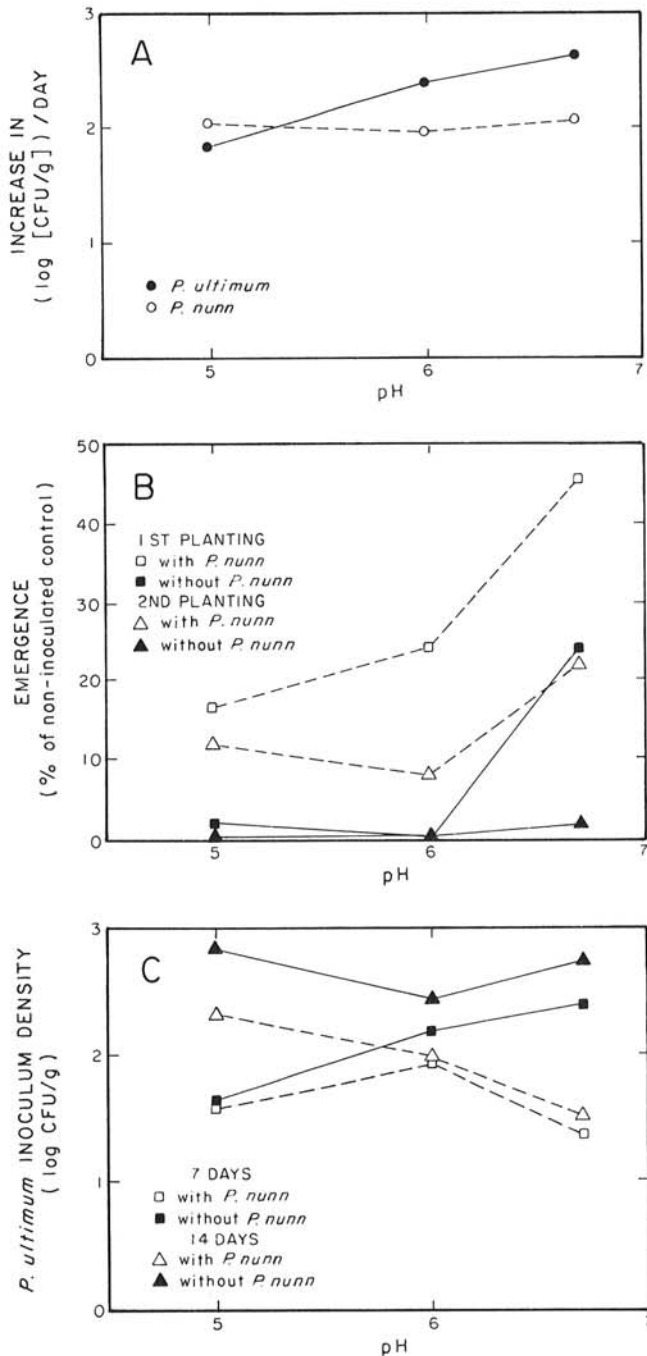

Fig. 2. A, Rate of increase over 7 days in population density of *Pythium ultimum* and *P. nunn* in aerated steamed soil at pH 5.0, 6.0, and 6.7. Initial inoculum density of *P. ultimum* = 100 colony-forming units (cfu) per gram, *P. nunn* = 300 cfu/g. **B,** Adjusted percent emergence of cucumber seeds grown at pH 5.0, 6.0, and 6.7 in aerated steamed soil infested with *P. ultimum* alone or *P. ultimum* plus *P. nunn*. Initial inoculum density of *P. ultimum* = 100 cfu/g, *P. nunn* = 300 cfu/g. Differences between the inoculated control and each treatment with *P. nunn* were significant at pH 6.7 and 6.0 in the first planting and only at pH 6.7 in the second planting, $P \leqslant 0.05$. **C,** Inoculum density of *P. ultimum* in aerated steamed soil at pH 5.0, 6.0, and 6.7, with and without *P. nunn*. Initial inoculum density of *P. ultimum* = 100 cfu/g, *P. nunn* = 300 cfu/g. Differences in inoculum density between the inoculated control and each treatment with *P. nunn* were significant only at pH 6.7, $P \leqslant 0.05$.
