# Effects of Soil Texture and Matric Potential on Sporangium Production by *Phytophthora parasitica* var. *nicotianae*

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## ABSTRACT

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Mycelial mats of *Phytophthora parasitica* var. *nicotianae* grown on nylon mesh in 5% V-8 juice broth were incubated in the sand fraction of a Wagram fine sandy loam at constant matric potentials ranging from 0 to −15 bars. After 2 days of incubation, few to no sporangia were produced on mats at 0 millibars (mb) and at −10 mb, production was erratic at −20 and at −30 mb, while >140 sporangia per square millimeter were produced between −40 mb and −15 bars. Sporangium production also was observed in five soils or their sand fractions maintained at constant matric potentials between +2 mb (flooded) and −40 mb. Soil texture was a critical factor in determining the highest matric potential at which sporangia were consistently produced; −40 mb in the sand fraction of a fine sandy loam, −20 mb in the sand fraction of a sandy loam, and 0 mb in a coarse sand. Sporangium production was abundant in Grantham silt loam, a soil material conducive to development of tobacco black shank, but were inhibited over a range of matric potentials in two soil materials (Duplin sandy loam and Coxville sandy loam) characterized as suppressive to black shank. Sporangium production was inhibited in untreated (compared to pasteurized) Norfolk sandy loam even though the soil was conducive to disease development. Soil pasteurization did not influence sporangium production in the Grantham, Duplin, or Coxville soil materials. The effects of matric potential on sporangium production by *P. p.* var. *nicotianae* were modified by soil texture, soil pasteurization, and unknown factors contributing to suppression of black shank disease in several soils.

The production and germination of sporangia of *Phytophthora* spp. are mediated by many environmental factors (8). Since sporangia play a major role in the epidemiology of Phytophthora root rots, knowledge of how these factors influence sporangium production is important. Sporangia may germinate either directly to produce germ tubes or secondary sporangia, or indirectly to produce motile zoospores which are considered the primary infective propagule of many *Phytophthora* spp. (8). Matric potential is perhaps the most important factor that influences the production and mode of sporangium germination in soil (8). Matric potential determines the percentages of air- and water-filled pores in soil, and sporangia form in response to the availability of both water and air. In most *Phytophthora* species, sporangia are produced in soils at matric potentials from near saturation to −4 bars (8). At saturation, soil pores are filled with water and the lack of sufficient aeration may inhibit sporangium production (9,17). In soils at potentials lower than −4 bars, sporangium production is reduced or prevented, but the mechanism of inhibition is unknown (8). Effects of matric potential on sporangium production depend on many factors including the species of *Phytophthora*, the depth in soil of the colonized substrate, and the nature of the substrate on which the vegetative mycelium is growing (10). In most studies, matric potential (not water content) of soil determines sporangium production (2,3,10). Differences observed in sporangium production in different soils at the same matric potential have been attributed to the effects of texture and pore size distribution (21), the effects of contact surfaces and nutrients on microbial activities (1,10,21), and the presence of antagonistic soil microorganisms (4,16). Suppression of diseases caused by *Phytophthora* spp. in certain soils also has been attributed to reduction of sporangium production and hyphal lysis by microbial antagonists (4,16).

Black shank is a root and crown disease caused in tobacco (*Nicotiana tabacum* L.) by *Phytophthora parasitica* Dast. var. *nicotianae* (Breda de Haan) Tucker (14). Under field conditions, spread of *P. p.* var. *nicotianae* from a point source of inoculum in the absence of cultivation was related to the level of host resistance and the presence of surface water (19). These observations illustrated the importance of host and environment on secondary inoculum production and dissemination within a growing season. In addition, soils conducive and suppressive to black shank development have been observed (6,20). The effects of matric potential and soil type on sporangium production of this pathogen has not been determined. Sporangium production for *P. parasitica*, a similar organism, was reported to be inhibited at 0 mb, restricted at −10 mb, and abundant from −25 to −300 mb (13).

The objectives of this study were to determine the effects of matric potential, soil texture, and soils conducive and suppressive to black shank development on sporangium formation by *P. p.* var. *nicotianae*.

