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SOIL, ROOTSTOCK, AND CLIMATIC FACTORS AFFECT POPULATIONS OF *PHYTOPHTHORA NICOTIANAE* IN SOUTH FLORIDA CITRUS PLANTINGS

DIANE B. BRIGHT AND JAMES H. GRAHAM[1]
University of Florida, IFAS
Citrus Research and Education Center
Soil and Water Science Department
700 Experiment Station Road
Lake Alfred, FL 33850

MICHAEL S. IREY AND LESLIE E. BAUCUM
U.S. Sugar Corporation
Clewiston, FL 33440

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Abstract. **Phytophthora nicotianae Breda de Haan is endemic in Florida citrus groves and causes fibrous root rot when rhizosphere populations develop to damaging levels. Annual surveys of populations of *P. nicotianae,* soil characteristics, and plant nutrient status were conducted in two citrus plantings on major rootstocks and soil series typical of the southern flatwoods: Grove 1 from 1998-2000, and Grove 2 in 1999 and 2001. In Grove 1, *P. nicotianae* populations on rootstocks over 3 years ranked: Cleopatra mandarin > Carrizo citrange > sour orange > Swingle citrumelo = Palestine sweet lime > Volkamer lemon. *P. nicotianae* populations were highest in Myakka fine sand; intermediate in Immokalee, Margate, Holopaw, Basinger, and Riviera fine sands; and lowest in Holopaw (Lime Substratum), Boca, and Oldsmar fine sands. Populations were higher in spodosols than entisols and alfisols with the exception of Oldsmar series. *P. nicotianae* populations were positively correlated with % clay and negatively correlated with % sand. Saturated hydraulic conductivity of soil series was predictive of *P. nicotianae* populations when rainfall was high in 1999, but not predictive in relatively dry years. *P. nicotianae* populations were weakly correlated with soil and plant nutrient status. In Grove 2, ranking of *P. nicotianae* populations for rootstocks was similar to that in Grove 1. Relationships with rootstock susceptibility, soil drainage, and rainfall patterns define where and when *P. nicotianae* populations reach damaging levels, as well as the management tactics that are most effective to maintain root health.**

Phytophthora nicotianae Breda de Haan (syn. *P. parasitica*) is a soilborne fungus-like organism endemic to Florida citrus groves. This *Phytophthora* sp. causes fibrous root rot, foot rot on susceptible rootstocks, and, occasionally, brown rot of fruit on early season citrus varieties (Graham and Menge, 1999; Graham and Timmer, 2004). While foot rot of the trunk and brown rot are easily detected above ground, *Phytophthora* damage to fibrous roots belowground is difficult to assess directly. Therefore, soil samples are collected from the root zone of mature groves to measure the populations of the pathogen in the rhizosphere by a quantitative assay (Graham and Menge, 1999; Timmer et al., 1988). Populations of *P. nicotianae* are considered damaging when they reach 10 to 15 propagules per cubic centimeter (cm^3) of rhizosphere soil (Graham and Timmer, 2004).

In fine textured soils, water-holding capacity greatly affects *Phytophthora* populations in the soil (Sidebottom and Shew, 1985). Central Florida ridge groves are predominantly on entisols—sandy mineral soils low in organic matter, natural fertility, and water holding capacity. These soils have weak or no diagnostic subsurface layers, are generally well drained, and only occasionally support damaging populations of *Phytophthora* on susceptible rootstocks (Graham and Menge, 1999). South Florida flatwoods groves are mostly located on spodosols and alfisols with diagnostic subsurface layers at varying depth in the soil profile. Spodosols contain an acidic subsurface hardpan composed of aluminum and iron cemented together with organic matter. In alfisols, the subsurface layer is loamy material consisting of a mixture of mostly clay and sand with little silt that has a relatively high water holding capacity. These hardpan layers may reduce soil hydraulic conductivity (SHC), the maximum rate that water can move through a soil when it is saturated. Depending on the depth of these restrictive soil layers, periodic or prolonged saturation of soils may promote root damage and reduce rooting depth of citrus in the flatwoods (Castle et al., 2004; Obreza et al., 1993). When the root zone is periodically saturated, conditions are favorable for *P. nicotianae* to infect fibrous roots within hours and destroy roots within 4 to 6 weeks (Graham and Menge, 1999; Kosola et al., 1995; Widmer et al., 1998). In flatwoods groves, proper internal drainage of the beds and careful irrigation management are essential for regeneration of roots. Increasing internal drainage of poorly drained beds with tile is crucial to long-term sustainability of fibrous root health (Graham and Menge, 1999; Graham and Timmer, 2004).

