Prediction of Potato Dry Rot Based on the Presence of *Fusarium* in Soil Adhering to Tubers at Harvest

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ABSTRACT

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A tuber disk technique for predicting dry rot of potato (*Solanum tuberosum*) before harvest was developed and compared with other tuber baiting methods. The technique distinguished between pathogenic and nonpathogenic forms of *Fusarium*. The absolute inoculum potential of Fusarium dry rot pathogens in soil adhering to tubers after lifting could be determined quantitatively. Correlations between assessments of dry rot as it occurs in naturally infected tubers and assessments according to the whole tuber technique ($r = 0.92$), the naturally infected and the tuber disk technique ($r = 0.98$), and the whole tuber and tuber disk techniques ($r = 0.96$) were highly significant ($P \leq 0.001$). The tuber disk technique requires only a few tubers, soil samples are easily collected and handled, and results are obtained within 8–10 days. This inexpensive, simple technique could be used commercially to predict the risk of storage rot development.

Additional keywords: inoculum density

Potato dry rot in South Africa is caused by eight *Fusarium* spp. (25) and is considered the most important storage disease of tubers (31). The incidence of tuber dry rot varies among production areas and among individual fields (10,14). Annual losses of 60% have been reported (31). The pathogens occur in soil adhering to tubers (3,6,8,11,12,19,21) and usually invade tissue injured during lifting or grading (7,8,19,21,28). Dry rot develops during storage.

A reliable system is needed for predicting the dry rot potential of a potato crop before harvest. Ideally, such a system should help make judgments about the suitability, nature, and duration of storage as well as the need for postharvest fungicide applications (1,10). Plant bioassays and tuber baiting techniques have been developed for predicting the Fusarium dry rot potential of field soils (1,4,6,7,9,10,12,14,19, 20,28,29). These methods assess inoculum levels and tuber susceptibility (14,29), but they cannot discriminate among soilborne pathogens causing similar symptoms (9). The procedures are also time-consuming, and results are not available before decisions on control and storage strategies must be made.

A potato baiting technique that gives a quantitative evaluation of the absolute inoculum potential of *Pythium aphanidermatum* in naturally infested sugar beet field soils has recently been described (23,24). The calculated potential estimates the maximum capacity of a pathogen population for infecting a population of host plants under conditions that are optimal for infection (16). We investigated a similar method for assessing the absolute inoculum potential of *Fusarium* spp. associated with potato dry rot in South African field soils.

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MATERIALS AND METHODS

Soil samples. Samples were obtained from potato fields in the Transvaal highveld (27 farms), eastern Orange Free State (24 farms), and from field plots at the Vegetable and Ornamental Plant Research Institute (VOPRI) at Roodeplaat. The cropping history of the fields in the production areas was mostly unknown, but potatoes are usually rotated (after 3–4 yr) with maize or wheat. VOPRI samples were taken from plots with a 3-yr rotation with *Eragrostis curvula* (Schrad.) Nees (weeping lovegrass), a plot planted previously with vegetables, and a plot of potatoes planted in a virgin soil. Samples (1 kg) of soil that had adhered to tubers when they were lifted were collected from operating grading machines, air-dried for 24 hr, and stored at 5 C in paper bags.

Preliminary studies with tuber disks. Soil samples from potato fields were randomly selected and sieved through 1-mm mesh sieves. The tuber disk technique described by Stanghellini and Kronland (23) was adapted to bait soilborne *Fusarium* spp.

Experiment 1. Petri dishes (9 cm in diameter, three per sample) were filled with 24 g of soil from three samples. Sound, unblemished tubers (cv. Vanderplank), selected at harvest from potato plants grown under commercial conditions in field plots at VOPRI, were washed under running tap water to remove adhering soil, surface-disinfested (3% sodium hypochlorite, 15 min), and allowed to dry. Ten disks (5 mm in diameter, 10 mm thick) were cut from tubers with a cork borer approximately halfway between the rose and heel ends. The disks were placed on the soil surface in each petri dish and incubated at 25 ± 2 C. (This incubation temperature was used throughout the investigation.)