## MATERIALS AND METHODS

The soil materials and soils used included: the sand fraction (particles <53 μm)of Wagram fine sandy loam, a coarse builder's sand, two soils conducive to black shank development (Grantham silt loam and Norfolk sandy loam), and two soils suppressive to black shank development (Duplin sandy loam and Coxville sandy loam) (20). Excepting the coarse sand, all soils were collected from the upper 15 cm of the AP horizon of fallow fields. The soils were air dried, sieved through a 2-mm screen, and stored in polyethylene bags at room temperature until used. The sand fraction of some soils was obtained by wet sieving the soil through a 53-μm sieve and drying the retained fraction at 105 C. The coarse sand also was washed on a 53-μm sieve before use to remove finer particles. Soil moisture release curves were obtained for each soil material (Figs. 1 and 2) by using Büchner funnel tension plates (0 to −200 mb) (10 mb = 0.1 kPa) and a ceramic pressure plate (−100 mb to −15 bars) (12). Water content at each matric potential was determined by drying soils at 105 C overnight. Percent sand, silt, and clay (Table 1) was determined by using the hydrometer method (5). Soils for some experiments were steam pasteurized at 60 C for 1 hr.

Mycelial mats of *P. p.* var. *nicotianae* were produced by stripping mycelia from 6- to 10-day-old cultures grown on oatmeal agar (11)

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at 28 C and blending the mycelium in 125 ml of sterile deionized water for 1 min at low speed in a Waring blender. A 5-ml aliquot of the resulting suspension was pipetted into a 9-cm-diameter petri plate containing 15 ml of 5% clarified V-8 juice broth and a single 7-cm square piece of 100-$\mu$m nylon mesh (Tetko Inc., Elmsford, NY). After 2 days, the mycelium had grown over and through the nylon mesh. The mats were washed three times in deionized water, cut into 1-cm squares, and placed between two 2-cm squares of 30-$\mu$m nylon mesh. No sporangia were present on mycelial mats prior to placement in soil.

Matric potentials ranging from +2 mb (water level 2 cm above the mycelial mat in soil) to −200 mb were controlled by using 6-cm-diameter Büchner funnel tension plates. Unless otherwise specified, the distance between the top of the porous plate and the top of a water reservoir was used to determine matric potentials. A 15-mm layer of soil was placed in each funnel, saturated from below, and mycelial mats were placed on the soil surface. A 5-mm layer of soil was placed over the mat and similarly saturated. Matric potentials were immediately established by using the soil surface and the top of the water resevior as reference points. Funnels were covered with plastic wrap to reduce evaporation and maintained in growth chambers at 24 C with a 14-hr photoperiod. After 2 days of incubation, mycelial mats were removed from the soil, rinsed, and stained with 0.05% crystal violet. The number of empty and full sporangia in five randomly chosen areas were counted on each mat. Upon removal of the protecting 30-$\mu$m mesh, the mycelial mat either remained on the 100-$\mu$m mesh or adhered to the 30-$\mu$m mesh. If the mycelial mat adhered to the 100-$\mu$m nylon mesh, the sample area corresponded to the area occupied by nine squares in the mesh (0.25 mm$^2$). If the mat adhered to the 30-$\mu$m mesh, the sample area counted was determined by using an ocular reticle (Whipple disc; Fisher Scientific). Sporangial counts were converted to sporangia per square millimeter for comparisons and statistical analysis. Water contents for the soils were determined in funnels and were comparable to the moisture release curves determined for each soil.

The effect of matric potentials between −200 mb and −15 bars on sporangium production in the sand fraction of the Wagram fine sandy loam was investigated by using a pressure plate apparatus. A 25-g sand sample was placed in a 5-cm-diameter rubber ring and a mycelial mat was buried in the sand in the center of the ring. The sand was saturated and allowed to equilibrate (average 5.5 hr, maximum of 14 hr) to the desired matric potential under positive air pressure, after which the pressure was released but mats were not removed from the sealed pressure chamber. Mycelial mats were incubated for a total of 2 days and then removed from the sand. Sporangia were counted as previously described. Water contents were determined in the sand samples in each replication, and were similar to values obtained for moisture release curves.