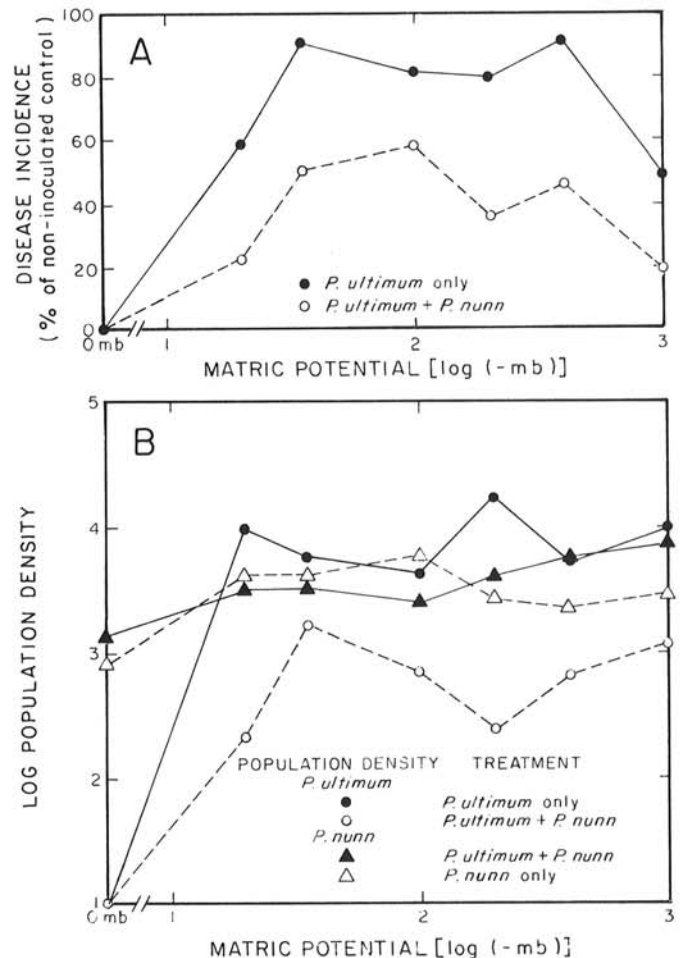
Fig. 3. A, Adjusted disease incidence of cucumber seeds grown at different matric potentials in aerated steamed soil infested with *Pythium ultimum* alone or *P. ultimum* plus *P. nunn*. Initial inoculum density of *P. ultimum* = 30 colony-forming units (cfu) per gram, *P. nunn* = 300 cfu/g. Differences between the inoculated control and each treatment with *P. nunn* were significant at all matric potentials except saturation, $P \leqslant 0.05$. **B,** Population densities of *P. ultimum* and *P. nunn* after 7 days in aerated steamed soil at various matric potentials. Initial inoculum density of *P. ultimum* = 30 cfu/g, *P. nunn* = 300 cfu/g. Differences in inoculum density of *P. ultimum* between the inoculated control and each treatment with *P. nunn* were significant at all matric potentials except −1,000 mb and saturation, $P \leqslant 0.05$.