Disks were removed after 24 hr, and adhering soil and mycelium were washed away with tap water. Disks were then surface-disinfested for 2 min in 70% ethanol, rinsed for 3 min in sterile distilled water, and allowed to dry on sterile paper towels in a laminar airflow cabinet. Each disk was sliced into five sequential sections (each 2 mm thick), starting from the surface that had been in contact with the soil. The sections were plated on a selective rose bengal-glycerin-urea (RbGU) medium for *Fusarium* (30) and incubated under a light bank (fluorescent plus black light; 12-hr photoperiod).

Colonies were examined after 7 days with a light microscope under low magnification (×10). Growth from colonies of single *Fusarium* spp. was transferred directly to the carnation leaf agar (CLA) section of divided petri dishes (5). Single-spore isolates of each species were obtained directly (25) from colonies of mixed cultures. Spores were transferred to the CLA section of divided petri dishes and incubated for 48 hr under a light bank as before.

Agar plugs (2–3 mm^3) were cut aseptically from the leading edge of developing colonies, transferred to the potato-dextrose agar (PDA) section of divided dishes, and incubated under a light bank for 10–14 days as before. *Fusarium* spp. were identified following Nelson et al (17). Colonization of different sections of the tuber disks by *Fusarium* spp. was also determined.

Experiment 2. Petri dishes (10 per sample) were filled with 24 g of soil from two samples. Disks (5 mm in diameter, 5 mm thick) were prepared from freshly lifted potato tubers (cv. Up-to-Date) and placed in petri dishes as described before. A water agar plug (5 mm in diameter, 3 mm thick) was then placed on top of each potato disk. The dishes were divided into two groups and incubated for 24 and 48 hr, respectively. The disks were

then removed. Tuber disks were separated, disinfested, and dried as described before.

In experiment 1, we found that fusaria that did not incite dry rot were confined almost exclusively to tissue in contact with soil, whereas the dry rot fusaria occurred above this zone. In experiment 2, therefore, we discarded the 2-mm section sliced from the portion of the dried disks that had been in contact with the soil. The remainder of each disk and the water agar plugs were plated on RbGU medium and incubated as before. The percentages of tuber disks and water agar plugs that were colonized by *Fusarium* spp. were determined after 7 days.

Experiment 3. Petri dishes (20 per sample) were filled with 24 g of soil from two samples, and tuber disks (5 mm in diameter, 5 mm thick) were prepared from freshly lifted or physiologically old (kept after harvest in paper bags for 90 days at 5 C and 50–70% relative humidity) potato tubers (cvs. Up-to-Date and Vanderplank) as described before. Ten disks were placed on top of the soil in each petri dish, incubated for 24 hr, disinfested, dried, and cut as before. The remaining portions of the dried disks were plated on RbGU medium and incubated. The percentage of tuber disks colonized by *Fusarium* spp. was determined after 7 days.

Population density and inoculum potential. Five techniques for estimating population density and inoculum potential were applied with each of the soils collected.

Soil dilution plate technique. Air-dried, sieved soil was ground in a mortar and pestle. Subsamples (0.25 g) were added to 100 ml of 0.1% water agar. Suspensions were shaken on a wrist-action shaker for 30 min, and 1-ml volumes were then spread on the surface of RbGU medium. Plates were incubated for 7–10 days under a light bank as before. The number of colonies of *Fusarium* per subsample was determined microscopically (×10) and converted to number of propagules per gram of soil.

Debris technique. Soils were treated for isolation of *Fusarium* spp. from plant debris as described by Marasas et al (13). Debris, mainly potato plant tissue, was air-dried overnight on sterile paper towels and stored in paper envelopes in a desiccator until tested. Two hundred pieces (2–5 mm long, 0.3–1 mm in diameter) of debris from each sample were plated on RbGU medium (10 pieces per plate). Plates were incubated for 7–10 days under a light bank as before. *Fusarium* spp. that developed from each piece of debris were identified, and the incidence of each species was expressed as a percentage of the total number of isolates of *Fusarium*.