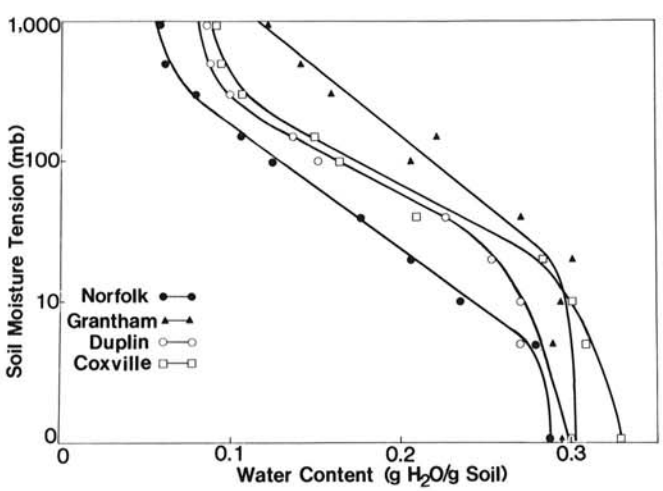


**Fig. 1.** Moisture release curves for sands used to determine effects of matric potential and texture on sporangium production by *Phytophthora parasitica* var. *nicotianae*. Sieved soils were wet sieved over a 53-$\mu$m sieve.

Experiments were conducted to determine the effects of matric potential, soil texture, and soil pasteurization on sporangium production. All experiments were replicated over time. The numbers of replications and observations per replication (mycelial mats) varied with experiment and ranged from three to six replications and from two to six observations (mycelial mats) per replication with five sporangial counts per observation. A single isolate of *P. p.* var. *nicotianae* obtained from flue-cured tobacco was used in all experiments. Additional isolates from flue-cured and burley-type tobacco were used in some experiments to test for isolate effects. A randomized complete block design was used in all experiments. Data were analyzed by analysis of variance and differences were determined by using the Waller-Duncan $k$-ratio $t$-test.

## RESULTS

Sporangium production by *P. p.* var. *nicotianae* was greatly affected by soil matric potential. In the sand fraction of Wagram fine sandy loam, few to no sporangia were produced at 0 and −10 mb and >140 sporangia per square millimeter were produced between −40 mb and −15 bars (Fig. 3). Production was erratic at −20 and −30 mb with either few or >140 sporangia per square millimeter produced on mats in different replications and

TABLE 1. Percent sand, silt, and clay contents of soil materials used to determine effects of matric potential and texture on sporangium formation by *Phytophthora parasitica* var. *nicotianae*[a]

| Soil materials | Particle sizes (mm) of sand (%) | | | | Sand (%) | Silt (%) | Clay (%) |
|---|---|---|---|---|---|---|---|
| | >2 | 2–0.5 | 0.5–0.25 | 0.25–0.05 | | | |
| Wagram | 0 | 9 | 23 | 68 | 100 | 0 | 0 |
| Norfolk | 0 | 20 | 59 | 21 | 65 | 30 | 5 |
| Coarse sand | 13 | 68 | 14 | 7 | 100 | 0 | 0 |
| Grantham | 0 | 8 | 38 | 54 | 16 | 67 | 17 |
| Duplin | 0 | 16 | 63 | 21 | 55 | 34 | 11 |
| Coxville | 0 | 13 | 58 | 28 | 51 | 33 | 16 |

[a] Size classes for partial sizes as determined by using the U.S. Department of Agriculture system of soil classification.