Citrus rootstocks vary widely in resistance and/or tolerance to *P. nicotianae* based on the populations they support in their rhizospheres (Agostini et al., 1991; Graham 1990, 1995a). When growing in soils amenable for optimal horticultural performance, Swingle citrumelo [*Citrus paradisi* Macf. × *Poncirus trifoliata* (L.) Raf.] is considered to be resistant because it does not sustain high populations of *P. nicotianae* and is able to regenerate fibrous roots after infection (Graham, 1990, 1995a). However, recent experience indicates Swingle citrumelo root systems are unsuited for poorly or excessively drained soil series (Castle et al., 2004) and for this reason may lack resistance to *Phytophthora* spp. (Adair et al., 2000; J. H. Graham and J. T. Taylor, unpublished data). Volkamer lemon (*C. volkameriana* Tan. & Pasq.) is considered to possess tolerance because it supports varying levels of *Phytophthora* (Kosola et al., 1995) and growth of new fibrous roots following infection is dependent upon seasonal and soil environmental conditions (Graham, 1995a). Carrizo citrange (*C. sinensis* × *P. trifoliata*), sour orange (*C. aurantium* L.), Cleopatra mandarin (*C. reticulata* Blanco), sweet orange [*C. sinensis* (L.) Osbeck], and Palestine sweet lime (*C. limettioides* Tanaka) are susceptible to root rot, often support high densities of *P. nicotianae*, and suffer root loss when heavily infected (Agostini et al., 1991; Graham, 1990, 1995a; Timmer et al.,

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[1]Corresponding author, e-mail: jhg@crec.ifas.ufl.edu.

1991). Trees on these rootstocks may respond to fungicide applications provided the damaging populations are sustained and not attributable to anoxic conditions that kill roots in poorly drained sites (Timmer et al., 1989).

The objective of this study was to identify the major factors—soil, rootstock, and climatic conditions—that promote damaging populations of *P. nicotianae* in flatwoods citrus groves. Annual surveys were conducted from 1998 to 2001 in two large citrus plantings of bedded citrus in South Florida encompassing the major rootstocks and soil types typical of the flatwoods.

Materials and Methods

Two groves in Hendry County, Florida were selected.

Grove 1 (11,471 acres). Sweet orange trees (*C. sinensis* cvs. 'Hamlin' and 'Valencia') on Cleopatra mandarin, Carrizo citrange, sour orange, Swingle citrumelo, Palestine sweet lime, and Volkamer lemon rootstocks were planted between 1986 and early 1991. Trees were grown under standard fertilization and microsprinkler irrigation practices for flatwoods citrus production. Soil series and order were identified, and data for soil texture and SHC of the surface A horizon were obtained from soil survey of the grove location (Anonymous, 1990). Samples for nutrient and *Phytophthora* analysis were taken from the tree drip line during the Summers in 1999, 2000, and 2001, mostly in June and July. A total of 321, 270, and 396 samples were taken during 1998, 1999, 2000, respectively, each sample representing 10 acres of grove. In each 10-acre block, 13 soil cores (1" diameter × 12" depth) from three interior double-row beds were collected in a serpentine manner across the beds, resulting in approx 39 samples per 10 acres. For leaf samples, two to three leaves (4-6 months old) were taken from the same trees as the soil samples for a total of 120-150 leaves per 10 acres. Subsamples of leaves and soils were dried and ground for nutrient analysis. Soil was extracted with 0.5 N ammonium acetate (pH 4.8). Leaf tissue was digested in nitric acid-hydrogen peroxide. Extracted nutrients, except phosphorus and nitrogen, were analyzed by inductively coupled plasma atomic emission spectroscopy (ICP-AES). Phosphorus was analyzed colorimetrically (Murphy and Riley, 1962; Watanabe and Olsen, 1965). Nitrogen was determined by combustion/reduction by means of a Perkin Elmer 2410 Nitrogen analyzer.

Subsamples of soil for recovery of *P. nicotianae* were diluted in 0.25% water agar (10 cm^3 soil in 90 mL water agar) and 1 mL of the soil suspension was plated onto each of five plates of PARPH (pimaricin-ampicillin-rifampcin-pentachloronitrobenzene-hymexazol) semi-selective agar medium (Timmer et al., 1988). Colony forming units were identified as *P. nicotianae* by colony morphology on PARPH and the counts were expressed as propagules per cm^3 soil.