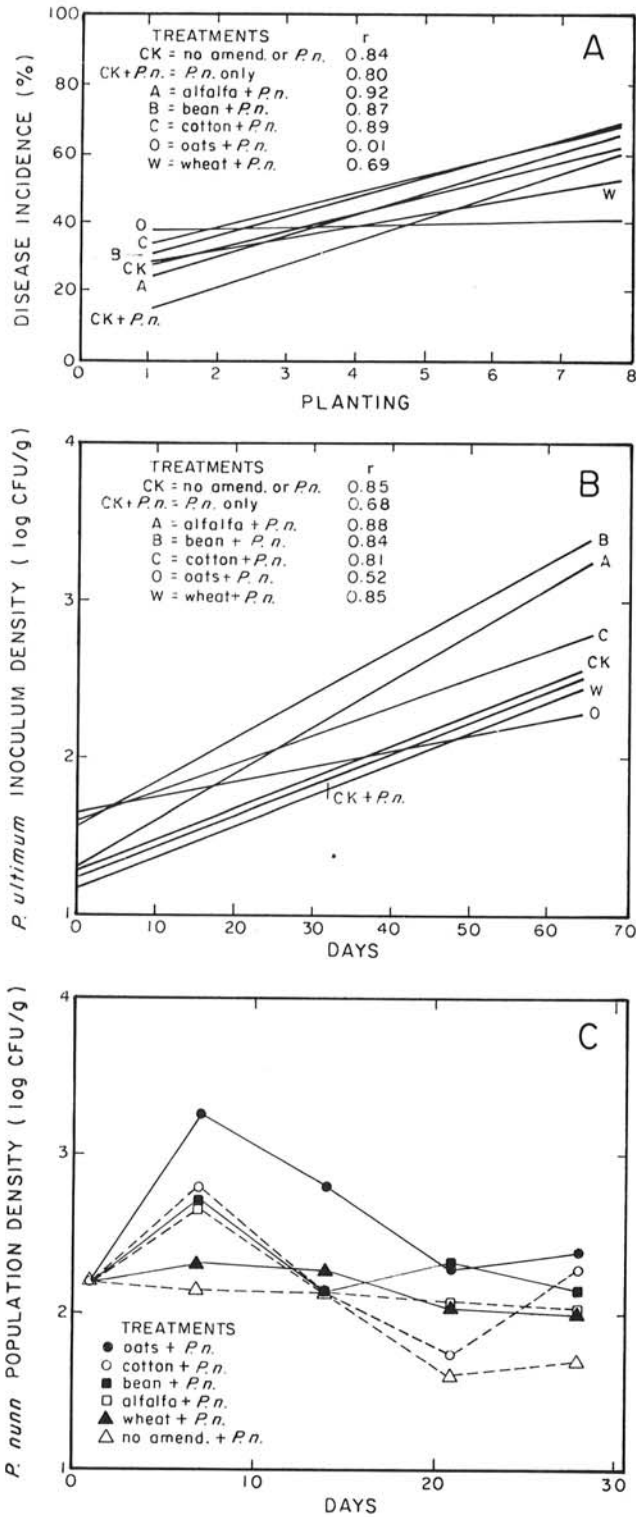
Fig. 4. A, Percent damping-off of successive plantings of cucumbers in Nunn sandy loam amended with organic amendments and *Pythium nunn* (*P. n.*). Indigenous population density of *P. ultimum* = 20–30 colony-forming units (cfu) per gram, *P. nunn* = < 10 cfu/g. All organic amendments added at 0.3% (w/w). Inoculum of *P. nunn* added at 300 cfu/g. All correlation coefficients significant at *P* = 0.05, except for treatments O and W. B, Inoculum density of *P. ultimum* over time in Nunn sandy loam amended with organic amendments and *P. nunn*. All organic amendments added at 0.3% (w/w). Inoculum of *P. nunn* added at 300 cfu/g. All correlation coefficients significant at *P* ≤ 0.05, except for treatments O and CK + *P. n*. C, Population density of *P. nunn* over time in Nunn sandy loam amended with organic amendments and *P. nunn*. All organic amendments added at 0.3% (w/w). Inoculum of *P. nunn* added at 300 cfu/g.

