Verticillium dahliae Interactions with *V. albo-atrum* 'Group 2' and *V. tricorpus* and Their Effects on Verticillium Wilt Disease Development in Potato

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ABSTRACT

***Verticillium dahliae* is a strong soil-borne pathogen that causes early dying of potato plants. Pathogen population dynamics were studied during disease development following combined inoculations of potato with *V. dahliae* and various other *Verticillium* species. In greenhouse and field studies, three *Verticillium* species were examined: *V. dahliae*, *V. albo-atrum* 'group 2' and *V. tricorpus*. Potato plants were inoculated with two out of the three species in various combinations of an aggressive (*V. dahliae*) and weak (*V. albo-atrum* 'group 2' or *V. tricorpus*) pathogen either on the same date or with a weak species followed by an aggressive species four days later. Plant and soil samples were collected and relative population levels (RPLs) of each pathogen were determined using polymerase chain reaction (PCR) techniques. In combinations where pathogens were inoculated at the same time, RPLs of the weaker species did not exceed those of the aggressive species. In combinations where the weaker species were inoculated first, followed by *V. dahliae* four days later, the two weaker species were still not able to exceed RPLs of *V. dahliae*. Visual wilt symptoms, however, were significantly lower than co-inoculations at the same time and the single inoculation studies. Implications of these findings on epidemiological aspects of these host-pathogen interactions are discussed.**

RESUMEN

***Verticillium dahliae* es un poderoso patógeno habitante del suelo que causa muerte prematura de plantas de papa. La dinámica poblacional del patógeno ha sido estudiada durante el desarrollo de la enfermedad después de inoculaciones combinadas de papa con *V. dahliae* y varias otras especies de *Verticillium*. En estudios de invernadero y campo, se examinaron tres especies de *Verticillium*: *V. dahliae*, *V. albo-atrum* 'grupo 2' y *V. tricorpus*. Plantas de papa fueron inoculadas con dos de las tres especies en diferentes combinaciones de un patógeno agresivo (*V. dahliae*) y uno débil (*V. albo-atrum* 'grupo 2' o *V. tricorpus*) en la misma fecha o con una especie débil seguida de una agresiva cuatro días después. Se colectaron muestras de planta y de suelo y se determinaron los niveles de población relativa (RPLs) utilizando técnicas de reacción en cadena de la polimerasa (PCR). En las combinaciones donde los patógenos fueron inoculados al mismo tiempo, los RPLs de las especies débiles no excedieron a aquellas de las especies agresivas. En combinaciones en las que las especies débiles fueron inoculadas primero, seguidas de *V. dahliae* cuatro días después, las especies más débiles no fueron capaces de exceder los RPLs de *V. dahliae*. Los síntomas visuales, sin embargo fueron significativamente menores que las co-inoculaciones simples de un mismo tiempo. Se discuten las implicancias de estos hallazgos sobre aspectos epidemiológicos de las interacciones huésped-patógeno.**

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ADDITIONAL KEY WORDS: host-pathogen interactions, pathogen combinations

ABBREVIATIONS: VD, *Verticillium dahliae*; VT, *Verticillium tricorpus*; VA2, *Verticillium albo-atrum* 'group 2'; RPL, relative population level

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INTRODUCTION

Verticillium species are soil-borne and tuber-borne fungal pathogens that infect the vascular system of a variety of economically important crops, including potato, cotton and tomato (Dobinson 1995; Heinz and Platt 2000; Jeger et al. 1996; Mahuku and Platt 2002; Schnathorst 1981). In potato production areas, premature plant death, declining tuber yields and diseased tubers are major problems caused by Verticillium wilt. *Verticillium dahliae* Kleb. is a strong soil-borne pathogen found on Prince Edward Island (Platt 1986). *Verticillium dahliae* (VD) favours warm temperatures of 24 to 28 C and forms microsclerotia that can survive 10 to 30 years (Tjamos and Fravel 1995). There are several management strategies available, including soil fumigation, crop rotation, host resistance, planting disease-free seed and soil solarization. Although no single practice will provide complete control of Verticillium wilt (Davis 1985; Powelson and Rowe 1993), chemical treatments tend to be the most effective and most widely used (Davis et al. 1996; Dobinson 1995). Due to high costs and adverse environmental concerns, other efficient and less harmful methods of control are needed (Keinath et al. 1991; Powelson and Rowe 1993). The effects of green manures as a biological control for Verticillium wilt of potato have been studied and showed an ability to significantly reduce pathogen populations (Davis et al. 1996).