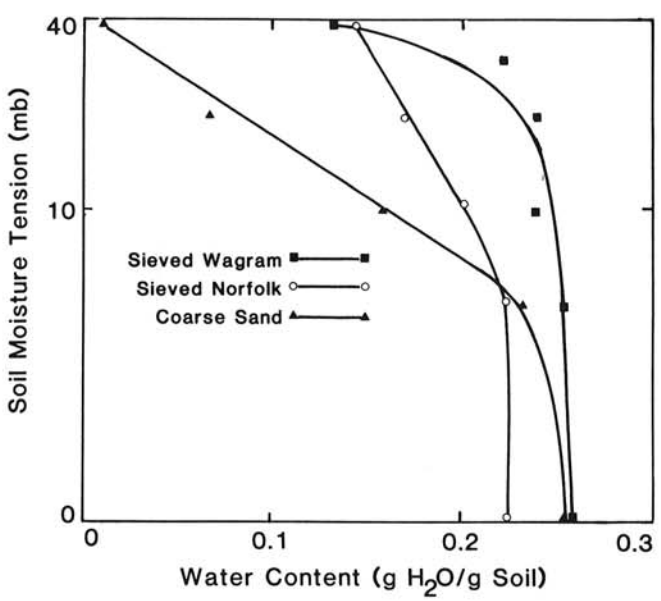


**Fig. 2.** Moisture release curves for Wagram fine sandy loam, Norfolk sandy loam, and a coarse builder's sand used to determine effects of matric potential, texture, and soil pasteurization on sporangium production by *Phytophthora parasitica* var. *nicotianae*.

observations. Sporangia were produced abundantly (>140 sporangia per square millimeter) in 21% of the mycelial mats at −20 mb and in 84% of the mats at −30 mb. Few or no sporangia were produced on remaining mats.

Sporangium production varied with soil texture, and a significant interaction between soil texture and matric potential was observed (Table 2). Sporangium production was greater in the sand fractions of the Wagram and Norfolk soils than in the other soils (Table 2). The highest matric potential at which sporangia were consistently produced was 0 mb in the Grantham silt loam and in the coarse sand, −10 mb in the Norfolk sandy loam, 20 mb in the sand fraction of the Norfolk sandy loam, and −40 mb in the sand fraction of the Wagram fine sandy loam (Table 2). Sporangium production also was determined for two fungal isolates at −20 mb in 10 samples of the sand fraction of the Wagram and Norfolk soils. Sporangia were produced in only 6% of the mycelial mats in the sand fraction of the Wagram soil and in 73% of the mycelial mats in the sand fraction of the Norfolk soil. The two isolates behaved similarly in all ten samples of both soils.

Soil pasteurization and soil type also influenced sporangium production. Sporangium production in soil materials suppressive to black shank development (Duplin and Coxville) and in the unpasteurized Norfolk was erratic over the range of matric potentials tested. Sporangium production in these soil materials ranged from 0 to >50 sporangia per square millimeter compared to consistent sporangium production (>50 sporangia per square millimeter) in the conducive Grantham soil (Table 3). Sporangium production was not affected by pasteurization except in the Norfolk soil where sporangium production was greater following pasteurization (Table 3).

TABLE 2. Sporangium production by *Phytophthora parasitica* var. *nicotianae* in different soil materials and sand fractions at different matric potentials

| Matric potential (mb) | Soil materials or sand fractions and sporangia per mm$^2$ | | | | |
|---|---|---|---|---|---|
| | Sand fraction of Wagram[y] | Sand fraction of Norfolk[y] | Norfolk | Coarse sand | Grantham |
| +2 | 0 a[z] | 0 a | 0 a | 0 a | 0.7 a |
| 0 | 0.2 a | 1.1 a | 1.2 a | 24 b | 44 b |
| −5 | 0.2 a | 0.7 a | 0.1 a | 50 b | 30 b |
| −10 | 1.4 a | 2.9 a | 9 a | 58 b | 35 b |
| −20 | 9.8 a | 174 b | 71 b | 48 b | 78 b |
| −40 | 154 b | 214 b | 73 b | 28 b | 79 b |

[y] Sand fraction obtained by wet sieving soil over 53-$\mu$m screen. Sporangial counts converted to sporangia per square millimeter.

[z] Values are the average of five replications with two observations (mycelial counts) per replication and five sporangial counts per observation. Values in a column followed by the same letter do not differ, $P = 0.05$, according to the Waller-Duncan $k$-ratio $t$-test.