ultimum (16). Damping-off generally is most severe at lower soil temperatures (11,30). The same trend also was evident with Pythium root rots (3,15,26). In addition, the saprophytic growth rate of *P. ultimum* was reduced at lower temperatures (Fig. 1B). Lifshitz and Hancock (18) observed two to four times greater population densities of *P. ultimum* at 26 C than at 17 C, which is similar to our results (Fig. 1B). Their experiments, done in steamed soil, showed a temperature optimum similar to that of in vitro studies. In raw soil, the optimum temperature for growth was much lower, suggesting interactions with other soil microbes (9). From these and other studies, it is apparent that the effect of temperature on disease is primarily related to effects on the host plant. At low temperatures, seedlings are more susceptible because of a decrease in the rate of emergence and root growth and concomitant longer exposure to the pathogen in the period while the host is susceptible. In our experiments, the biological control agent *P. nunn* applied to the aerated steamed soil was unable to protect seedlings at lower temperatures (Fig. 1C), although inoculum densities of *P. ultimum* were reduced when *P. nunn* was
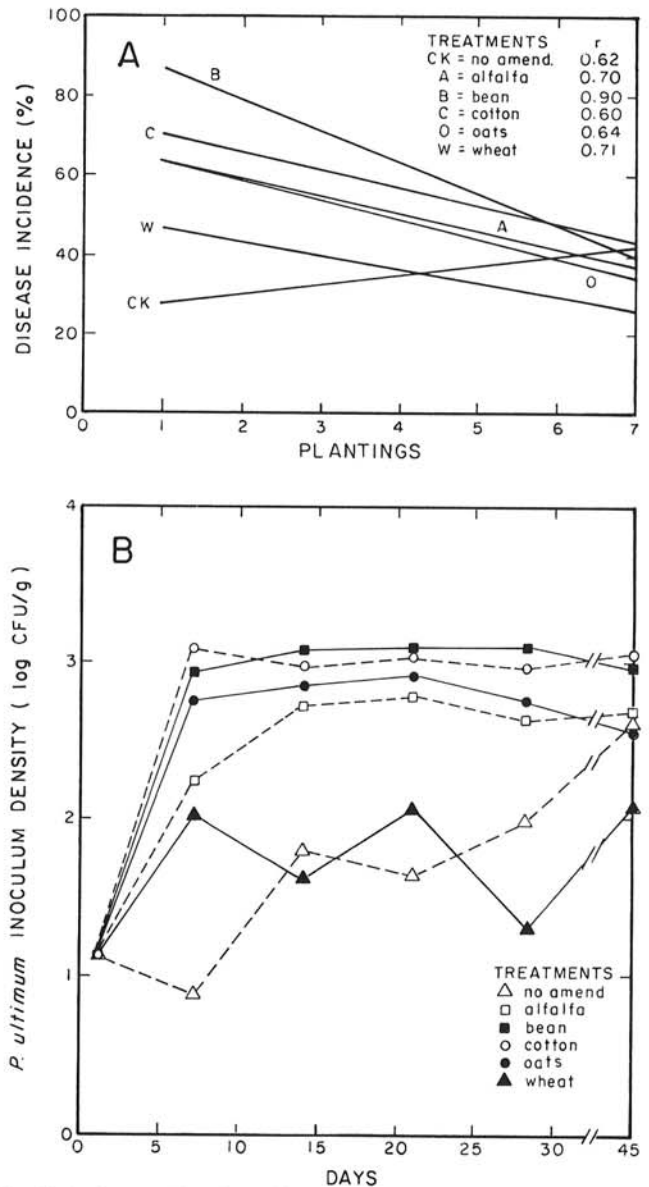