It is thought that biological control techniques may provide an economical and environmentally safe approach to controlling Verticillium wilt disease (Davis 1985; Keinath et al. 1991). Plant-pathogenic fungi have been known to infect closely related species, as these agents have diverse host-pathogen relationships (Lucas 1998). *Verticillium tricorpus* Isaac has been recommended as a biological control agent against VD (Davis et al. 2000). In potato, VD is often found in association with *Verticillium tricorpus* (VT), which has been described as a weak pathogen with intermediate saprophytic ability (Isaac 1953; Mahuku et al. 1999). A study by Heinz and Platt (2000) suggests that studying the population dynamics of these species in combi-

TABLE 1—*Foliar wilt symptoms expressed following inoculation of potato plants with various combinations of* Verticillium *species.*

Study Site	Inoculated Pathogens	Foliar Wilt	
	(VD/VA2)	**(%)**	**FProb/LSD**
Greenhouse	VD+VA2	7	0.001/0.792
	VD	32	
	VA2	0	
Field	VD+VA2	52	0.001/0.826
	VD	94	
	VA2	7	
	VA2+4dVD	48	
	(VD/VT)	**(%)**	**FProb/LSD**
Greenhouse	VD+VT	7	0.001/0.686
	VD	32	
	VT	0	
Field	VD+VT	50	0.001/0.853
	VD	94	
	VT	10	
	VT+4dVD	45	

Note: Pathogen inoculations = *Verticillium dahliae* (VD), *V. albo-atrum* 'group 2' (VA2), *V. tricorpus* (VT), VD+VA2 at same time (VD+VA2), VD+VT at same time (VD+VT), VA2 + 4 day delay then VD (VA2+4dVD) and VT + 4 day delay then VD (VT+4dVD); FProb= F probability value from ANOVA tests; LSD = least significant difference of means at $P<0.05$. Visual wilt symptoms were recorded for the greenhouse and field studies at 37 and 63 days post inoculation, respectively.

TABLE 2—*Mean relative population levels (RPLs) of* Verticillium dahliae *(VD) and* V. albo-atrum *'group 2' (VA2) in soil and plant tissue samples following inoculation with the pathogens in various combinations.*

Sample Type	Study Site	Pathogen Inoculations	Pathogen Detected	Mean RPLs	FProb/LSD
Soil	Greenhouse	VD+VA2	VD	1.82	0.85/NS
		VD+VA2	VA2	1.96	
		VD	VD	1.94	
		VA2	VA2	2.24	
	Field	VD+VA2	VD	2.72d	0.001/0.621
		VD+VA2	VA2	2.08bc	
		VD	VD	2.68cd	
		VA2	VA2	1.30a	
		VA2+4dVD	VD	2.44cd	
		VA2+4dVD	VA2	1.58ab	
Roots	Greenhouse	VD+VA2	VD	1.82	0.11/NS
		VD+VA2	VA2	1.96	
		VD	VD	2.96	
		VA2	VA2	2.56	
	Field	VD+VA2	VD	2.72d	0.001/0.605
		VD+VA2	VA2	2.08bc	
		VD	VD	1.80b	
		VA2	VA2	0.80a	
		VA2+4dVD	VD	2.44cd	
		VA2+4dVD	VA2	1.58b	