TABLE 3. Sporangium production by *Phytophthora parasitica* var. *nicotianae* at −40 mb matric potential in pasteurized and untreated soil materials

| Soil material | Soil condition and sporangia per mm$^2$[y] | |
|---|---|---|
| | Pasteurized | Untreated |
| Norfolk | 76 a[z] | 11 b |
| Grantham | 60 a | 43 a |
| Coxville | 3 b | 3 c |
| Duplin | 0 b | 1 c |

[y] Soil materials steam pasteurized at 60 C for 1 hr. Sporangial counts converted to sporangia per square millimeter.

[z] Values are the average of three replications with four observations (mycelial mats) per relication and five sporangial counts per observation. Values in a column followed by the same letter do not differ, $P = 0.05$, according to the Waller-Duncan $k$-ratio $t$-test.

## DISCUSSION

Most species of *Phytophthora* produce sporangia in soils at matric potentials from near saturation to −4 bars (8). Similar results were obtained in this study for *P. p.* var. *nicotianae* in the sand fraction of Wagram fine sandy loam. Sporangium production was minimal near saturation, erratic between −20 and −30 mb (the range of matric potentials within which air-filled pore spaces are becoming available [Fig. 2]), and consistently high at potentials <−40 mb (Fig. 3). Abundant sporangium production at −15 bars as observed in this study has not been reported previously for *P. parasitica* or for any *Phytophthora* sp. (7,10). Several factors may account for this difference. Other researchers used *Phytophthora* spp. that may be more sensitive to dry conditions in the soil (7,10). Also, water content in the sand fraction of the Wagram soil changed only slightly between −100 mb and −15 bars which is not true for less sandy soils in which water content would decrease more gradually over this range of potentials. Preparation of mycelial mats used in this experiment also was different than in some previous experiments. For example, Duniway (7) air-dried mycelial mats to the potential of the soil before placing them in soil to maintain soils at the proper matric potential. Gisi et al (10) used a pressure plate to obtain low matric potentials, but maintained the pressure for the entire 2-day incubation period. Evidence from preliminary experiments suggest that continuous positive air pressure corresponding to −15 bars potential adversely affected mycelium appearance and sporangium production. Finally, sporangium initiation may have begun while the sand was equilibrating from a higher matric potential and then continued at potentials normally too low for sporangium initiation. Sporangium initiation has been reported to occur in *P. parasitica* (3) within 90 min of placement in a soil extract and within 30 min in *P. cambiovora* (22). Sporangium production by *P. parasitica* continued at 0 mb, a potential normally suppressive to sporangium production after initiation at −150 mb. Further research is required to determine if sporangium formation, once initiated, continues at low matric potentials.

The effects of matric potential on sporangium production by *P. p.* var. *nicotianae* were modified by soil texture. Texture affected the highest potential at which sporangia were produced. Sporangia were produced at successively higher matric potentials as the percentage of coarse sand increased: 0 mb in the coarse sand, −20 mb in the sand fraction of the Norfolk sandy loam, and −40 mb in the sand fraction of Wagram fine sandy loam. Increasing the percentage of coarser particles creates larger pore spaces that drain at increasingly higher matric potentials (Fig. 2). Sporangium production may therefore be in response to the availability of air-filled pore spaces. This hypothesis is supported by the erratic