Fig. 5. A, Percent damping-off of successive plantings of cucumbers in Nunn sandy loam treated with organic amendments only. Indigenous population density of *Pythium ultimum* = 20–30 colony-forming units (cfu) per gram, *P. nunn* = <10 cfu/g. All organic amendments added at 0.3% (w/w). All correlation coefficients not significant at *P* = 0.05. B, Inoculum density of *P. ultimum* over time in Nunn sandy loam treated with organic amendments. All organic amendments added at 0.3% (w/w).

added (*unpublished*). Cooler season plants such as spinach are less susceptible to *P. ultimum* at lower temperatures because of faster emergence (16) and might be protected by *P. nunn* at such temperatures. In preliminary experiments, *P. nunn* significantly reduced damping-off of spinach at 15 C (*unpublished*).

High soil moisture and anaerobic conditions affect the physiology of plant roots (5) and increase the severity of Pythium damping-off and root rots (2,15,26,30). Some researchers also hypothesized that seedling damping-off increases at higher water potentials because of an influence on diffusion of exudates from the seed rather than a direct effect on the activity of *P. ultimum* (6,13). For example, Brown and Kennedy (4) showed that exudation from soybean seeds is much greater under anaerobic conditions. Such soil environments also might provide conditions necessary for rapid diffusion of exudates (31). Griffin (8) found that water suction has no effect on the growth rate of *P. ultimum* in the range of 1–392 mb and speculated that *P. ultimum* may be more tolerant of poor gas exchange than other fungi. Hancock (9) observed no significant reduction in growth until the osmotic potential was below −10 bars. Sporangium germination was not inhibited until osmotic potential was below −20 to −30 bars. We observed that the saprophytic increase of *P. ultimum* was approximately the same at all matric potentials from −20 mb to −1,000 mb (Fig. 3B). However, no *P. ultimum* was detected in water-saturated soils after 1 wk. Similarly, Lifshitz and Hancock (18) observed the greatest inoculum density increases at matric potentials of −0.25, −0.50, and −1.0 bars, with no increase at saturation. In contrast, saprophytic increase of *P. nunn* was similar at all matric potentials tested (Fig. 3B), and it exhibited some saprophytic increase in saturated soils. In addition, *P. nunn* was effective in reducing population densities of *P. ultimum* and damping-off at all matric potentials tested (Fig. 3), suggesting that biological control by *P. nunn* is not limited by high matric potentials. Thus, *P. nunn*, like other *Pythium* spp., is ecologically adapted to high-moisture soils and might have a potential biocontrol application in that niche.

Interpretation of the effects of soil pH on Pythium damping-off is difficult. Soil pH influences other soil factors, such as solubility of minerals and ionization of salts and acids. Griffin (7) demonstrated that damping-off is more severe when plants adapted to high pH are grown at low pH, and vice versa. In vitro studies revealed that pH does not have major effects on the growth rate of *P. ultimum*, especially in the range of 5.0–7.0. Griffin suggested that soil pH directly influences the vigor of the host, rather than directly affecting the growth of the pathogen. We observed that the saprophytic increase of *P. ultimum* was somewhat lower at pH 5.0 (Fig. 2A), similar to in vitro studies reported by Lifshitz and Hancock (18). *P. nunn* was not significantly influenced by soil pH values in this range (Fig. 2A); however, no significant reductions in disease incidence (Fig. 2B) or pathogen inoculum density (Fig. 2C) were observed at pH 5.0. Lifshitz et al (19) described a similar trend.

Many workers have reported that the addition of immature green crop debris (9,27,32,33), sucrose (12), cornmeal (21), glucose (22), or oatmeal (34) results in an increased severity of Pythium diseases. Because *Pythium* spp. are excellent pioneer colonists (1) due to their rapid germination and high growth rate, the availability of a readily utilizable food source could increase the inoculum potential of *Pythium* spp. and subsequent disease.

In contrast to the situation where organic amendments initially induced greater disease incidence than in controls, no increase in damping-off was observed in comparison with unamended controls when *P. nunn* was added with the treatments. In the latter case, no increase in inoculum potential of *P. ultimum* may have occurred. The one exception was in the first few plantings in the oatmeal treatment where disease incidence was greater than in the unamended control. In later plantings, however, disease incidence was less than in the control, an indication of disease suppression. This was the same treatment in which the population densities of *P. nunn* were significantly higher than in any other treatment at 7 days and where inoculum of *P. ultimum* was the lowest at the end of the experiment. This suggests that *P. nunn* played a role in

disease suppression.