Natural infections. One hundred tubers that had been mechanically damaged (cuts and punctures) by grading machines during harvesting were collected from each of the four Roodeplaat plots. The tubers were kept in crates at 25 ± 2 C and 50–70% relative humidity to promote natural development of dry rot (26). After 6 wk, tubers were cut in half at the infection site, and five disks (2 mm^3) were dissected at random from the periphery of discolored tissue of each tuber, plated on PDA, and incubated for 4–5 days under a light bank as before. Developing colonies were examined microscopically (×10), and organisms other than *Fusarium* were identified directly. Single spores of *Fusarium* spp. were transferred to CLA and PDA for identification. The percentage of infections caused by dry rot *Fusarium* spp. (singly or in combinations) was regarded as an estimate of the absolute inoculum potential.

Whole tuber technique. In a modification of the technique of McKee and Boyd (14), sound, unblemished tubers from Vanderplank potato plants, grown under commercial conditions in field plots at VOPRI, were selected at harvest, surface-disinfested (3% NaOCl, 15 min), and allowed to dry. Tubers (75–150 g) were pressed against a sterilized rigid peg (5 mm in diameter, 10 mm long) to wound them on both sides about halfway between the rose and heel ends. Fifty tubers were inoculated by placing air-dried, sieved soil (about 0.5 g) into each wound with a sterile spatula. Control tubers were wounded but not inoculated.

Tubers were wrapped in paper bags and incubated at 50–70% relative humidity for 6 wk to allow development of dry rot. The occurrence of *Fusarium* spp. in discolored tissue was then determined as for natural infections. Absolute inoculum potential was estimated as the percentage of infections caused by dry rot *Fusarium* spp. (singly or in combination).

Tuber disk method. Disks (5 mm in diameter, 5 mm thick) from freshly lifted Up-to-Date tubers were prepared, incubated on sieved soil, disinfested, dried, and cut as described in experiment 3. The remainder of each disk was plated on RbGU medium and incubated, and the absolute inoculum potential was determined as previously described.

RESULTS

Colonization of tuber disks by soil-borne *Fusarium* spp. During the initial 24 hr, fusaria penetrated the first 2-mm section of 94.4% of the disks. Colonization decreased in sections farther from the soil contact zone: on average, 60.0, 56.7, 17.7, and 4.4% of the sections 2–4, 4–6, 6–8, and 8–10 mm, respectively, from the soil contact surface were colonized.

Several *Fusarium* spp. occurred in the first 2 mm of the disks (Table 1). *F. compactum* (Wollenw.) Gordon, *F. moniliforme* Sheldon, and *F. subglutinans* (Wollenw. & Reinking) Nelson, Toussoun & Marasas were not dry rot pathogens (25). Dry rot *Fusarium* spp. predominated in sections cut from the top 6 mm of disks. Common saprophytes were rarely found. *F. oxysporum* Schlecht. emend. Snyd. & Hans. penetrated farther than other fusaria and was isolated singly from 83.3% of the sections cut from the top 2 mm of colonized disks.

Fusarium spp. colonized significantly ($P \leq 0.01$) more tuber disks than water agar plugs. More baits ($P \leq 0.01$) were colonized after 48 hr of incubation than after 24 hr. After 48 hr, the disks had dried out, and some were covered by a mycelial mat, which hampered isolation. *F. scirpi* Lambotte & Fautr. and *F. acuminatum* Ell. & Ev. were isolated from tuber disks but not from water agar plugs. In contrast, *F. oxysporum* was isolated more frequently from water agar plugs than from tuber disks (*data not shown*). *Fusarium* spp. colonized more disks ($P \leq 0.01$) of cultivar Up-to-Date than of Vanderplank and more physiologically old (stored) than freshly lifted tubers (*data not shown*).