TABLE 2—*Continued.*

Sample Type	Study Site	Pathogen Inoculations	Pathogen Detected	Mean RPLs	FProb/LSD
Lower stem	Greenhouse	VD+VA2	VD	1.60	0.13/NS
		VD+VA2	VA2	1.00	
		VD	VD	1.60	
		VA2	VA2	0.82	
	Field	VD+VA2	VD	2.14	0.28/NS
		VD+VA2	VA2	1.22	
		VD	VD	2.34	
		VA2	VA2	2.12	
		VA2+4dVD	VD	1.16	
		VA2+4dVD	VA2	1.62	
Mid stem	Greenhouse	VD+VA2	VD	0.94b	0.001/0.494
		VD+VA2	VA2	0.18a	
		VD	VD	1.30b	
		VA2	VA2	0.44a	
	Field	VD+VA2	VD	1.70	0.38/NS
		VD+VA2	VA2	1.04	
		VD	VD	1.70	
		VA2	VA2	1.24	
		VA2+4dVD	VD	0.88	
		VA2+4dVD	VA2	0.84	
Top stem	Greenhouse	VD+VA2	VD	0.68bc	0.001/0.436
		VD+VA2	VA2	0.08a	
		VD	VD	1.08c	
		VA2	VA2	0.36ab	
	Field	VD+VA2	VD	1.50	0.09/NS
		VD+VA2	VA2	0.94	
		VD	VD	1.44	
		VA2	VA2	0.66	
		VA2+4dVD	VD	0.60	
		VA2+4dVD	VA2	0.60	
Tuber stem-end	Greenhouse	VD+VA2	VD	0.25ab	0.001/0.331
		VD+VA2	VA2	0.50b	
		VD	VD	0.00a	
		VA2	VA2	0.20ab	
	Field	VD+VA2	VD	0.90b	0.001/0.349
		VD+VA2	VA2	0.35a	
		VD	VD	1.30c	
		VA2	VA2	0.35a	
		VA2+4dVD	VD	1.25c	
		VA2+4dVD	VA2	0.10a	
Tuber eye-end	Greenhouse	VD+VA2	VD	0.00	NA
		VD+VA2	VA2	0.00	
		VD	VD	0.00	
		VA2	VA2	0.00	
	Field	VD+VA2	VD	0.65b	0.001/0.206
		VD+VA2	VA2	0.00a	
		VD	VD	0.75b	
		VA2	VA2	0.00a	
		VA2+4dVD	VD	0.00a	
		VA2+4dVD	VA2	0.00a	

Note: Pathogen inoculations = *Verticillium dahliae* (VD), *V. albo-atrum* 'group 2' (VA2), VD + VA2 at the same time (VD+VA2), VA2 + 4 day delay then VD (VA2+4dVD); Mean RPLs = mean of four replicates from all five sampling dates; FProb = F probability value from ANOVA tests; LSD = least significant difference of means at $P<0.05$; NS = not significant; NA= not available.

nation may reveal more information about the competitiveness and possible moderating effects of VT on more aggressive species such as VD. A new Verticillium isolate, *V. albo-atrum* 'group 2' (VA2) described by Robb et al. (1993), is thought to be similar to VT in that it is also a weak potato pathogen (Mahuku et al. 1999). It is may be possible that VA2 may also have some moderating effects on more aggressive VD.

As part of a MSc. degree thesis, greenhouse and field experiments were conducted. Potato plants were inoculated with various combinations of an aggressive pathogen and a weaker pathogen. Polymerase chain reaction (PCR) techniques were used to assess relative population levels (RPLs) within plant tissue and soil samples to determine if the weaker pathogens had any effects on populations of aggressive pathogens. Additional plants were inoculated with a single species for comparison.

MATERIALS AND METHODS

A greenhouse experiment conducted in 2003 at the Agriculture and Agri-Food Canada Crops and Livestock Research Centre in Charlottetown, Prince Edward Island, was arranged and conducted in the same manner as a previous greenhouse experiment by Robinson et al. (2007). Approximately 30 days after planting, all pots in a randomly selected plot were inoculated with a single species (VD, VA2 or VT) or a pathogen combination (VD+VT or VD+VA2). The control group was inoculated with water. Each of the six treatments was replicated four times. One plant per plot was destructively sampled at 1, 3, 10, 20 and 37 days post-inoculation.