Mean propagule counts per block by rootstocks averaged across soil series or by soil series averaged across rootstocks were subjected to the PROC GLM (SAS Institute, Cary, N.C.). Mean separations were made by Student-Newman-Keuls multiple range test at $P < 0.05$. Correlations between propagule counts per block across rootstocks and soil series for several factors including soil physical characteristics, soil nutrient status, and plant nutrient concentration were tested by the PROC CORR (SAS Institute, Cary, N.C.).

Grove 2 (3371 acres). Sweet orange trees (*C. sinensis* cvs. 'Hamlin' and 'Valencia') on Cleopatra mandarin, F-80-3 (citrumelo, *C. paradisi* × *P. trifoliata*) Carrizo citrange, Swingle citrumelo, and Volkamer lemon rootstocks were planted in 1990 and 1991. Soils series were identified as for Grove 1. Samples for soil nutrient and *Phytophthora* analysis were taken during the summers of 1999 and 2001, mostly in June and July as in Grove 1. A total of 162 and 120 samples were taken during 1999 and 2001, respectively, each representing 10 acres of grove. As appropriate, data analyses were conducted as for Grove 1.

Results

Grove 1. Mean populations of *P. nicotianae* for the 1998-2000 seasons varied significantly on the six rootstocks surveyed (Table 1). Counts ranged from 5.4 propagules per cm^3 soil for Volkamer lemon to 30.4 propagules per cm^3 soil for Cleopatra mandarin, which had significantly higher populations than all other rootstocks except Carrizo citrange. Carrizo and sour orange supported intermediate levels of *P. nicotianae*, whereas Swingle citrumelo, Palestine sweet lime, and Volkamer lemon supported significantly lower populations than the most susceptible rootstocks. Populations of *P. nicotianae* also varied significantly among the fine sand soil series, ranging from 7.1 to 34.1 propagules per cm^3 soil (Table 2). Myakka supported the highest populations, followed by Immokalee, Margate, Holopaw, and Basinger with intermediate populations, and Riviera, Holopaw LS, Boca, and Oldsmar with the lowest. Higher densities of *P. nicotianae* were found in spodosols than entisols and alfisols with the exception of the spodosol, Oldsmar.

Although the soil series were all classified as fine sands (Table 2), based on the large sample size (n = 738 10-acre blocks), a lower percentage of sand and a higher percentage clay were significantly associated with elevated *Phytophthora* populations (Table 3). Saturated hydraulic conductivity (SHC) of the soils was negatively correlated ($P < 0.001$) with populations of *P. nicotianae* in 1999, a heavy rainfall year (Table 4). No correlation was found in the drier years of 1998 and 2000.

Higher populations of *P. nicotianae* were correlated with lower concentrations of leaf nutrients (Table 5). However, correlations were only significant for nitrogen, phosphorus, calcium, and copper. In addition, higher propagule densities of *P. nicotianae* were correlated with elevated soil pH and higher levels of phosphorus, calcium, and magnesium in the soil (Table 6).

Grove 2. Phytophthora populations averaged for the 1999 and 2001 seasons varied significantly on the six rootstocks surveyed (Table 7). As in Grove 1, Cleopatra mandarin supported the highest population of *P. nicotianae* (42.6 propagules per cm^3 soil), which was significantly different from the lowest population found on Volkamer lemon (1.0 propagules per

Table 1. Propagule density of *Phytophthora nicotianae* associated with different rootstocks at Grove 1 from 1998 to 2000.[z]

Rootstock	No. of 10-acre blocks	*P. nicotianae* propagules/cm^3 soil
Cleopatra mandarin	161	30.4 a
Carrizo citrange	175	24.6 ab
Sour orange	190	19.4 bc
Swingle citrumelo	172	12.4 cd
Palestine sweet lime	31	11.4 cd
Volkamer lemon	60	5.4 d

[z]Significant differences ($P < 0.05$) among rootstocks (averaged across soil series) are indicated by unlike letters according to Student-Newman-Keuls multiple range test.

Table 2. Propagule density of *Phytophthora nicotianae*, saturated hydraulic conductivity (SHC), and sand, silt, and clay composition of the surface A horizon of fine sand (FS) soils at Grove 1 from 1998-2000.