Table 1. Incidence of *Fusarium* spp. isolated from five sections cut sequentially from potato tuber disks and incubated for 24 hr at 25 ± 2 C on soil from three potato fields[a]

	Disk section[b]				
***Fusarium* sp.**	**1**	**2**	**3**	**4**	**5**
F. oxysporum	22.9	51.0	58.2	44.0	83.3
F. solani	13.7	27.9	38.1	45.7	16.7
F. equiseti	48.0	11.5	3.7	10.3	0
F. scirpi	7.9	7.3	0	0	0
F. compactum	1.6	2.2	0	0	0
F. moniliforme	1.7	0	0	0	0
F. sambucinum	1.0	0	0	0	0
F. graminearum	2.2	0.1	0	0	0
F. subglutinans	1.0	0	0	0	0

[a]Tuber disks (5 mm in diameter, 10 mm thick) were incubated in petri dishes (10 disks per dish, three dishes per soil sample) filled with soil that had adhered to tubers when they were lifted. Soil samples were from the Transvaal highveld of South Africa.

[b]Each disk was sliced into five sequential sections (2 mm thick), starting from the surface that had been in contact with the soil. *Fusarium* spp. in sections were determined after incubation on rose bengal-glycerin-urea medium. Values are percentages of total isolates of *Fusarium* spp. and are the means of 30 disks incubated on three different soils.

Inoculum density and inoculum potential of potato soils. Table 2 shows the relative frequency of *Fusarium* spp. in plant debris recovered from the different potato soils, and in baits used for assessing the absolute inoculum potential of these soils. *F. oxysporum* was the predominant *Fusarium* sp. recovered from tuber baits, discolored tissue of naturally infected tubers, and plant debris. It was isolated more frequently from debris recovered from soil from the two dryland production areas (eastern Orange Free State and Transvaal highveld) than from the tuber baits. However, in the Roodeplaat soil it occurred at distinctly lower levels in debris than in tuber baits. *F. solani* (Mart.) Appel & Wollenw. emend. Snyd. & Hans., one of the major colonizers of tuber baits, was isolated infrequently from plant debris. It was also isolated less frequently from tuber baits inoculated with soil from Roodeplaat than from tuber baits inoculated with soil from the dryland production areas. Several *Fusarium* spp. (e.g., *F. crookwellense* Burgess, Nelson & Toussoun, *F. scirpi, F. acuminatum,* and *F. graminearum* Schwabe) occurred infrequently in plant debris and were seldom isolated from tuber disks.

Inoculum density of the 51 soils from the dryland production areas, as determined by soil dilution, ranged between 560 and 10,360 propagules of *Fusarium* per gram of soil (average values of 3,880 and 3,792 for soils of the eastern Orange Free State and Transvaal highveld, respectively). The absolute inoculum potential of these soils, determined by the two tuber baiting techniques, ranged between 2 and 94%.

The correlation ($r = 0.96$) between the assessments from the whole tuber and the tuber disk techniques was highly significant ($P \leq 0.001$). The relationship between inoculum density as determined by the soil dilution plate technique and the absolute inoculum potential as determined by the whole tuber or tuber disk technique was also highly significant ($P \leq 0.001$) (Table 3). However, the relationship was not striking and was meaningless for untransformed data. Data from the plant debris assay did not correlate positively with data from either of the tuber baiting methods.

Inoculum densities, expressed as propagules of *Fusarium* per gram of soil, in the four Roodeplaat field plots ranged between 500 (virgin soil) and 7,880 (soil previously planted with vegetables). The absolute inoculum potential of *Fusarium* spp. that cause dry rot, as determined with tuber disk baits, whole tubers, and naturally infected tubers, was lowest for the virgin soil (8, 6, and 3%, respectively) and highest for soil previously planted with vegetables (46, 39, and 23%, respectively). The potential of each soil, as assessed with tuber disk baits and whole tubers, was substantially higher than indicated by the incidence of naturally infected tubers. However, the relative values of the four soils, as ranked by the different bioassays, were essentially the same (*data not shown*).

Correlations between assessments obtained with naturally infected tubers and the whole tuber technique ($r = 0.92$), naturally infected tubers and the tuber disk technique ($r = 0.98$), and the whole tuber and tuber disk techniques ($r = 0.96$) were highly significant ($P \leq 0.001$). Regression analysis indicated significant positive linear relationships between the population density of *Fusarium* as determined by soil dilutions and the absolute inoculum potential as determined by the various tuber techniques (Table 3). No significant ($P \leq 0.05$) correlations could be found between the data obtained with plant debris and data from either of the tuber baits or the population density of *Fusarium*.