In 2003, a field experiment was conducted at the Agriculture and Agri-Food Canada Harrington Research Farm in

Prince Edward Island. It was identical in design to that of a previous field experiment by Robinson et al. (2007). Approximately 30 days after planting, randomly chosen plots were inoculated with a single species (VD, VA2 or VT) or a pathogen combination (VD+VT or VD+VA2). The remaining plots were inoculated with a weak pathogen followed by an aggressive pathogen four days later (VA2+4dVD or VT+4dVD). The control group was inoculated with water. Each of the eight treatments was replicated four times. Three plants per plot were destructively sampled at 1, 6, 15, 28 and 63 days post inoculation.

The experiments conducted for this study also duplicated the materials and methods from Robinson et al. (2007). The only difference was the substitution of *V. dahliae* for *V. albo-atrum* 'group 1'. Both experiments were conducted in the same manner, though the results were different.

Polymerase chain reaction was used to identify the pathogens. The resulting bands were examined and ranked according to visual intensity, which is related to the concentration of the pathogen's DNA, using a series of verticillium DNA standards with known concentrations for comparison. A table showing the comparison of band intensity to concentration as well as a gel photograph figure demonstrating the band intensities were both published earlier by Robinson et al. (2007).

RESULTS

Pathogen Interactions Between VD and VA2

At 37 days post-inoculation, visual wilt symptoms of plants inoculated in the greenhouse with VD+VA2, were at 7% (Table 1). Inoculation with VD alone affected 32% of the plants, while inoculation with VA2 affected 0%. Compared to the VD single

TABLE 3—*Mean relative population levels of* Verticillium dahliae *(VD) and* V. tricorpus *(VT) in soil and plant tissue samples following inoculation with the pathogens in various combinations.*

Sample Type	Study Site	Pathogen Inoculations	Pathogen Detected	Mean RPLs	FProb/LSD
Soil	Greenhouse	VD+VT	VD	1.60	0.11/NS
		VD+VT	VT	2.48	
		VD	VD	1.94	
		VT	VT	2.24	
	Field	VD+VT	VD	2.84c	0.001/0.486
		VD+VT	VT	1.60a	
		VD	VD	2.68c	
		VT	VT	2.00ab	
		VT+4dVD	VD	2.86c	
		VT+4dVD	VT	2.30bc	
Roots	Greenhouse	VD+VT	VD	2.82c	0.001/0.356
		VD+VT	VT	1.54a	
		VD	VD	2.96c	
		VT	VT	2.16b	
	Field	VD+VT	VD	2.26b	0.04/0.683
		VD+VT	VT	1.28a	
		VD	VD	1.60ab	
		VT	VT	1.32a	
		VT+4dVD	VD	1.62ab	
		VT+4dVD	VT	1.10a	
Lower stem	Greenhouse	VD+VT	VD	1.88b	0.001/0.589
		VD+VT	VT	0.30a	
		VD	VD	1.60b	
		VT	VT	0.82a	
	Field	VD+VT	VD	1.46bc	0.001/0.667
		VD+VT	VT	0.40a	
		VD	VD	2.34d	
		VT	VT	1.04ab	
		VT+4dVD	VD	2.02cd	
		VT+4dVD	VT	1.52bc	
Mid stem	Greenhouse	VD+VT	VD	1.38b	0.001/0.534
		VD+VT	VT	0.08a	
		VD	VD	1.10b	
		VT	VT	0.44a	
	Field	VD+VT	VD	1.02b	0.02/0.603
		VD+VT	VT	0.30a	
		VD	VD	1.70c	
		VT	VT	0.66ab	
		VT+4dVD	VD	1.06b	
		VT+4dVD	VT	0.90ab	
Top stem	Greenhouse	VD+VT	VD	0.98b	0.001/0.467
		VD+VT	VT	0.14a	
		VD	VD	1.08b	
		VT	VT	0.36a	
	Field	VD+VT	VD	0.64ab	0.02/0.539
		VD+VT	VT	0.20a	
		VD	VD	1.44c	
		VT	VT	0.50ab	
		VT+4dVD	VD	0.42ab	
		VT+4dVD	VT	0.76b	