Soil series	Soil order	No. of 10-acre blocks	*P. nicotianae* propagules/cm³ soil	SHC (cm/hr)	Sand (%)	Silt (%)	Clay (%)
Myakka FS	Spodosol	35	34.1 a[y]	57.8	98.1	1.2	0.7
Immokalee FS	Spodosol	181	24.3 ab	32.9	96.7	2.0	1.3
Margate FS	Entisol	16	21.9 ab	10.8	97.0	1.5	1.5
Holopaw FS	Alfisol	91	19.9 ab	50.6	97.2	1.2	1.6
Basinger FS	Entisol	238	18.7 ab	40.1	98.4	1.2	0.4
Riviera FS	Alfisol	21	15.5 b	19.7	96.3	2.6	1.0
Holopaw LS[z]	Alfisol	86	13.7 b	—	—	—	—
Boca FS	Alfisol	37	12.3 b	85.2	98.4	1.2	0.4
Oldsmar FS	Spodosol	18	7.1 b	71.6	97.2	2.0	1.8

[z]LS = Limestone substratum.
[y]Significant differences ($P < 0.05$) among soil series (averaged across rootstocks) are indicated by unlike letters according to Student-Newman-Keuls multiple range test.

cm³ soil). Populations of *P. nicotianae* on F-80-3, Carrizo citrange, and Swingle citrumelo were intermediate.

Propagule densities of *P. nicotianae* did not vary significantly with soil series, even though a wide range of populations was found (Table 8). Fewer blocks were sampled for each soil series in Grove 2 than in Grove 1, which may account for the lack of significant differences among soil series. All samples soils were alfisols, except Oldsmar, that supported populations above the damage threshold of 15 propagules per cm³ soil.

Table 3. Correlation of soil texture parameters and propagule density of *Phytophthora nicotianae* (1998-2000) at Grove 1.[z]

Soil texture parameter	Correlation coefficient (r)	P
Sand (%)	-0.1309	0.0003
Silt (%)	0.0267	0.4605
Clay (%)	0.1887	<0.0001

[z]Based on 738 observations (across rootstocks and soil series).

Table 4. Rainfall for 1998, 1999, 2000[z] and correlation of saturated hydraulic conductivity with propagule density of *Phytophthora nicotianae* at Grove 1.[y]

Year	Rainfall (inches)	Correlation coefficient (r)	P
1998	46.5	0.0226	0.6864
1999	63.3	-0.3001	<0.001
2000	40.8	-0.0423	0.4167

[z]Rainfall data from SWFREC Immokalee weather station.
[y]Based on 370 observations each year (across rootstocks and soil series).

Table 5. Correlation of citrus leaf nutrient status and propagule density of *Phytophthora nicotianae* (1998-2000) at Grove 1.[z]

Nutrient	Correlation coefficient (r)	P
Nitrogen	-0.0747	0.0364
Phosphorus	-0.0766	0.0319
Potassium	-0.0248	0.4876
Calcium	-0.0846	0.0177
Magnesium	-0.0035	0.9231
Copper	-0.0842	0.0183

[z]Based on 785 observations (across rootstocks and soil series).

Discussion

Annual surveys in two large plantings of bedded citrus in South Florida confirm that rootstocks, characteristics of soils, and rainfall patterns may substantially influence endemic *Phytophthora* activity. Populations above the damage threshold of 15 propagules per cm³ soil occurred on the rootstocks well known to be susceptible to root rot caused by *P. nicotianae*: Cleopatra mandarin, Carrizo citrange, and sour orange (Graham and Menge, 1999). Similarly, those rootstocks known to possess some field resistance and /or tolerance, Swingle citrumelo and Volkamer lemon supported lower populations. F-80-3, a citrumelo, supported damaging populations as observed in previous screening trials of this rootstock for *Phytophthora* resistance (Graham, 1995b).

Table 6. Correlation of soil nutrients and pH with propagule density of *Phytophthora nicotianae* (1998-2000) at Grove 1 and 2.[z]

	Grove 1 (1998-2000)		Grove 2 (1999 & 2001)	
Nutrient	Correlation coefficient (r)	P	Correlation coefficient (r)	*P*
Phosphorus	0.0973	0.0062	0.2621	<0.001
Potassium	0.0215	0.5466	-0.0680	0.2931
Calcium	0.0709	0.0464	0.0613	0.3437
Magnesium	0.0682	0.0555	0.1273	0.0484
Soil pH	0.0700	0.0495	0.2813	<0.001

[z]Based on 789 and 241 observations (across rootstocks and soil series) in Grove 1 and 2, respectively.