Increases in disease incidence over unamended controls were observed at the first plantings (Fig. 5A) when organic amendments were added to raw soil without *P. nunn*; by the fifth planting, however, disease incidence in all treatments were not significantly different. It is not clear whether this reduction in disease incidence was due to *P. nunn* or to general microbiological activity and competition. However, the native populations of *P. nunn* increased to the same levels after 28 days as in treatments where 300 cfu/g of *P. nunn* were added in the beginning. The increase in inoculum densities of *P. ultimum* was more rapid in treatments in which *P. nunn* was not added with the amendment (Fig. 5B) than when it was added (Fig. 4B).

Inoculum density of *P. ultimum* and disease incidence were not always correlated. This suggests that other factors in inoculum potential besides density were affected by *P. nunn*. For example, when bean or cotton leaves were added to raw soil, the population density of *P. ultimum* from days 7 to 45 was constant at 1,000–2,000 cfu/g (Fig. 5B). Yet disease incidence decreased from 98 to 40% in the bean leaf treatment and from 68 to 43% in the cotton leaf treatment (Fig. 5A). Further research is needed to elucidate the exact mechanisms of suppression in raw soil.

P. nunn, added at only 300 cfu/g, eliminated the explosive buildup of inoculum potential of *P. ultimum* in the presence of immature crop debris. This evidence indicates that *P. nunn* can compete with *P. ultimum* for the same substrates. Our results also established that *P. nunn* and *P. ultimum* occupy overlapping environmental niches. Thus, *P. nunn* has potential for use as a successful biological control agent against *P. ultimum*.

LITERATURE CITED

1. Barton, R. 1961. Saprophytic activity of *Pythium mamillatum* in soils. II. Factors restricting *P. mamillatum* to pioneer colonization of substrates. Trans. Br. Mycol. Soc. 44:105-118.
2. Bateman, D. F. 1961. The effect of soil moisture upon development of poinsettia root rots. Phytopathology 51:445-451.
3. Bateman, D. F., and Dimock, A. W. 1959. The influence of temperature on root rots of poinsettia caused by *Thielaviopsis basicola*, *Rhizoctonia solani*, and *Pythium ultimum*. Phytopathology 49:641-647.
4. Brown, G. E., and Kennedy, B. W. 1966. Effect of oxygen concentration on Pythium seed rot of soybean. Phytopathology 56:407-411.
5. Burstrom, H. G. 1965. The physiology of plant roots. Pages 154-169 in: Ecology of Soil-Borne Plant Pathogens. K. F. Baker and W. C. Snyder, eds. Univ. California Press, Berkeley.
6. Flentje, N. T. 1964. Pre-emergence rotting of peas in South Australia. II. Factors associated with the soil. Aust. J. Biol. Sci. 17:651-664.
7. Griffin, D. M. 1958. Influence of pH on the incidence of damping-off. Trans. Brit. Mycol. Soc. 41:483-490.
8. Griffin, D. M. 1963. Soil physical factors and the ecology of fungi. II. Behavior of *Pythium ultimum* at small water suctions. Trans. Brit. Mycol. Soc. 46:368-372.
9. Hancock, J. G. 1977. Factors affecting soil populations of *Pythium ultimum* in the San Joaquin Valley of California. Hilgardia 45:107-122.
10. Harman, G. E., Chet, I., and Baker, R. 1981. Factors affecting *Trichoderma hamatum* applied to seed as a biocontrol agent. Phytopathology 71:569-572.
11. Hoppe, P. E. 1949. Differences in Pythium injury to corn seedlings at high and low temperatures. Phytopathology 39:77-84.
12. Johnson, L. F., Hsieh, C. C., and Sutherland, E. D. 1981. Effects of exogenous nutrients and inoculum quality on the virulence of *Pythium ultimum* to cotton hypocotyls. Phytopathology 71:629-632.
13. Kerr. 1964. The influence of soil moisture on infection of peas of *Pythium ultimum*. Aust. J. Biol. Sci. 17:676-685.
14. Klute, A. 1986. Water retention: Laboratory methods. In: Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods, 2nd ed. American Society of Agronomy. In press.
15. Kraft, J. M., and Roberts, D. D. 1969. Influence of soil water and temperature on the pea root rot complex caused by *Pythium ultimum* and *Fusarium solani* f. sp. *pisi*. Phytopathology 59:149-152.
16. Leach, L. D. 1947. Growth rates of host and pathogen as factors determining the severity of pre-emergence damping-off. J. Agric. Res. 75:161-179.