TABLE 3—*Continued.*

Sample Type	Study Site	Pathogen Inoculations	Pathogen Detected	Mean RPLs	FProb/LSD
Tuber stem-end	Greenhouse	VD+VT	VD	0.10a	0.001/0.332
		VD+VT	VT	0.00a	
		VD	VD	0.00a	
		VT	VT	0.75b	
	Field	VD+VT	VD	1.00cd	0.001/0.413
		VD+VT	VT	0.10a	
		VD	VD	1.30d	
		VT	VT	0.65bc	
		VT+4dVD	VD	0.50ab	
		VT+4dVD	VT	0.70bc	
Tuber eye-end	Greenhouse	VD+VT	VD	0.00a	0.001/0.218
		VD+VT	VT	0.25b	
		VD	VD	0.00a	
		VT	VT	0.20ab	
	Field	VD+VT	VD	0.25b	0.001/0.239
		VD+VT	VT	0.00a	
		VD	VD	0.75c	
		VT	VT	0.10a	
		VT+4dVD	VD	0.10a	
		VT+4dVD	VT	0.35b	

Note: Pathogen inoculations = *Verticillium dahliae* (VD), *V. tricorpus* (VT), VD + VT at the same time (VD+VT), VT + 4 day delay then VD (VT+4dVD); Mean RPLs = mean of four replicates from all five sampling dates; FProb = F probability value from ANOVA tests; LSD = least significant difference of means at $P<0.05$; NS = not significant.

inoculations, the percentage of foliar wilt in VD+VA2 greenhouse-inoculated plants was significantly lower. At 63 days post-inoculation, visual wilt symptoms of plants inoculated in the field with VD+VA2 were recorded at 52% (Table 1). Plants inoculated with VD alone affected 94% of the plants, while VA2 affected 7%. These results show that the percentage of foliar wilt was greater in the field than in the greenhouse. The results from the field, however, were recorded after a greater number of days post-inoculation. Compared to the VD single inoculation, the percentage of foliar wilt in VD+VA2 field-inoculated plants was significantly lower. In the field, at 63 days post inoculation, the visual wilt symptoms of VA2+4dVD were 48%. These results were significantly less than those resulting from the other field combination, VD+VA2.

In the greenhouse combination of VD+VA2, mean RPLs of both species in the soil were not significantly different (Table 2). The field combination of VD+VA2 had mean RPLs of VA2 in the soil that were significantly lower than those of VD. Mean RPLs of VA2 were significantly lower than those of VD in the combination VA2+4dVD. The VD single inoculation was not significantly different from either combination. In the roots, mean RPLs of both species in the greenhouse combination VD+VA2 were not significantly different (Table 2). The field combinations VD+VA2 and VA2+4dVD had significantly lower mean RPLs of VA2 than VD. The VD single inoculation had significantly lower mean RPLs than did VD in both combinations. In the mid and top stem parts for the greenhouse combination, VA2 mean RPLs were significantly lower than those of VD (Table 2). There were no significant differences in the lower stem. The field combinations VD+VA2 and VA2+4dVD had no significant differences in mean RPLs. In the tubers, mean RPLs of VA2 in the greenhouse combination were not significantly different than those of VD in the tuber stem-end (Table 2). There were no results for the tuber eye-end in the greenhouse. The field combinations VD+VA2 and VA2+4dVD had significantly lower mean RPLs of VA2 in the stem-end and eye-end.

Pathogen Interactions Between VD and VT

At 37 days post-inoculation, visual wilt symptoms of plants inoculated in the greenhouse with VD+VT were at 7% (Table 1). Inoculation with VD alone affected 32% of the plants, while inoculation with VT affected 0%. Compared to the VD single inoculations, the percentage of foliar wilt in VD+VT greenhouse-inoculated plants was significantly lower. At 63 days post-inoculation, visual wilt symptoms of plants inoculated in the field with VD+VT were recorded at 50% (Table 1). Plants inoculated with VD alone affected 94% of the plants, while VT affected 10%. These results are similar to those in the greenhouse, but the percentage of foliar wilt was greater in the field. Those results, however, were recorded after a greater number of days post-inoculation. In the field at 63 days post-inoculation, the visual wilt symptoms of VT+4dVD were 45%. These results were higher than those of the greenhouse combination and significantly lower than those of the other field combination VD+VT. Compared to the VD single inoculation in the field, the percentage of foliar wilt resulting from both combinations was significantly lower.