DISCUSSION

Accurate prediction of the destructiveness of a soilborne disease requires knowledge of many factors. The most important of these variables are the measurement of the population density and the assessment of the absolute inoculum potential of the particular soilborne pathogen (2,16,24). Caution should be exercised when comparing determinations of inoculum densities of soilborne *Fusarium* spp. because a particular method may favor selective isolation of a certain species (15). Methods for measuring inoculum density also fail to distinguish between pathogenic and nonpathogenic forms of a

Table 2. Incidence of *Fusarium* spp. in plant debris recovered from soils[a] from potato fields and from baits used to assess the absolute inoculum potential of these soils

	Incidence (% of total)									
	Eastern Orange Free State			Transvaal highveld			Roodeplaat			
Fusarium sp.[b]	Soil debris[c]	Whole tuber[d]	Tuber disk[e]	Soil debris[c]	Whole tuber[d]	Tuber disk[e]	Soil debris[c]	Whole tuber[d]	Tuber disk[e]	Naturally infected tubers[f]
*F. oxysporum**	57.5	49.2	51.7	64.6	51.7	44.6	57.5	75.4	72.6	97.4
*F. solani**	16.3	43.8	46.2	12.6	42.3	49.2	18.0	24.6	19.7	2.6
*F. equiseti**	12.6	2.7	1.2	8.5	2.5	4.4	9.5	0	7.7	0
*F. scirpi**	4.3	0.5	0	5.3	1.3	0.1	0.2	0	0	0
*F. sambucinum**	2.1	1.6	0.4	1.0	1.0	1.2	0	0	0	0
F. subglutinans	1.4	0	0	4.4	0.2	0	0	0	0	0
F. reticulatum	2.5	0.1	0	0.3	0.1	0	0	0	0	0
F. moniliforme	0.5	0	0	1.4	0.2	0.1	0.2	0	0	0
F. chlamydosporum	0.2	0	0	0.6	0.1	0	0	0	0	0
F. nygamai	0.8	0	0.2	0	0.2	0.1	13.8	0	0	0
*F. crookwellense**	0.7	1.0	0.2	0	0	0	0	0	0	0
F. compactum	0.2	0.2	0.1	0.5	0.1	0.3	0.8	0	0	0
F. dimerum	0.2	0	0	0.3	0	0	0	0	0	0
*F. acuminatum**	0.4	0.5	0	0	0	0	0	0	0	0
F. graminearum group 1*	0.1	0.4	0	0.4	0.3	0	0	0	0	0
F. merismoides	0.2	0	0	0	0	0	0	0	0	0
F. graminearum group 2	0	0	0	0.1	0	0	0	0	0	0

[a] Soil that adhered to tubers when they were lifted was collected from operating grading machines in eastern Orange Free State (24 farms), the Transvaal highveld (27 farms), and Roodeplaat (four field plots) and stored at 5 C in paper bags.

[b] An asterisk indicates that the *Fusarium* sp. is associated with dry rot of potatoes in South Africa.

[c] Two hundred pieces (2–5 mm long, 0.3–1 mm in diameter) of washed and dried debris from each soil sample were plated on rose bengal-glycerin-urea medium (10 pieces per plate).

[d] Sound, unblemished, surface-disinfected tubers (cv. Vanderplank) were inoculated by placing approximately 0.5 g of air-dried, sieved soil into wounds made with a sterilized rigid peg.

[e] Tuber disks (5 mm in diameter, 5 mm thick, cv. Up-to-Date) were incubated on soil in petri dishes (10 disks per dish, 10 dishes per sample).

[f] Tubers (100 per sample) mechanically damaged by grading machines during harvest were incubated to promote dry rot development.

pathogen, or between more and less aggressive forms of a specific *Fusarium* sp. (2,22,24).