17. Lifshitz, R., Dupler, M., Elad, Y., and Baker, R. 1984. Hyphal interactions between *Pythium nunn* and several soil fungi. Can. J. Microbiol. 30:1482-1487.

18. Lifshitz, R., and Hancock, J. G. 1983. Saprophytic development of *Pythium ultimum* in soil as a function of water matric potential and temperature. Phytopathology 73:257-261.

19. Lifshitz, R., Sneh, B., and Baker, R. 1984. Soil suppressiveness to a plant pathogenic *Pythium* species. Phytopathology 74:1054-1061.

20. Lifshitz, R., Stanghellini, M., and Baker, R. 1984. A new species of *Pythium* isolated from soil in Colorado. Mycotaxon 20:373-379.

21. Liu, S. Y., and E. K. Vaughn. 1965. Control of Pythium infection of table beet seedlings by antagonistic microorganisms. Phytopathology 55:986-989.

22. Luna, L. V., and Hine, R. B. 1964. Factors influencing saprophytic growth of *Pythium aphanidermatum* in soil. Phytopathology 54:955-959.

23. Mircetich, S. M., and Kraft, J. M. 1973. Efficiency of various selective media in determining *Pythium* population in soil. Mycopathol. Mycol. Appl. 50:151-161.

24. Paulitz, T. C., and Baker, R. 1987. Biological control of Pythium damping-off of cucumbers with *Pythium nunn*: Population dynamics and disease suppression. Phytopathology 77:335-340.

25. Paulitz, G., Windham, M., and Baker, R. 1985. *Pythium nunn*—A potential biological control agent. (Abstr.) Phytopathology 75:1326-1327.

26. Pieczarka, D. J., and Abawi, G. S. 1978. Influence of soil water potential and temperature on severity of Pythium root rot of snap beans. Phytopathology 68:766-772.

27. Sawada, Y., Nitta, K., and Igarashi, T. 1964. Injury of young plants caused by the decomposition of green manure. I. Causal agent of injury. Soil Sci. Plant Nutr. 10:163-170.

28. Scher, F. M., and Baker, R. 1980. Mechanism of biological control in a Fusarium-suppressive soil. Phytopathology 70:412-417.

29. Schofield, R. K., and Taylor, A. W. 1955. The measurement of soil pH. Soil Sci. Soc. Am. Proc. 19:164-167.

30. Short, G. E., and Lacy, M. L. 1976. Factors affecting pea seed and seedling rot in soil. Phytopathology 66:188-192.

31. Stanghellini, M. E., and Hancock, J. G. 1971. Radial extent of the bean spermosphere and its relation to the behavior of *Pythium ultimum*. Phytopathology 61:165-168.

32. Trujillo, E. E., and Hine, R. B. 1965. The role of papaya residues in papaya root rot caused by *Pythium aphanidermatum* and *Phytophthora parasitica*. Phytopathology 55:1293-1298.

33. Watson, A. G. 1970. The effect of cover crops incorporated into field soil on *Pythium ultimum* populations and inoculum potentials. (Abstr.) Phytopathology 60:1537.

34. Yarwood, C. E. 1966. Detection of *Pythium* in soil. Plant Dis. Rep. 50:791-792.