Table 7. Propagule density of *Phytophthora nicotianae* associated with rootstocks at Grove 2 in 1999 and 2001.

Rootstock	No. of 10-acre blocks	*P. nicotianae* propagules/cm³ soil[z]
Cleopatra mandarin	19	42.6 a
F-80-3	27	25.8 ab
Carrizo citrange	62	23.9 ab
Swingle citrumelo	131	20.6 ab
Volkamer lemon	6	1.0 b

[z]Significant differences ($P < 0.05$) among rootstocks (averaged across soil series) are indicated by unlike letters according to Student-Newman-Keuls multiple range test.

Table 8. Propagule density of *Phytophthora nicotianae*, saturated hydraulic conductivity (SHC), and sand, silt, and clay composition of the surface A horizon of fine sand (FS) soils at Grove 2 in 1999 and 2001.

Soil series	Soil order	No. of 10-acre blocks	*P. nicotianae* propagules/cm³ soil	SHC (cm/hr)	Sand (%)	Silt (%)	Clay (%)
Boca + Boca DP[z]	Alfisol	13	35.2 a[x]	85.2	98.4	1.2	0.4
Pineda LS[y]	Alfisol	20	26.2 a	33.5	98.2	0.7	1.1
Holopaw FS	Alfisol	45	25.9 a	50.6	97.2	1.2	1.6
Oldsmar LS[y]	Spodosol	24	19.6 a	71.0	98.5	0.5	1.0
Holopaw LS[y]	Alfisol	108	18.2 a	50.6	97.2	1.2	1.6

[z]DP = Depressional.
[y]LS = Limestone Substratum.
[x]No significant differences ($P < 0.05$) among soil series (averaged across rootstocks) are indicated by like letters according to Student-Newman-Keuls multiple range test.

Soils with higher clay content and lower sand content were more conducive for *Phytophthora* activity even though the surface horizons vary over a narrow range from well-drained to moderately drained. Spodic soils with potentially restrictive organic subsoil layers tended to support higher *Phytophthora* populations than entisols and alfisols with loamy subsoils. The exception is the spodosol, Oldsmar, which serves to point out that the depth to the subsoil layer is also important in determining the effect of drainage characteristics on root health (Castle et al., 2004). This depth is difficult to assess without direct observation of the soil profile due to its fluctuating depth and disturbance by the bed construction process. Nevertheless, soil series with lower SHC were associated with elevated populations of *P. nicotianae* after 1999—an El Niño year of heavy rainfall. After drier years in 1998 and 2000, the soils apparently were not saturated often or long enough to affect *Phytophthora* populations. Taken together, the variation in responses of *P. nicotianae* in different soil series support the need for careful irrigation management and maintenance of optimum internal drainage in bedded profiles through the use of tiles in poorly drained soils.

In Grove 1, negative relationships of population of *P. nicotianae* with nitrogen, phosphorus, calcium, and copper were significant but weak. These negative correlations may suggest incipient deficiency in tree nutrients. Plant nutrition is known to affect susceptibility to pathogens, and specifically, phosphorus deficiency promotes root rot of citrus seedlings caused by *P. nicotianae* (Graham and Egel, 1988). Susceptibility of tissues may be higher because phosphorus deficiency increases leakage of nutrients from roots (Ratnayake et al., 1978), which increases attraction and infection of roots by *Phytophthora* zoospores (Khew and Zentmeyer, 1973). Conversely, nutrient deficiencies might be a result of a compromised fibrous root system due to *Phytophthora* root infection that leads to reduction in root uptake of mineral nutrients. Therefore, increased rhizosphere activity of *P. nicotianae* may be a cause rather than an effect of nutrient deficiency.

In contrast, the weakly positive relationship of *P. nicotianae* with soil phosphorus, magnesium, and pH in both groves, and calcium in Grove 2, is difficult to explain. In a previous study of tobacco, elevation of pH from 5 to 7 increased black shank caused by *P. nicotianae* (*P. parasitica* var. *nicotianae*), but relationships with potassium, calcium, and magnesium were weak or inconclusive (Kincaid et al., 1970).

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