On the other hand, assessments of the absolute inoculum potential, which involve collection of soils from fields and a host bioassay, estimate the maximum capacity of a pathogen population to infect a population of susceptible host plants under conditions that are optimal for infection (16). Our study showed that the potato tuber disk technique provides an effective quantitative estimate of the absolute inoculum potential of Fusarium dry rot pathogens in soil adhering to tubers after lifting. The technique proved to be reliable in the sense that the slopes of regression lines calculated from data obtained with soils from separate regions or soils with different histories of potato cultivation did not differ significantly from each other. This simple, inexpensive technique could be applied to predict the risk of storage rot. Unlike other tuber bioassays (10,14,28), few tubers are needed, soil samples are easily collected and handled, and results are available within 8–10 days.

The *Fusarium* spp. that cause dry rot are primarily regarded as tuberborne fungi (6,11,12,19,27), and propagules in soil adhering to tubers are known to cause tuber rot (3,8,14,18,22). Soils for the tuber disk bioassay should therefore not be sampled by conventional techniques (19), but rather should be collected from tubers during lifting or grading. To predict the risk of Fusarium dry rot for a particular crop, tubers should be sampled and soil collected from them about 14 days before harvest. The same tubers should be used to prepare the baits, to exclude differences in susceptibility among cultivars or among tubers of the same cultivar (9,19,28,29).

A survey of identical tuber lots indicated that *F. oxysporum* and *F. solani* were the major *Fusarium* spp. associated with the dry rot disease complex in the two dryland production areas (25). *F. equiseti* (Corda) Sacc., *F. sambucinum* Fuckel, *F. scirpi, F. crookwellense, F. acuminatum,* and *F. graminearum* were minor pathogens. The same *Fusarium* spp. were also isolated from tuber disks incubated on these soils, although at higher frequencies than from naturally infected tubers. However, the different *Fusarium* spp. occurred in naturally infected tubers and colonized tuber disks in similar orders of magnitude. Only *F. sambucinum* appeared less commonly in colonized disks than in naturally infected tubers. Pathogen populations or pathogenicity may have decreased during the 3–5 mo that potato field soils were stored at 5 C before being tested. *F. sulphureum* (*F. sambucinum*) has been reported to decline in soil after 6 mo at 4 C (9).

F. oxysporum was also the major pathogen isolated from tuber disks incubated on Roodeplaat soils. This organism was almost solely responsible for dry rot of naturally infected tubers.

The tuber disk technique is an effective and reliable way to assess the relative frequencies of dry rot *Fusarium* spp. in soil adhering to tubers. The method could also be useful in planning control strategies. For example, on certain farms the so-called "minor" *Fusarium* spp., such as *F. equiseti* and *F. crookwellense,* were recovered at relatively high frequencies from both tubers and soils. The dry rot *Fusarium* spp. differ substantially in their temperature requirements. At low temperatures, "minor" species like *F. acuminatum* and *F. crookwellense* are distinctly more pathogenic than *F. oxysporum* or *F. solani* (26).

The rates at which different sections of tuber disks were colonized showed that *F. oxysporum* and *F. solani* grow the fastest and are the most competitive *Fusarium* spp. This pattern of colonization may explain the predominance of these wound pathogens in lesions that develop following the introduction of mixed inocula (25). It might also account for their preponderance in soil adhering to tubers, thus ensuring subsequent development of dry rot.

Table 3. Regression analysis[a] of data on inoculum density and absolute inoculum potential of potato fields soils obtained by different techniques

Independent variable (x)	Dependent variable (y): Whole tuber technique	Tuber disk technique	Naturally infected tubers
Eastern Orange Free State and Transvaal highveld soils			
Inoculum density[b]	$y = -32.14 + 11.17x$ $a = 19.49, b = 2.43$ $r = 0.60$***	$y = -111.7 + 19.44x$ $a = 39.50, b = 4.92$ $r = 0.57$***	
Roodeplaat soils			
Inoculum density[b]	$y = -73.42 + 11.84x$ $a = 70.10, b = 21.07$ $r = 0.86$*	$y = -83.24 + 13.84x$ $a = 47.03, b = 11.33$ $r = 0.97$***	$y = -49.69 + 8.07x$ $a = 14.48, b = 5.93$ $r = 0.97$***

[a] Three asterisks indicate significance at $P = 0.001$; one asterisk indicates significance at $P = 0.05$.
[b] Log_2 propagules of *Fusarium* per gram of soil.

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