In the greenhouse combination VD+VT, mean RPLs of both species in the soil were not significantly different (Table

3). In the field combination VD+VT, mean RPLs of VT were significantly lower than those of VD. In the field combination VT+4dVD, mean RPLs of were not significantly different. Mean RPLs of VD in both combinations were not significantly different than those of the VD single inoculation. In the roots, mean RPLs of VT in the greenhouse combination VD+VT, were significantly lower than those of VD (Table 3). The field combination VD+VT also had significantly lower mean RPLs of VT than those of VD, and the combination VT+4dVD did not differ significantly. In all stem parts for the greenhouse combination, VT mean RPLs were significantly lower than those of VD (Table 3). In the field combination VD+VT, mean RPLs of VT were significantly lower than those of VD in the lower and mid stems. In the top stem differences were not significant. Compared to the VD single inoculation, mean RPLs of VD in the VD+VT combination were significantly lower. The field combination VT+4dVD had mean RPLs of VT that were not significantly different than those of VD in all stem parts. Compared to the VD single inoculation, VD in the VT+4dVD combination was significantly lower in the mid and top stem. In the tubers, mean RPLs of VT in the greenhouse combination were significantly higher than those of VD in the tuber eye-end, and there were no significant differences in the tuber stem-end (Table 3). The field combination VD+VT had significantly lower mean RPLs of VT in the stem-end and significantly higher levels of VT in the eye-end. In the combination VT+4dVD, VT was detected at significantly higher levels than VD in the tuber eye-end. There were no significant differences between the species in the tuber stem-end for the combination VT+4dVD. In both tuber parts the VD single inoculation had higher mean RPLs than did VD in the time-delayed combination.

DISCUSSION

The aggressive pathogen VD was able to maintain higher mean RPLs than did VA2 and VT in both the greenhouse and field experiment. Even though mean RPLs were higher than the weaker pathogens, VD levels in the greenhouse stems were generally low. This may explain the low percentage of plants with visual wilt symptoms (7%). These results were compared to plants that were inoculated with VD only. The mean RPLs from the greenhouse combinations and VD single inoculation were not significantly different from each other. However, the percentage of foliar wilt from the single inoculation (32%) was significantly higher than that from the combinations. This may indicate that although VT and VA2 did not exceed VD mean RPLs, they appear to have some role in suppressing VD pathogenicity. The weaker pathogens may have reduced the pathogenicity of the aggressive species through competition for space and nutrients within the plant, a process known as hyphal interference (Lucus 1998). In the field combinations VD+VA2 and VD+VT, VD mean RPLs and percentage of visual wilt symptoms were higher than those in the greenhouse and showed no suppression by VA2 or VT. This may have been due to naturally occurring VD populations that have been known to survive in the soil for more than 10 years (Easton et al 1992; Keinath et al 1991; Tjamos and Fravel 1995). These naturally occurring VD populations have been shown to affect uninoculated plants to an extent that is similar to that of inoculated plants, and the results obtained from the control group verified this (unpublished data).

In combinations where plants were inoculated with a weak pathogen followed by VD four days later, the weaker pathogens did not colonize all sample types at mean RPLs greater than VD. Although there were no significant differences between the levels of VA2 and VD in the stems, VD mean RPLs were significantly higher than those of VA2 in the soil and roots. This again may possibly be due to natural population levels of VD in the soil. Because of naturally occurring population levels of VD, inoculation with VA2 prior to VD would not be as effective in suppressing the aggressive pathogen. When present in delayed combination with VT, VD again maintained higher mean RPLs in the soil, roots, lower and mid stem; however, differences in all plant parts were not significant.