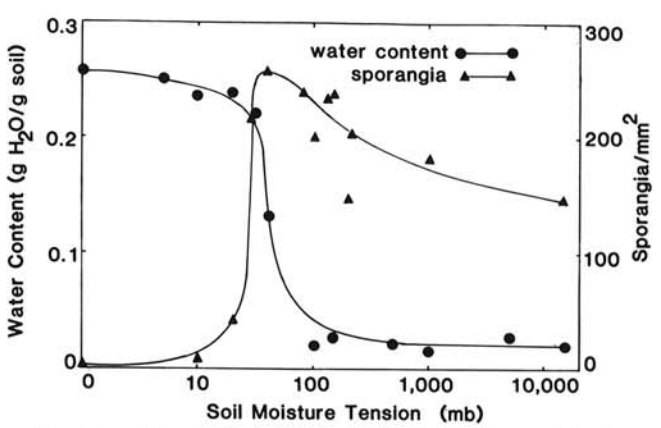


**Fig. 3.** Relationships of soil matric potential to sporangium production by *Phytophthora parasitica* var. *nicotianae* in the sand fraction of Wagram fine sandy loam, and the moisture release curve for the sand fraction of that soil. Values for the sporangium production curve are an average of three to six replications with two to six observations (mycelial mats) per replication and five sporangial counts per observation.

sporangium production at −20 and −30 mb in the sand fraction of the Wagram soil. At −20 mb, 21% of the mycelial mats produced abundant sporangia while at −40 mb, most mycelial mats (83%) produced abundant sporangia. In some tests, sporulating and nonsporulating mats were in the same funnel. Similar erratic behavior was observed in several isolates of *P. p.* var. *nicotianae* (J. R. Sidebottom, *unpublished*). Because of the relatively uniform pore size in the sand fraction of Wagram soil, pores begin to drain rapidly between −20 and −30 mb. The availability of air-filled pores around each mycelial mat at these potentials may be quite variable and might account for the variation in sporangium production between replications and even in different positions in the same funnel. A similar response was observed in the sand fraction of the Norfolk soil at −10 and −20 mb. Sterne and McCarver (21) reported a similar response with *P. parasitica* and *P. cryptogea* while investigating the effects of matric potential on sporangium production in a coarse sand, a clay loam, and two artificial "soils" composed of uniform glass beads which had moisture characteristics similar to those of the natural soils. For both species, sporangium production from mycelial mats was restricted to −250 mb in the two finer-textured "soils," whereas sporangium formation occured at −50 mb in the two coarser "soils." This difference was attributed to effects of texture on pore size distribution and aeration (21).

However, soil aeration was not the only effect of texture on sporangium production. Sporangia were produced at saturation in Grantham silt loam, a considerably finer-textured soil than the coarse sand and presumably with more restricted aeration. Some other property of this soil must be affecting production. Sporangium production was lower in unfractionated Norfolk and Wagram soil than in the sand fraction of these soils. MacDonald and Duniway (15) also reported greater sporangium production by *P. cryptogea* and *P. megasperma* in the sand fraction of a fine sandy loam than in the unfractionated soil.

Interactions between soil texture and matric potential are important since texture is a stable property of the soil and its effects on sporulation may be more predictable than those associated with other soil characteristics. However, since texture of the soil may affect a variety of factors including aeration, reactive surfaces, nutient availability, and microbial interactions, it is difficult to determine the exact mechanism of texture × matric potential interactions.

Sporangium production was also affected by soil type and pasteurization. In the Duplin and Coxville soil materials, which are suppressive to black shank development, sporangium production was reduced compared to sporangium production in the Grantham, which is a conducive soil material. Sporangium production was not affected in Duplin or Coxville soils by pasteurization, raising pH with KOH, or wetting soils with a complete nutrient solution instead of deionized water (J. R. Sidebottom, *unpublished*). Sporangium production was similarly suppressed in the Duplin and Coxville soils collected from the same sites 8 mo after the original collections. Sporangium production also was reduced or erratic in unpasteurized Norfolk soil material, which is conducive. In this instance, however, reduction appears to be biotic in nature since production was significantly higher following pasteurization of the soil. The Norfolk soil was the only soil tested in which sporangium production was affected by soil pasteurization.

As with other species of *Phytophthora*, production of sporangia of *P. p.* var. *nicotianae* was greatly affected by soil matric potential. However, these effects were modified by texture. Sporangium production was inhibited in some soils at or near saturation, but not in all. When just the sand fraction of a soil was used, the percentage of coarse sand particles appeared to affect whether sporangia were produced at these high matric potentials. Sporangium production was also affected by properties contributing to suppression of the black shank disease. Sporangium production was low and erratic in two suppressive soil materials.

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