It is thought that VT may be used as a biological control agent against VD because of its weak pathogenic nature (Davis et al. 2000; Heinz and Platt 2000). Compared to the VD single inoculation, all combinations indeed had fewer foliar wilt symptoms. However, visual wilt symptoms from the delayed combinations VA2+4dVD and VT+4dVD were not significantly different from those of the other field combinations. Therefore, the initial soil populations of VD may not have given the weaker species a chance to colonize the plants without interference. Further delayed combination studies in a greenhouse environment will help to clarify the role of natural VD soil populations and help elucidate possible moderating abilities of VA2 and VT. Also, additional studies involving different concentration levels of weak and aggressive species may help to clarify the potential of using weaker species as biological control agents.

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LITERATURE CITED

Davis JR. 1985. Approaches to control of potato early dying caused by *Verticillium dahliae*. Am Potato J 62:177-185.

Davis JR, DO Everson, LH Sorensen and AT Schneider. 2000. Association of *Verticillium tricorpus* with soil suppressiveness of verticillium wilt of potato. *In*: EC Tjamos, RC Rowe, JB Heale and DR Fravel (eds), Advances in Verticillium Research and Disease Management. APS Press, St. Paul, MN, USA. pp 347-351.

Davis JR, OC Huisman, DT Westermann, SL Hafez, DO Everson, LH Sorensen and AT Schneider. 1996. Effects of green manures on verticillium wilt of potato. Phytopathology 86:444-453.

Dobinson KF. 1995. Genetic transformation of the vascular wilt fungus *Verticillium dahliae*. Can J Bot 73:710-715.

Easton GD, ME Nagle and MD Seymour. 1992. Potato production and incidence of *Verticillium dahliae* following rotation to nonhost crops and soil fumigation in the state of Washington. Am Potato J 69:489-502.

Heinz RA and HW Platt. 2000. A competitive PCR-based assay to quantify *Verticillium tricorpus* propagules in soil. Can J Plant Pathol 22:122-130.

Isaac I. 1953. A further comparative study of pathogenic isolates of verticillium: *V. nubilum* Pethybr. and *V. tricorpus* sp. nov. Trans Br Mycol Soc 36:180-195.

Jeger MJ, GA Hide, PHJF Van Den Boogert, AJ Termorshuizen and P Van Baarlen. Pathology and control of soil-borne fungal pathogens of potato. Potato Res 39:437-469.

Keinath AP, DR Fravel and GC Papavizas. 1991. Potential of *Gliocladium roseum* for biological control of *Verticillium dahliae*. Phytopathology 81:644-648.

Lucas JA. 1998. Biological control of plant disease. *In*: Plant Pathology and Plant Pathogens, Ed 3. Blackwell Science Ltd., Malden, MA, USA. pp 233-248.

Mahuku GS and HW Platt. 2002. Molecular evidence that *Verticillium albo-atrum* Grp 2 isolates are distinct from *V. albo-atrum* Grp 1 and *V. tricorpus*. Mol Plant Pathol 3(2):71-79.

Mahuku GS, HW Platt and P Maxwell. 1999. Comparison of polymerase chain reaction based methods with plating on media to detect and identify verticillium wilt pathogens of potato. Can J Plant Pathol 21:125-131.

Platt HW. 1986. Varietal response and crop loss due to Verticillium wilt of potato caused by *V. albo-atrum*. Phytoprotection 67:123-127.

Powelson ML and RC Rowe. 1993. Biology and management of early dying of potatoes. Ann Rev Phytopathol 31:111-126.

Robb J, R Moukhamedov, X Hu, HW Platt and RN Nazar. 1993. Putative subgroups of *Verticillium albo-atrum* distinguishable by PCR-based assays. Physiol and Mol Plant Pathol 43:423-436.

Robinson N, HW Platt and L Hale. Interactions of various *Verticillium* species in combination with *V. albo-atrum* on verticillium wilt disease development in potato. Amer J Potato Res 84:133-141.

Schnathorst WC. 1981. Life cycle and epidemiology of *Verticillium*. *In*: M Mace, A Bell and C Beckman (eds), Fungal Wilt Diseases of Plants. Academic Press Inc., New York, NY. pp 81-111.

Tjamos EC and DR Fravel. 1995. Detrimental effects of sublethal heating and *Talaromyces flavus* on microsclerotia of *Verticillium dahliae*. Phytopathology 85:388-392.